Climate change and salmonid life history variation

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Abstract—A model is developed to predict some effects of climate change on anadromous fish. A review the relevant biology of salmonids, focusing on three species of Pacific salmon and on Atlantic salmon, shows that there is sufficient commonality to this biology that we can conceive of a "general salmon" model, which is then tailored to consider a particular species in a particular situation. Such a model is developed for the Atlantic salmon (*Salmo salar* L.) and is used to study the effects of climate change on its patterns of development and maturation. The main variables in this model are the weight and length of the fish (assumed to be related allometrically), the metabolic rate of the fish (a measure of how potential growth is converted into realized growth) and environmental properties such as food availability and water temperature. The main predictions are the pattern of development (maturation and smoltification) and feeding behavior in the stream. Given these predicted patterns of development and behavior, we can address the response to climate change. For example, if climate change leads to an overall decrease in the availability of food, then returning fish will be smaller (as expected). However, the return timing may change too, depending upon the metabolic rate. Similarly, assuming that streams are warmed by climate change, leads to a clear prediction about switches in the patterns of smolting as a function of size of the fish and metabolic rate. Methods for testing the proposed models are described.

INTRODUCTION

ANADROMOUS fish such as the salmonids, which spend their lives both in freshwater and sea water, are ideal organisms for the study of the biological response to climate change (MOONEY, 1991). First, because of the differences in volumes, direct climate change in the form of global warming is more likely to affect stream environments through rising water temperature long before lake or ocean environments are affected (HILL and MAGNUSON, 1990; MAGNUSON *et al.*, 1990). For example, in a study of two Norwegian rivers, JENSEN (1992) predicted that climate change will lead to increased growth rates and survival of parr, a decrease of smolt age, a higher proportion of mature male parr, and changes in the timing and size of smolt runs. Assuming that schools are smaller because of a temporally less concentrated smolt run, Jensen predicted a decrease in survival from smolt to adult. Second, fish also will be subject to indirect effects of climate change such as modification of surface currents and zooplankton distributions due to changing wind patterns. JENSEN (1992) predicted that climate change may affect the distribution, total production, and sea

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age and size at maturity of salmon. Third, although we tend to think of interspecific differences characterizing the salmonids (e.g. GROOT and MARGOLIS, 1991; STOLZ and SCHNELL, 1991), there is an enormous amount of *intra-specific* variation; it is this existing variation which will form the basis of the first response of organisms to changing climate.

NEITZEL *et al.* (1991) attempted to predict such biological response through the use of the fossil record by comparing the modern physical environment with that of the Middle Holocene. In this paper, I describe an alternative approach in which life history models of salmonids are developed in sufficient detail that we will be able to predict the response to climate change and habitat modification.

There has been so much work on the life history of salmon that it cannot all be reviewed here. This work has focused on either maturation or on the emigration from freshwater to sea water (smolting). Many problems remain, however, particularly from the perspective of a predictive theory. For example, HANKIN and McKELVEY (1985) note that conventional life history theory does not take into account egg size or other advantages of large size and raise the general question: Why is observed age of maturity of chinook larger than that predicted by standard life history theory? HEALEY (1987) found that smolting and maturation were driven by more than a critical size, that the usual environmental explanation of variation was wanting, and that (p. 116) "...populations nevertheless display a wide range of sizes and ages at maturity. This suggests that some combination of sizes and ages confers greater fitness than a single size and age".

How are we to understand this variation and what are we to do about the failure of existing theories of life history? It is remarkable that virtually all existing theories on the maintenance of alternative phenotypes or seasonal polyphenism ignore the physiological state of the organism and assume that knowledge of age is sufficient to explain all of the life history (e.g. SCHAFFER, 1979; CASWELL *et al.*, 1984; MORAN, 1992; ROFF, 1992; STEARNS, 1992). That is, age is usually treated as a state.

Over the last 8 years, my collaborators and I have developed a theory of life history and behavior that is focused on the physiological state of the organism and the interactions between the environment, physiological response and expected lifetime reproduction (MANGEL and CLARK, 1988; MANGEL and LUDWIG, 1992). Underlying the theory is a "backward" approach to understanding life history. We begin with a terminal measure of expected reproductive success and then work backwards in time, asking at each time and stage of the life history for the suite of behaviors or developmental patterns that will achieve the largest terminal value. Once the optimal pattern of behavior and development is known, the reproductive success associated with different patterns can also be assessed rapidly using the same kind of backward dynamic iteration. These methods can be used to understand interspecific and intraspecific variation in the salmonids and the response of these organisms to climate change. Over the last 3 years, in collaboration with Felicity Huntingford (Glasgow University), Neil Metcalfe (Glasgow University) and John Thorpe (Freshwater Fisheries Laboratory, Pitlochry, Scotland), I have developed condition-dependent life history models for Atlantic salmon. These will be described in detail below, and I shall show how such models can be used to assess the biological response to climate change.

This paper has two main parts. First, I review the biology of salmonids, arguing that there is sufficient commonality among the salmonids that we can develop a "general salmon" model, which can then be tailored to look at particular species in particular situations. In addition to Atlantic salmon (*Salmo salar*), I focus on three species of

Table 1. Maximum percentage contribution to any population of different life history combinations of chinook salmon (HEALEY, 1986)

	Ocean Years				
	1	2	3	4	5
Stream years					
0	50	35	53	12	1
1*	19	56	77	60	12
2	t†	t	t	2.0	t

*Fish with the 1.0 lifestyle were observed at 1%.
†t = trace (present).

Oncorhynchus: chinook (*O. tshawytscha*), sockeye (*O. nerka*) and steelhead (*O. mykiss*). Steelhead is picked for the analogy with Atlantic salmon in that both species are potential repeat spawners (iteroparous organisms) rather than single spawners (semelparous organisms). Chinook in California and sockeye in British Columbia are both traditionally strong populations at the boundaries of their habitats; we would thus expect them to be particularly sensitive to climate change and other forms of habitat modification. This assumption depends, to some extent, on the local adaptations of stocks to their natal streams. For example, if there is especially strong local adaptation, then southern-most stocks might be best able to deal with global warming. In any case, the differences in growth and behavior of geographically distinct species can be a powerful tool for considering the effects of climate change. Second, I develop a model for Atlantic salmon and show how that model can be used to predict the response (patterns of development, behavior and reproduction) of the fish to climate change. GISKE *et al.* (1992) recently embarked upon a study of Capelin (*Mallotus villosus* Mueller) in the Barents Sea, and there is some similarity between their approach (also based on dynamic, state variable models) and the one described here. A general theme of some of the other papers in this volume is that one needs to try to incorporate behavior into models for the interaction of physical and biological processes. In this paper and NONACS *et al.* (1993), we show that behavior matters and provide examples of how the behavior of organisms can be incorporated into models involving physical and biological process.

SALMONID LIFE HISTORY VARIATION AND BEHAVIOR

Natural selection was once described as the rudder that propels the vessel of evolution (MOORE, 1979); variation is the wind in the metaphor (MAYR, 1991). The enormous range of interspecific life history variation in the salmonids is well known (see e.g. GROOT and MARGOLIS, 1991; STOLTZ and SCHNELL, 1991, especially p. 96). However, in focusing on interspecific variation, we may tend to ignore intraspecific variation. The work reported here is based on two phenomena of intraspecific variation.

First, a rather general phenomenon: Pacific salmon (HEALEY, 1987) can be character-ized by a matrix containing Fresh Water Years and Sea Water Years (Tables 1–3). In addition to the data shown in Table 1, there are five major life histories for chinook parr in terms of movement from emergence, through (and residence in) estuaries, to the ocean (PEARCY, 1992).

Table 2.   Maximum percentage contribution to any population of
different life histories of sockeye salmon (HEALEY, 1986)

	Ocean Years				
	1	2	3	4	5
Stream years					
0		t*	0.1	t	
1	2.2	89.2	50.7	66.5	7.2
2†	1.4	58.3	63.2	8.9	
3†	1.7	15.4	4.6	t	
4†	t	0.3	t		

*t = trace (present).
†Trace levels of 2.0, 3.0, and 4.0 observed.

Table 3.   Maximum percentage contribution to the Wad-
dell Creek (California) population of different life histor-
ies of steelhead (based on data in SHAPOVALOV and TAFT,
1954)

	Ocean Years*		
	1	2	3
Stream years			
1	11.5	7.2	0.5
2	51.1	41.9	0.5
3	30.2	10.7	0.2
4	5.1	1.6	0.3

*Fish spawning for the first time. There are also
second, third and fourth time spawners.

Second, a more specific phenomenon: If a group of sibling Atlantic salmon are started in
the spring of the year of their emergence on unlimited rations, the initial size distribution is
roughly Gaussian. By the fall of that year, however, the distribution has bifurcated into a
bimodal distribution (Fig. 1). The larger fish (the Upper Modal Group, UMG) continue
feeding over the winter and smolt after one year in the river. The smaller fish (the Lower
Modal Group, LMG) become anorexic over the winter (i.e. lose appetite, METCALFE and
THORPE, 1992), spend much of their time during the winter hiding in the rocks rather than
feeding, and smolt after at least one more year in the river. In the rivers of northern
Scotland, Scandinavia and Canada, the fish may take three, four or five years before
smolting (METCALFE and THORPE, 1990). To model this phenomenon requires linking the
states of individual fish, and of the environment and a measure of reproductive success.
Such models can be used to explore the effects of climate change.

How is this variation to be understood? There are a number of possible approaches.
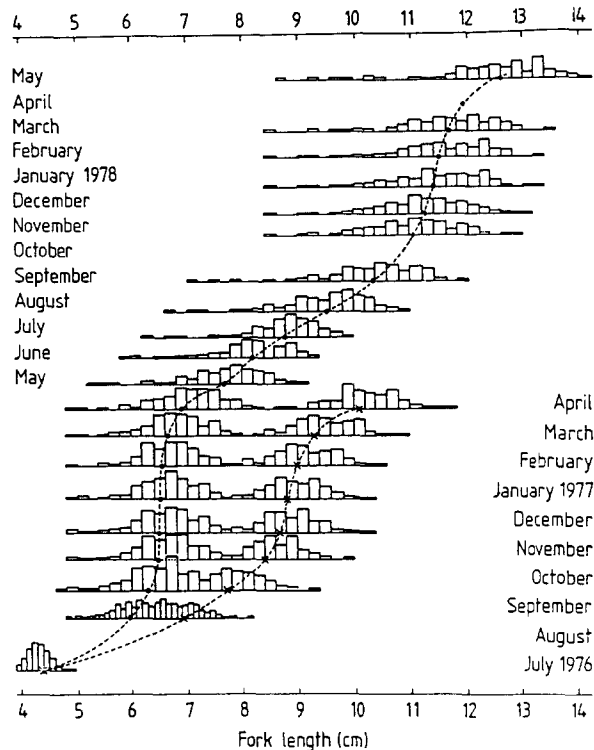First, we might take the "engineering" approach: Variation is simply noise, and what we

Fig. 1.　The development of a bimodal size distribution from a unimodal size distribution of Atlantic salmon siblings. From Thorpe *et al.* (1992).

see are imperfect attempts to achieve a single "perfect" life history. Second, we might take the caricature of the "Adaptationist approach": Each combination of freshwater and seawater years is an exactly optimal life history for some environment. (This is a thinly veiled version of the engineering approach, in a wider array of environments.) Third, we might recognize from the outset that "Variation is the core of biology" (Berry, 1989) and that our objective must be to understand how this variation can be maintained by the interaction of the environmental and physiological factors within a framework of expected reproduction. That is, the variety of observed life histories represents the interaction of the varieties of genetic potential under the proximate control of environmental factors, constrained by relative reproductive success.

THE COMPONENTS OF A "GENERAL SALMONID" MODEL

In this section, I shall review studies on the particulars of salmonid life histories. In the course of this review, it shall become apparent that there are a number of general features common to the wide range of salmonids. In this sense, it is possible to construct a model of a "General Salmonid" by capturing the salient biological properties. We then need to specify the details of parameters and functional relationships for different species; below I shall show how this can be done for Atlantic salmon. It is helpful to focus on the life cycle:

feeding and growth, survival, smolting, and maturation. Overlying all of these is genetic variation which is the first source of intraspecific variability, but not the last.

Growth rate, smolting and maturation

PARKER and LARKIN (1959) found that in freshwater, male and female steelhead grow at approximately the same rate. In salt water, males grow significantly faster than females. In addition, they found that growth rate was inversely related to eventual life history events in both fresh and salt water. Slow growing steelhead failed to become smolts at completion of the second growth year and remained an additional year in freshwater. Fast growing individuals migrated at the completion of the second growth year. In salt water, the two freshwater growth groups further subdivided into fast and slow growing fractions; those growing faster in sea water matured following the first ocean growth year, whereas the slower growing fraction took an extra year to mature. Similar results have been observed for Atlantic salmon (SIMPSON and THORPE, 1976; HIGGINS, 1985). In fact, it appears to be a general result that rapid growth in fishes is correlated with early maturation (THORPE et al., 1983). BRETT (1965, 1971) gives general relationships concerning metabolic rate, appetite, size and activity. SHELBOURN et al. (1973) measured the effects of temperature and size on specific growth rate in sockeye. These, and work by ELLIOT (1975, 1976), suggest that there is an optimum temperature for growth. However, the optimal temperature may itself depend upon the stage of life history. For example, in the case of Atlantic salmon optimal temperatures for incubation are about 7–8°C, for fry are about 17–18°C, for smolts a bit less, for adults about 12°C, for maturation of ovaries about 8–10°C and for spawning about 5°C (J. Thorpe, personal communication). Many of the data in the literature can be used to "tune" the models. For example, PARKER (1971) gives a range of growth rates varying from 0.7–1.4% of body weight per day. In estuaries, chinook grew at about 5.8% of their body weight per day, reaching 70 mm before migrating (HEALEY, 1980); sockeye growth rates can be 10% per month (RICKER, 1962).

General reviews of growth models are found in PARKER and LARKIN (1959), URSIN (1967) and BEYER (1989); these justify the basic principle of weight change based on anabolic factors minus catabolic factors. FROM and RASMUSSEN (1984) gave a general growth model for rainbow trout *Salmo gairdneri*, which involves considerable physiological detail. BEYER and LAURENCE (1980) developed a stochastic growth model of larval fish, without any temperature effects. Other models are those of SCHNUTE (1981), who focused on acceleration of weight rather than the rate of change of weight, and IWAMA and TAUTZ (1981).

Timing and the parr–smolt transformation

"Windows" for life history events (parr–smolt transformation and maturation) are common in the salmonids; this has been recognized for many years (e.g. SHAPAVOLOV and TAFT, 1954, especially Fig. 21; THORPE, 1986). The windows for chinook and steelhead may be wider than those for Atlantic salmon (NEITZEL et al., 1991) but they still clearly exist (WEDEMEYER et al., 1980). Some aspects of the parr–smolt transformation can occur independent of photo period in steelhead (WAGNER, 1974), but in general photo-period affects ATPase activity (ZAUGG, 1981), and by shifting the annual photo-period, it is possible to shift the window (THORPE et al. 1989). It is only those salmonids that spend a full

year or more in freshwater that exhibit smolting as a set of integrated physiological, behavioral and morphological changes in preparation for life in the sea; those which enter the sea within their first year of life show the transition more gradually (J. Thorpe, personal communication). We understand many details of physiology of smolting (HOAR, 1988), but it often appears confusing and contradictory. Part of the role of theory is to help organize observations into a quantitative and predictive format.

Survival

A key component of any salmonid model is the general phenomenon of decreasing risk of mortality with increasing size (McGURK, 1986; PEPIN, 1991); animals escape mortality by growth (also NONACS et al., 1994). Ocean survival of steelhead smolts varies from about 5% for 160 mm smolts to 25% for 190 mm smolts (WARD and SLANEY, 1988). Smolt to adult survival for sockeye rose from 5% (70 mm) to 15% for 90 mm fish (HENDERSON and CASS, 1991). RICKER (1962, 1976) presented a thorough study of the relationship between mortality and weight for sockeye and this is used below. In some cases the details of predation have been investigated. For example, merganser predation is important for both Pacific and Atlantic salmon and the intensity of predation clearly varies with size (WOOD, 1987; SJÖBERG, 1988; FELTHAM, 1990). Although there is a general decrease in mortality rate with size, marine survival is highly variable with a coefficient of variation for steelhead of 45%, for sockeye of about 50%, and for chinook of about 100% (PEARCY, 1992, Table 4.1). It is still not clear how predation and starvation interact to determine these rates and theory can help to elucidate the relationship.

Maturation: length, weight and fecundity

For females, reproductive success is reasonably characterized by fecundity, although more complicated alternatives are possible and can be justified (GISKE et al., 1993). There is an abundance of information on the relationship between female size and fecundity, for both Pacific salmon (e.g. HANKIN and McKELVEY, 1985; HEALEY and HEARD, 1984) and Atlantic salmon (e.g. MILLS, 1989). HANKIN (1986) showed that earlier releases of hatchery chinook result in faster growth rates, which encouraged earlier maturation. However, ZAUGG (1989) found that in the Columbia river the fraction of returning adult chinook was not correlated with size or time of release of fall run, underyearling salmon. For Atlantic salmon reproduction depends on total lifetime (river years plus sea years, THORPE et al., 1984). There seems to be a similar effect for sockeye (MANZER and MIKI, 1985). Additionally, older fish exhibit higher variability in fecundity and length.

Genetic variation

Condition dependent life history models, as described below, require inherent variability in the processes which lead to growth, smolting, and maturation. The salmonids are wealthy in such variation.

There is now an enormous amount known about the genetic variation of chinook along the entire western coast of North America (UTTER et al., 1989; WINANS, 1989; BARTLEY et al., 1992). CARL and HEALEY (1984) showed differences in both enzyme frequency and morphology among three juvenile life history types of chinook (immediate migration to

sea after emergence, 2 months in freshwater then migration, or full year in freshwater then migration) and propose that this genetic variability complicates management. In fact, there is evidence that ocean and stream chinook are different races (HEALEY, 1983; CLARKE et al., 1992). MORGAN and IWAMA (1991) give data that can be used to assess variability in metabolic rates, which have standard errors about 25% of the mean. HIGGINS and TALBOT (1985) found similar results in Atlantic salmon. This variation, presumably of a natural origin, will play a key role in the conceptual foundation of conditional life history models.

FOOTE et al. (1989) showed that there are allozyme differences in sockeye and kokanee (the land-locked form of sockeye). Furthermore, there are genetic differences in the early development and growth of sympatric sockeye and kokanee (WOOD and FOOTE, 1990). In particular, growth rates are more variable in kokanee than in sockeye and it appears that some of the metabolic variability is compensated by behavior. After reviewing all of the evidence, WOOD and FOOTE (1990) conclude that "these results provide strong evidence that emergence timing in salmonids is under stabilizing selection" (p. 2257). Such stabilizing selection is one of the assumptions underlying the models described below. It is also clear that there are genetic differences in the sea water adaptability of sockeye and kokanee (FOOTE et al., 1992).

Although traits such as growth rate, age of maturity, and size of maturity are heritable to some extent (RIDDELL, 1986; REFSTIE and STEINE, 1978), environmental variation is important in determining the development and behavior of the fish. The generally high phenotypic and genetic correlations between length and weight (REFSTIE and STEINE, 1978) mean that we can work with one of them (e.g. weight) and presume a parametrization of the other, at least for growing fish. In this regard, length is the natural structural variable since weight loss is more easily achieved than shrinkage.

THE PHYSICAL ENVIRONMENT AND POSSIBLE EFFECTS OF CLIMATE CHANGE

To understand how changes in the physical environment may affect the pattern of life history in the salmonids, I shall adopt a "behavioral ecology" approach (MANGEL and CLARK, 1988; KREBS and DAVIES, 1991). In particular, I shall ask for the suite of behaviors that maximize expected reproductive success under one set of environmental parameters and then compute the expected reproductive success assuming the same suite of behaviors but with changed environmental conditions. The behavioral ecology approach was recognized by WYNNE-EDWARDS (1962) in the very first figure of his book *Animal Dispersion in Relation to Social Behaviour*. This figure shows the correlation (0.85) between the number of pelagic birds and the abundance of plankton in the North Atlantic. These birds were mainly non-planktivorous, but concentrated in areas of high plankton density because that's where the fish would be. Recent work (AEBISCHER et al., 1990) has shown that this kind of correlation can span at least four trophic levels: phytoplankton, zooplankton, planktivorous fish and piscivorous birds.

Ocean environment

We can now characterize the temporal distribution of zooplankton (PARSONS et al., 1970) in the ocean. Even in the absence of climate change, there is considerable variation in the pattern of zooplankton abundance. For example, the maximum annual abundance

of zooplankton at station "P" in the northeast Pacific ocean has CV of about 50% (WARE and McFARLANE, 1989). Patchiness is important (MACKAS *et al.*, 1985) and climate change can clearly affect the pattern of patchiness (e.g. PARES-SIERRA and O'BRIEN, 1989). It is likely that offshore transport is a major determinant of the pattern of zooplankton and thus, implicitly of the fish themselves (CURY and ROY, 1989). River discharge and temperature, and oceanic variability affect the return pattern of sockeye (MYSAK *et al.*, 1986; HSIEH *et al.*, 1991). Ocean current simulations are reaching a sophisticated level (e.g. THOMSON *et al.*, 1992) that allows prediction of oceanic pattern and the surface currents and the distribution of fish. The salmonids have a "preferred range" of ocean temperature (PEARCY, 1992, p. 89) that can be used to predict ocean distribution (Fig. 6.2 in PEARCY, 1992). The same is true for the California Current, for which we are now in a position to predict the physical environment and its response to changes in wind stress and other forcing factors associated with climate change (PARES-SIERRA and O'BRIEN, 1989).

General reviews of the range of effects of climate change are found in CUSHING and DICKSON (1976), CUSHING (1982), FRYE (1983), SHEPHERD *et al.* (1988), BEAMISH and McFARLANE (1989) and HEALEY (1990). By comparison with the geologic record, NEITZEL *et al.* (1991) attempt to predict effects of warming on key characteristics of the rivers (their Table 2) and thus ultimate effects on the fish (their Table 5).

PEARCY and SCHOENER (1987) studied the changes of the biota in the North Pacific due to El Nino; a weakened California Current and strengthened Alaska Current lead to increased zooplankton production in the Gulf of Alaska and record production of salmonids there. On the other hand, El Niño caused anchovy growth rates to decrease (BUTLER, 1989) and feeding patterns of juvenile coho and chinook to change (BRODEUR *et al.*, 1992). There is environmental control of phytoplankton patchiness (THERRIAULT and PLATT, 1981) and this exerts at least some control on zooplankton patchiness. Zooplankton are transported by surface currents (WICKETT, 1966) that will be sensitive to changes in temperature and changes in the wind stress curl. In the California Current, a possible general argument runs as follows: a large-scale change in temperature on land will cause a change in wind stress curl, which will cause a change in surface currents and turbulence which will cause a change in zooplankton pattern, which will potentially cause a change in the feeding pattern and growth rate of the fish. That is, the major effects on phytoplankton and zooplankton from increased wind intensity will be increased turbulence (DAVIS *et al.*, 1991), which may increase or destroy zooplankton patchiness (depending upon the intensity of the turbulence). In any case, there may be profound consequences for the growth of all pelagic species. An alternative scenario, for waters further north, might be the following: due to warming, polar waters move south so that fish are able to reach these more productive waters sooner, which causes them to grow faster. In the computations reported in below, I focus on the first scenario.

Stream environment

Egg incubation time decreases with increasing temperature (WARE, 1975). HEMING and McINERNEY (1982) show that yolksac chinook grow faster at higher temperature but achieve smaller maximum tissue weight: at 12°C they reach about 600 mg (wet wt.) after 82 days but at 6°C they reach about 687 mg after 186 days. Growth rates (mm day^{-1}) of post larvae of marine fish are positively correlated with temperature and length (but specific growth rate—mm day^{-1}/mm of body length—is inversely correlated with length); total

mortality increases with temperature and decreases with length (Pepin, 1991). These results are similar to those of Boggs (1991) concerning anchovy. Neither Pepin nor Boggs considered salmonids explicitly, but we expect the general physiological principles to hold here as well. Catabolism increases with temperature (Ursin, 1979), and the proportion of available daily ration available for growth either decreases or peaks with temperature, depending upon the overall level of energy intake (Elliot, 1976). In general there is a "peaked" specific growth rate as a function of temperature (Brett, 1965; Brett and Glass, 1973; Elliot, 1975). For chinook in particular, we know that growth is affected by water temperature and by ration level interacting with water temperature (Neilson and Geen, 1984).

Logging on Carnation Creek, British Columbia, raised the temperature of the stream by removing cover; the fish emerged earlier (up to 6 weeks more growth was allowed), smolted smaller and sooner (Holtby, 1988). Holtby used a Monte Carlo "forward iteration" method (Mangel and Clark, 1988) to predict a 47% increase in smolt numbers but only a 9% increase in adults prior to the fishery (these are results of the simulations). Similar results were found in the River Fiddich, Scotland, where warm cooling effluent from distilleries increased river temperature by 1–3°C and caused the Atlantic salmon there to grow faster and to smolt a year earlier (Morrison, 1989; Thorpe et al., 1989). Squawfish predation on juvenile salmonids increases with temperature (Vigg and Burley, 1991). Survival of smolts of steelhead and chinook in the Sacramento River delta decreased with increasing temperature (Kjelson and Brandes, 1989). Both water flow and temperature affect timing of spawning in Atlantic salmon (Heggberget, 1988) and increasing water temperature causes earlier loss of smolt characteristics (hypo-osmoregulatory capacity) in Atlantic salmon (Duston et al., 1991). In principle, then, warming could affect the length of the window for the parr–smolt transformation.

A theory of condition dependent life history will provide a set of organizing principles for the maze of facts, and will allow prediction of the effects of climate change.

A MODEL FOR ATLANTIC SALMON

The state variable in the model for Atlantic salmon is the weight $W(t)$ of the fish at time t, with w denoting a particular value of the weight. Length is assumed to be related to weight through an allometric relationship of the form

$$L(t) = AW(t)^B \qquad (1)$$

where the parameters A and B, which vary for parr, post-smolt females, maturing and non-maturing males, are fit from data obtained at the Rowardennan Field Station or Stirling Aquatech Fish Farm, Oban. Weight can increase or decrease, but length can only increase.

The physiological state of the fish and the environment are linked through reproductive success and various developmental switches. At this time, we envision five developmental switches (Table 4; see Thorpe, 1991; Thorpe et al., 1992 and references there-in for justification of the timing).

In this description, emigration occurs during May and reproduction during November. We are fairly confident about the timing of F, $G1$, and $G2$ but less so concerning the timing of $E1$ and $E2$ (see Thorpe, 1991). The other physiological constraints are:

(1). A fish which continues gonad growth cannot initiate smolting, i.e. that $G2 = G1 = 1$ forces $E1 = E2 = 0$.

(2). A fish can only continue advanced gonad growth if it has initiated it, i.e. it is only possible for $G2 = 1$ if $G1 = 1$.

(3). A fish can only continue preparations for emigration if it has initiated them, i.e. that it is only possible for $E2 = 1$ if $E1 = 1$.

(4). If the advanced switch ($G2$ or $E2$) is set to 0, then the preliminary switch ($G1$ or $E1$) is reset to 0, regardless of its value.

(5). The somatic cost of reproduction is largest from April onwards.

(6). Fish which mature in November cease growth in July.

To illustrate these switches and how they affect behavior and development, denote by 0 a "negative" response to the developmental switch and by 1 a "positive" response to the developmental switch. Then a parr which smolts at age 1 would follow the pattern:

$$F \quad G1 \quad E1 \quad E2$$
$$1 \quad 0 \quad 1 \quad 1\text{—then to sea.}$$

A parr which smolts at age 2 could follow a number of patterns. Two examples are

$$F \ G1 \ E1 \ F \ G1 \ E1 \ E2 \qquad \text{or} \ F \ G1 \ E1 \ F \ G1 \ E1 \ E2$$
$$0 \ 0 \ 0 \ 1 \ 0 \ 1 \ 1\text{—to sea} \qquad 0 \ 0 \ 0 \ 0 \ 0 \ 1 \ 1\text{—to sea.}$$

The second pattern (not feeding in the winter before emigration) is not observed; but it is indeed possible. One of the purposes of the theory is to explain why such a pattern is not observed. Finally, a male which matures as a parr might follow

$$F \quad G1 \quad E1 \quad G2 \quad F$$
$$1 \quad 1 \quad 0 \quad 1 \quad 1\text{—breed}$$
$$1 \quad 1 \quad 0 \quad 1 \quad 0\text{—breed}$$
$$0 \quad 1 \quad 0 \quad 1 \quad 0\text{—breed}$$
$$0 \quad 1 \quad 0 \quad 1 \quad 1\text{—breed.}$$

These simple examples show why a dynamic, state variable model and the associated

Table 4.   *The developmental switches in the model of Atlantic salmon*

Developmental Switch	Date	Description
F	1 August	Whether to feed ($F = 1$) or to become anorexic ($F = 0$) during the winter months
$G1$	1 November	Whether to continue gonad ($G1 = 1$) growth or to switch it off ($G1 = 0$)
$E1$	1 December	Whether to initiate developments for emigration ($E1 = 1$) the next spring or not ($E1 = 0$)
$E2$	1 March	Whether to continue developments for emigration ($E2 = 1$) or to abort preparations ($E2 = 0$)
$G2$	1 April	Whether to continue advanced gonad growth ($G2 = 1$) or to abort ($G2=0$)

methods of backwards iteration and dynamic programming (MANGEL and CLARK, 1988) are required for the analysis of this problem. Let us assume that the parr does not mature, so that $G1 = G2 = 0$. Then a fish which smolts after 1 year has, in principle, two developmental paths:

$$
\begin{array}{ccc}
F & E1 & E2 \\
1 & 1 & 1 \\
0 & 1 & 1.
\end{array}
$$

Now it may be argued that we never see the second path and that it doesn't make sense, so it can be ignored. But this should be a conclusion of the theory, not an input. In principle, a parr that smolts after 2 years has ten possible developmental paths. Including the two maturation switches (which must be done for male parr, since they do mature in the river, but need not be done for female parr) leads to an enormous number of possible pathways. Using a simulation approach (a forward approach, MANGEL and CLARK, 1988; MANGEL and LUDWIG, 1992) is cumbersome and time consuming. The backward approach of stochastic dynamic programming immediately leads to the important landmarks in developmental and behavioral space (the "optimal" pattern of development and behavior, in response to size and time) and allows rapid evaluation of the fitness of alternative developmental pathways. The backward method starts with the final stage of life history (reproducing individuals) and then links (via "sequential coupling", MANGEL and CLARK, 1988) to previous stages working backwards through the life history.

The seawater model

In the seawater model, time is counted in months, with $t = 1$ corresponding to April. The $G1$ developmental switch occurs in November, i.e. $t = 8, 20, 32$, etc. and the $G2$ developmental switch occurs in April, i.e. $t = 1, 13, 25, 37$, etc. In addition, reproduction (R) occurs at $t=8, 20, 32$, etc. Although Atlantic salmon are iteroparous, the fraction of repeat spawners is usually low (rarely exceeding 10%, DUCHARME 1969), so that it is reasonable to begin by focusing on a single episode of reproduction and to assume that the physiological cost of reproduction is so high that the maturation behavior is shaped by consideration of only that single reproductive bout.

I presume that there is a maximum time, here $T = 80$, such that the fish must reproduce by T. (The precise value of T can be changed according to the particular species being modeled.) In order to reproduce at some time t_R, the fish must have responded positively to $G2$ at t_R-5 and to $G1$ at t_R-12. The simplest measure of expected reproductive success is the expected fecundity associated with maturation. Fecundity depends upon the length of the fish (THORPE et al., 1984):

$$V_{mat}(w) = \text{expected fecundity of a female of weight } w \text{ gms}$$

$$= a + bL(w). \tag{2}$$

Here $L(w)$, measured in cm, is determined by the allometric relationship (1) using the weight of the fish in July at the cessation of growth and the parameters (THORPE et al., 1984) are $a = -7750$, $b = 198$. Since a is negative, if the fish are small enough, $V_{mat}(w)$ computed from (2) will be negative; in that case we set it equal to 0. [In actual fact, very small females (of the order of 10 cm) can produce a few eggs—about 35—so that equation (2) is only

approximate (J. Thorpe, personal communication)]. THORPE *et al.*, found that different patterns of life history lead to different values of the parameters *a* and *b*. For example, if all river years were combined and fish with 1 or 2 sea years compared, the slopes *b* were statistically different ($P < 0.05$) but the intercepts *a* were not. On the other hand, when comparing combinations of all sea years but with different numbers of river years, the intercepts but not the slopes were statistically different (Table 2, THORPE *et al.*, 1984). Rather than trying to fit all of these patterns, these results are left as something to be explained by the model.

For times previous to *T*, we must characterize growth, survival and the developmental switches. In the characterization of growth, the current developmental physiology plays the role of a parameter. In all the analysis that follows, denote by *G*1 and *G*2 the variables of the developmental processes and denote by *g*1 and *g*2 their values (i.e. 0 or 1). The variable s will be used to measure time in days and the growth model for weight is (with explanation of parameters following)

$$\frac{dW}{ds} = f_{ue}[k_2 W^\beta \exp\left(-s_{cr1}g1 - s_{cr2}g2\right) - k_1 W^\alpha]. \tag{3}$$

In this equation f_{ue} is the "food utilization efficiency" and is assumed to measure the relative ability of an individual fish to convert net potential growth into real growth. The maximum potential gain for a fish of weight *W* is $k_2 W^\beta$ where both k_2 and β are constants (in the freshwater model described below they vary with season and temperature). The anabolic gain is reduced by a term associated with the somatic cost of reproduction s_{cri} for the developmental switch *Gi*. As described above, we expect $s_{cr1} \ll s_{cr2}$, but including both in the formulation allows flexibility. The catabolic term $k_1 W^\alpha$ is also determined by two constants k_1 and α. Equation (3) is a generalization of the standard von Bertalanffy equation (REISS, 1989)

$$\frac{dW}{ds} = c_2 W^{2/3} - c_1 W. \tag{4}$$

However, in the case of (3), the parameters were estimated from the Oban field cage data. Although an analytical solution of (4) is possible, in general, (3) must be solved numerically.

RICKER's (1976) result on the size dependence of survival leads to a monthly mortality rate

$$\mu_m(w) = 5.51 \ w^{-0.524}. \tag{5}$$

This can be converted to a daily mortality rate $\mu(w)$ by assuming that the fish survives a 30 day month with probability $\exp(-\mu_m(w)) = (1-\mu(w))^{30}$.

Next consider the developmental switches. Because developmental switches are fixed over intervals of 5 or 7 months, the "periods" of our model can be of that length (Fig. 2), and instead of using *t* to measure calendar time, we can use it to measure time in the natural periods of the fish. With this new characterization, the *G*1 developmental switch occurs at even values of the time variable and the *G*2 developmental switch occurs at odd values. At those even values, *G*2 is a state variable and at the odd values, *G*1 is a state variable. Thus, expected lifetime reproduction is characterized by two functions:
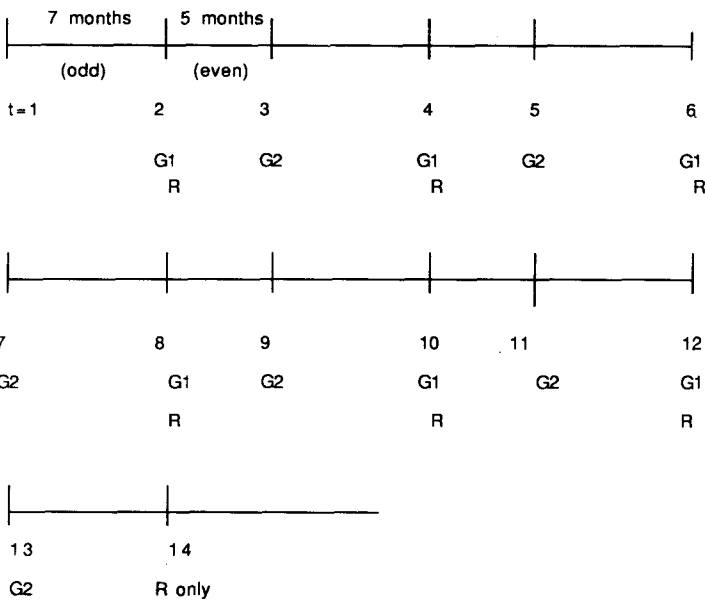
Fig. 2.   The timeline of development in the sea water model. Here time is measured in natural periods of the fish. In odd periods (April), the appropriate developmental switch is $G2$, and the value of $G1$ is a developmental state variable. In even periods (November), the reverse occurs.

$V_o(w, t, g1)$ = Expected lifetime reproduction for a fish of weight w at the start of *odd* period t (April of any year), when the value of the $G1$ developmental state variable is $g1$ and the developmental switch is $G2$;

$V_e(w, t, g2)$ = Expected lifetime reproduction for a fish of weight w at the start of *even* period t (November of any year), when the value of the $G2$ developmental state variable is $g2$ and the developmental switch is $G1$.   (6)

We can now derive the stochastic dynamic programming equations for these two fitness functions. We already have determined $V_e(w, 14, g2)$; it is given by equation (2). At $t = 13$, a fish only receives fitness if the choice of $G2$ is $g2 = 1$ and the current value of $G1$ is $g1 = 1$, so that

$$V_o(w, 13, g_1) = \begin{cases} \mathbf{S}_{mat}(w)V_{mat}(w'(w, 1, 1)) & \text{if } g_1 = 1 \text{ and choice is } g_2 = 1 \\ 0 & \text{otherwise} \end{cases} \quad (7)$$

where V_{mat} is the value of maturation from (2), $w'(w, 1, 1)$ is the weight of a fish in July, if it adopts $G1 = G2 = 1$ in April and $\mathbf{S}_{mat}$ is the survival of the fish from April to November in a year in which it matures. This could include fishing mortality in rivers, for example, although it is not done for the results reported below. In the case of an iteroparous fish, we would modify the maturation term in (7) to include expected reproduction after the current spawning event.

For previous times we have the iteration equations

$$V_e(w, t, g2) = max\{S'(t, t + 1)V_o(w'(w, 0, g2), t+ 1, 0);$$

$$S''(t, t + 1)V_o(w''(w, 1, g2), t + 1, 1)\}. \quad (8)$$

In this equation $S'(t, t+1, 0)$ and $S''(t, t+1, 1)$ are the probabilities of surviving from period t to period $t + 1$. They are determined by solving (3) and using (5) to determine accumulated mortality:

$$\mu_{acc}(t, t + 1) = \int_0^{Length^{(t)}} (1 - exp(-\mu(w(s)))) \, ds \quad (9)$$

where $Length(t)$ is the length of period t, measured in days and $exp(-\mu(w))$ is the probability that a fish of weight w survives a single day; then $S(t, t + 1) = exp(-\mu_{acc}(t, t + 1))$. Note that two different survival probabilities are needed because the different values of g_1 will lead to different growth rates. Also in (8), $w'(w, 0, g2)$ is the weight of a fish at the end of even period t given that its weight at the start is w and the values of $G1$ and $G2$ are 0 and $g2$ respectively; $w''(w, 1, g2)$ is similar except that the value of $G1$ is 1.

Next consider the dynamic programming equation in odd periods. This is slightly more complicated because reproduction occurs in the following even period if both developmental processes remain on. If $G1=0$, then the only choice of $G2=0$ so that

$$V_o(w, t, 0) = S'(t, t + 1)V_e(w'(w, 0, 0), t + 1, 0) \quad (10)$$

whereas if G1 = 1, we have

$$V_o(w, t, 1) = max\{S'(t, t + 1)V_e(w'(w, 0, 0), t + 1,0); S_{mat}(w)V_{mat}(w'(w, 1, 1))\}. \quad (11)$$

The numerical solution of (8,10,11) for the pattern of growth and maturation is straightforward, once one sees how the logic of alternating even and odd periods works.

The freshwater model

The freshwater timeline is more complicated because of the five developmental switches (Fig. 3). Here, the final period $T = 20$ to correspond to the $E2$ developmental switch. At that time, and at each other time, there will be one developmental switch and four

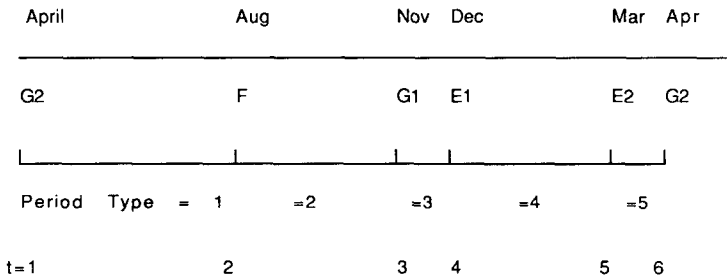| April		Aug		Nov	Dec		Mar	Apr
G2		F		G1	E1		E2	G2
Period	Type =	1	=2	=3		=4	=5	
t=1		2		3	4		5	6

Fig. 3. The timeline of the freshwater model, showing the five developmental switches and the five associated periods. As before, in each period there is exactly one developmental switch and four developmental state variables.

Table 5. The developmental state variables in the freshwater model for Atlantic salmon

Period type	Values	Appropriate developmental switch	Developmental state variables
One	1, 6, 11, 16	$G2$	$E1, E2, F, G1$
Two	2, 7, 12, 17	F	$E1, E2, G1, G2$
Three	3, 8, 13, 18	$G1$	$E1, E2, F, G2$
Four	4, 9, 14, 19	$E1$	$E2, F, G1, G2$
Five	5, 10, 15, 20	$E2$	$E1, F, G1, G2$

"developmental state variables" (Table 5), corresponding to the other developmental switches (which occur at different times).

To characterize growth, I first fit an equation similar to (3) to the Rowardennan field station data. This gave parameters that were constant. I then incorporated temperature and food availability that had a temporal pattern, normalized in such a manner that the yearly average of $k_2(t)$ was the same as in the fit for constant k_2. The daily temperature profile (HIGGINS and TALBOT 1985) is denoted by $T_d(s)$. Following the work of URSIN (1967, 1979) and ELLIOT (1976), I assume that the temperature dependence of anabolic changes has an optimum

$$a(T_d) = A_e - B_e(T_d - T_{ideal})^2 \tag{12}$$

where $a(T_d)$ is the temperature dependent anabolic factor, A_e and B_e are parameters, and T_{ideal} is the temperature that maximizes growth rate. Also following Ursin and Elliot, I assume that catabolic costs always increase with temperature

$$c(T_d) = \exp(-E_d/(273 + T_d)). \tag{13}$$

Note that although the temperature dependence of the anabolic term is symmetric with respect to temperature, the temperature dependence of the catabolic term is monotonic with temperature, so that the overall temperature dependence of growth will be asymmetric (URSIN 1967, 1979). Finally, I assume that there is a somatic cost s_{cei} of preparation for emigration, analogous to the one used for reproduction and depending upon the values of $E1$ and $E2$ developmental switches. With these assumptions, the growth model analagous to (3) for a fish that is continuously feeding ($f = 1$) is

$$\frac{dW}{ds} = f_{ue}\{a(T_d(s))\rho(s)k_2 W^\beta$$

$$\times \exp(-s_{cr1}g1 - s_{cr2}g2 - s_{ce1}e1 - s_{ce2}e2) - c(T_d(s))k_1 W^\alpha\} \tag{14}$$

In this equation, $\rho(s)$ is a relative measure of the availability of food at time s. We thus compute, using (14), the weight $w_i(w, e1, e2, 1, g1, g2)$ of a fish at the end of period i, given that its weight at the start of the period is w and that the values of the developmental switches are $e1, e2, f = 1, g1$ and $g2$.

Next consider the growth dynamics of a fish which adopts the anorexic behavior, $f=0$. In nature fish that become anorexic "ramp" their feeding level from fully active to anorexic, but I assume (for simplicity of calculation) that a fish adopting anorexic behavior switches feeding off in the middle of month 6 and back on in the middle of month 12. When it is not

feeding, a fish (i) forages just enough to maintain weight and (ii) reduces metabolic rate. Rewrite (14) as

$$\frac{dW}{ds} = ANA(W, s) - \delta(W)CAT(W, s) \tag{15}$$

where $ANA(W, s)$ and $CAT(W, s)$ are the anabolic and catabolic components of the growth function respectively and $\delta(W)$ is the reduction in catabolic costs which occur during anorexia. WRIGHT (1991) provides data that can be used to estimate the reduction in metabolic rate. Over the range of 1–20 g, an excellent ($r^2 = 0.989$) fit to Wright's data is obtained with $\delta(W) = 1.0181 - 0.33646 \log_{10}(W)$. The catabolic cost is paid by the fish regardless of the foraging behavior. Thus the daily catabolic cost is $\delta(W)CAT(W, s)$. If $\delta(W)CAT(W, s) > ANA(W, s)$, then the fish forages for the entire day and loses weight. Otherwise, it can forage for a fraction Δs of the day, determined by $ANA(W, s)\Delta s = \delta(W)CAT(W, s)$. Thus

$$\Delta s = \min\left\{1, \frac{\delta(W)CAT(W, s)}{ANA(W, s)}\right\}. \tag{16}$$

In this case, the allometric relationship (1) is

$$\log(L) = 0.317743 \log(W) + 3.84405. \tag{17}$$

In applying (17), we recognize that even though weight may decrease, length does not (so that condition will decrease when fish are losing weight).

Next consider mortality. PEPIN (1991) gives a length–mortality relationship:

$$\mu_{Pep}(L) = 0.25L^{-0.68}. \tag{18a}$$

McGURK (1986) published a mortality–weight allometric relationship spanning 12 orders of magnitude in dry weight (assumed to be 20% of wet weight). Although there is some discussion about it (FURNELL and BRETT, 1986), I have adopted it here as

$$\mu_{McG}(W) = 0.00787W^{-0.25}. \tag{18b}$$

In the computations reported below, I use (18b). Lacking better information, these equations combine all sources of mortality (e.g. starvation, disease, parasites and predators).

There is an additional mortality associated with smolting. In particular, the probability of death of a fish of length L that smolts is

$$\mu_{smolt}(L) = \begin{cases} \mu_{s1} & \text{if } L < L_{s1} \\ \mu_{s2} + [L - L_{s2}]\left(\dfrac{\mu_{s2} - \mu_{s1}}{L_{s2} - L_{s1}}\right) & \text{if } L_{s1} \leq L \leq L_{s2} \\ \mu_{s2} & \text{if } L > L_{s2} \end{cases} \tag{19}$$

where the μ_{si} and L_{si} are parameters (e.g. FELTHAM, 1990).

We are now ready to formulate the dynamic programming equations for the five different value functions. Starting at $t = T = 20$, a fish only receives fitness if $E1 = 1$, and it adopts $E2 = 1$ so that

$$V_{E2}(w, T, 1, g1, g2) = [1 - \mu_{smolt}(L(w))\,]V_o(w, 1, g1). \tag{20}$$

It is this equation that links the freshwater fitness with seawater fitness through $V_o(w, 1, g1)$. The values of entries in (20) show that a smolting fish gains no weight during the travel from the stream to the sea, enters the sea at period 1, transfers its current value of $G1$, and has associated fitness determined by the solution of the sea water model. For previous times, the $E2$ developmental switch involves either smolting or remaining in the stream; the fitnesses associated with these will be described below.

Working backwards, at $t = 19, 14, 9$ or 4, the period is four, the appropriate developmental switch is $E1$, and the associated value is $V_{E1}(w, t, e2, g1, f, g2)$ determined as the solution of the equation

$$V_{E1}(w, t, e2, g1, f, g2) = max_{e1=0,1}\{exp[-\mu_{ac4}(w, e1, e2, f, g1, g2)]$$
$$\times V_{E2}(w_4(w, e1, e2, f, g1, g2), t + 1, e1, g1, g2)\} \tag{21}$$

In this equation $\mu_{ac4}(w, e1, e2, f, g1, g2)$ is the accumulated mortality for a fish during period four when its weight at the start of the period is w and when the values of the developmental switches are $e1, e2, f, g1$, and $g2$; $w4(w, e1, e2, f, g1, g2)$ is the weight of the fish at the end of this period.

At $t = 18, 13, 8$ or 3, the period is three, the appropriate developmental switch is $G1$, and the fitness at these times is determined by

$$V_{G1}(w, t, e1, e2, f, g2) = max_{g1=0,1}\{exp[-\mu_{ac3}(w, e1, e2, f, g1, g2)]$$
$$\times V_{E1}(w_3(w, e1, e2, f, g1, g2), t + 1, e2, g1, f, g2)\} \tag{22}$$

with $\mu_{ac3}(w, e1, e2, f, g1, g2)$ and $w_3(w, e1, e2, f, g1, g2)$ having interpretation similar to those above.

At $t = 17, 12, 7$ or 2, the period is two, the appropriate developmental switch is F, and the fitness at these times is determined by

$$V_F(w, t, e1, e2, g1, g2) = max_{f=0,1}\{exp[-\mu_{ac2}(w, e1, e2, f, g1, g2)]$$
$$\times V_{G1}(w_2(w, e1, e2, f, g1, g2), t + 1, e1, e2, f, g2)\,\}. \tag{23}$$

At $t = 16, 11, 6$ or 1, the period is one and the appropriate developmental switch is $G2$. Here a simplification and a complication arise. The simplification is that there is no longer any choice in feeding (the anorexic period has either not yet started or has ended, depending upon the point of view which one adopts). However, if $G1 = 1$ and the fish adopts $G2 = 1$, then it will mature at the end of period two, in which case we must consider feeding behavior during period two. We thus use the growth model to compute $w_{12}(w, e1, e2, 1, 1, f)$ which is the weight of a fish at the end of period 2, if it has weight w at the start of period one and adopts the designated values for the developmental switches. Now a parr which has not spent any time at sea may have lower fecundity than an adult of the same weight. Hence, reduce the value of maturation [given by (2)] by a factor $f_0 \leq 1$. Thus the fitness $V_{parr,mat}$ of a fish which matures in this manner is

$$V_{parr,mat}(f) = f_0\ exp\,[-\mu_{ac12}(w, e1, e2, 1, 1, f)]V_{mat}(w_{12}(w, e1, e2, 1, 1, f)). \tag{24}$$

Two values of f are allowed in (24) since the fish could continue feeding or not before maturing.

We can now write the iteration equation for $V_{G2}(w, t, e1, e2, g1)$. First, if $g1 = 0$, then as before the only choice is $G2=0$ and

$$V_{G2}(w, t, e1, e2, 0) = \exp\left[-\mu_{ac1}(w, e1, e2, 0, 0)\right]$$
$$\times V_F\{(w, e1, e2, 0, 0), t + 1, e1, e2, 0, 0)\} \quad (25)$$

whereas if $g1 = 1$ either value of $G2$ is possible so that

$$V_{G2}(w, t, e1, e2, 1) = \max \{\max_{f=0,1}\{V_{\text{parr,mat}}(f)\};$$

$$\exp\left[-\mu_{ac1}(w, e1, e2, 0, 0)\right]V_F(w_1(w, e1, e2, 0, 0), t + 1, e1, e2, 0, 0)\}. \quad (26)$$

The right hand side of (26) is interpreted as follows: even if the parr matures, there are still two different feeding levels possible; the "max" inside the brackets takes care of these. The term involving $V_F(w_1(w, e1, e2, g1, 0), t + 1, e1, e2, 0, 0)$ is the expected fitness if the value of $G2 = 0$.

At $t = 15, 10, 5$ or 0 the period is five and the developmental switch is $E2$. Once again, the fish is assumed to be feeding. In addition, if the value of $E1 = 1$, and if the value of $E2 = 1$, the fish must emigrate. Thus, if $e1 = 1$ there are two choices for $E2$ and

$$V_{E2}(w, t, 1, g1, g2) = \max \{[1 - \mu_{\text{smolt}}(L(w))]V_0(w, 1, g1);$$

$$\exp\left[-\mu_{ac5}(w, 0, 0, g1, g2)\right]V_{G2}(w_5(w, 0, 0, g1, g2), t + 1, 0, 0, g1)\}. \quad (27)$$

The first term on the right hand side of (27) corresponds to $E2 = 1$, in which case the fish smolts. The second term corresponds to $E2 = 0$, in which case further development occurs in the stream.

Similarly, if $e1 = 0$ the only choice is $E2 = 0$ so that

$$V_{E2}(w, t, 0, g1, g2) = \exp\left[-\mu_{ac5}(w, 0, 0, g1, g2)\right]V_{G2}(w_5(w, 0, 0, g1, g2), t + 1, 0, 0, g1)\}$$
$$(28)$$

The solution of equations (20)–(28) then leads to predictions about the patterns of development and feeding behavior.

A simplification of the freshwater model

A simplification of the freshwater model is possible if we assume (i) that early maturation does not occur (so $G1 = G2 = 0$) and (ii) that the feeding and emigration switches are linked so that $F = 1$ implies $E1 = E2 = 1$ and $F = 0$ implies that $E1 = E2 = 0$. The former assumption is pretty reasonable if we focus on females and there are proximate mechanisms (J. Thorpe, personal communication) that support the latter assumption.

With these simplifications, the focus of the model is the feeding switch each August. If a fish of weight w in August continues feeding, we need to know its weight $w'(w)$ the following May (at the time of emigration) and the survival probability $S_f(w)$ for this fish from August to May. Alternatively, if a fish of weight w in August adopts the anorexic behavioral pathway, we need to know its weight $w''(w)$ the following August and the survival probability $S_{an}(w)$ from the current year to the next year, taking into account the weight dynamics described in equations (12)–(16).

We can now work with yearly periods and let

$V_{Fr}(w, t)$
= Expected reproductive success of a fish in freshwater in year t,
when its weight in August is w. (29)

Assuming that the fish can stay at most T years in freshwater, we have the end condition $V_{Fr}(w,T) = 0$, because emigration must occur in May and the specified time is August (i.e. it is too late in the last year for the fish to gain any reproductive success). For previous years, we compute the value of continuing to feed and the value of anorexia.

If the fish continues to feed in year t, then it emigrates the following May at weight $w'(w)$. Hence the value of feeding is

$$V_{feed}(w, t) = (1 - \mu_{smolt}(w'(w)))S_f(w)V_o(w'(w), 1, 0). \tag{30}$$

That is, if the fish survives to the following May, and survives smolting, it receives the expected reproductive success starting at weight $w'(w)$ in the ocean in period 1 with $G1=0$. The value, in terms of expected reproductive success, for a fish that follows the anorexic pathway is

$$V_{an}(w, t) = S_{an}(w)V_{Fr}(w''(w), t + 1). \tag{31}$$

That is, its expected reproductive success is determined by survival to the next August, and the expected reproductive success from that point on, given the new weight $w''(w)$.

Combing these equations we have

$$V_{Fr}(w, t) = \max\{V_{an}(w, t), V_{feed}(w, t)\} \tag{32}$$

This single equation replaces the set of coupled equations (21)–(28). As it is solved backwards, starting at $t = T - 1$, for each value of t and weight w, we obtain the optimal feeding behavior, pattern of smolting and the associated expected reproductive success.

SOME TYPICAL RESULTS

In this section, I present some typical results of the models developed in the previous section. To investigate the effects of climate change, the assumptions are (i) in the freshwater stage the main effect of climate change will be warming of the water (either directly through temperature increase or indirectly through changed precipitation), and (ii) in the seawater stage, the main effect of climate change will be a change in the patterns of zooplankton distribution (numbers and/or spatial distribution) leading to decreased food availability. (As described above, the alternative of increased food availability is feasible and could also be investigated.) That is, we determine the behaviors under one set of environmental conditions, but then go forward in time (Mangel and Clark, 1988) under the changed circumstances.

The seawater stage

It is easiest to begin with the seawater stage. Here we characterize the growth of the salmon using equation (3) and from that the expected reproductive success. We can simply run the growth model, ignoring the developmental constraints, with a base case value of k_2

and then with a changed value k_{2c}, which here is taken to be 80% of the base case value. This will cause the fish to grow more slowly, but will not lead to starvation (cf GISKE and AKSNES, 1992; AKSNES and GISKE, 1993). The results for a very fast growing fish (Fig. 4) show that under the scenario of climate change the fish grow slower and have poorer survival, leading to a decrease in expected reproductive success. Note that if there were no constraints, we could read off the "optimal" time for maturation (which, because of the reproductive window, occurs at $t = 8, 20, 32, \ldots$) from Fig. 4. We thus see that under the base case we predict highest fitness for fish that mature at $t = 20$ months at sea, but nearly equal fitness for fish that mature at $t = 8$. However, under the climate change scenario these are reversed, and the general prediction is that the maturing fish would be returning sooner (at $t = 8$) and smaller. This figure can be viewed as a "fitness surface" (sensu MANGEL and LUDWIG, 1992).

A more complicated treatment of climate change would assume that

$$k_{2c} = k_2 \exp\left(Z - \frac{\sigma^2}{2}\right) \tag{33}$$

where Z is a normally distributed random variable with mean 0 and variance σ^2. The motivation behind this description is that climate change will increase the variability of k_2, because of changed patterns of zooplankton, but maintain the mean value. Alternatively, we could assume that both the mean and variance change, but the assumption underlying (33) allows a focus on the role of increased stochasticity in the environment. Now length and survival are random variables so that expected reproductive success is also a random variable. We can study, however, how the average (over realizations of k_{2c}) expected reproductive success depends upon the variance σ^2 (Fig. 5). Here we see that the environmental variance becomes especially important at values $\sigma^2 > 1$, in which case there is a noticeable decline in average expected reproductive success.

However, the fish are constrained by the developmental switches. Using the full theory, we focus both on growth and the values of the developmental switches. For example, for a fish with $f_{ue} = 1$, smolt length 124 mm and weight 25 g, we predict that the fish will reproduce after 943 days at sea, at length 664 mm. Such a fish has a probability of surviving of 0.012, which is commensurate with the range of survival reported in Table 8 of BLEY and MORING (1988). Note that this value is achieved without any "tuning" of the model to match empirical results.

Under the climate change scenario in which k_2 is reduced by 20%, the same fish will still reproduce after 943 days at sea, but its length is now predicted to be 534 mm and the probability of survival is 3.6×10^{-3}. We thus see two effects of climate change: reduced size at return and reduced survival. However, the pattern of return is not changed.

This is not so if we consider a fish with $f_{ue} = 2$. A fish starting at the same size under the base case scenario exhibits the pattern of growth and maturation leading to reproduction after 578 days at sea, at length 682 mm, with survival probability 0.087. Thus, in the base case, f_{ue} differentiates between fish which mature at 1 sea year and those which mature at 2 sea years. Under the scenario of climate change, this same fish delays reproduction for an entire year, so that reproduction now occurs after 943 days at sea, at length 647 mm and ocean survival probability 0.02. Thus, the pattern of maturation changes in response to the decreased food supply. In addition, the fish actually loses condition at sea during the latter time. Again, we see the importance of the developmental constraints in characterizing the overall reproductive success. Some of the variation in maturation rates seen in
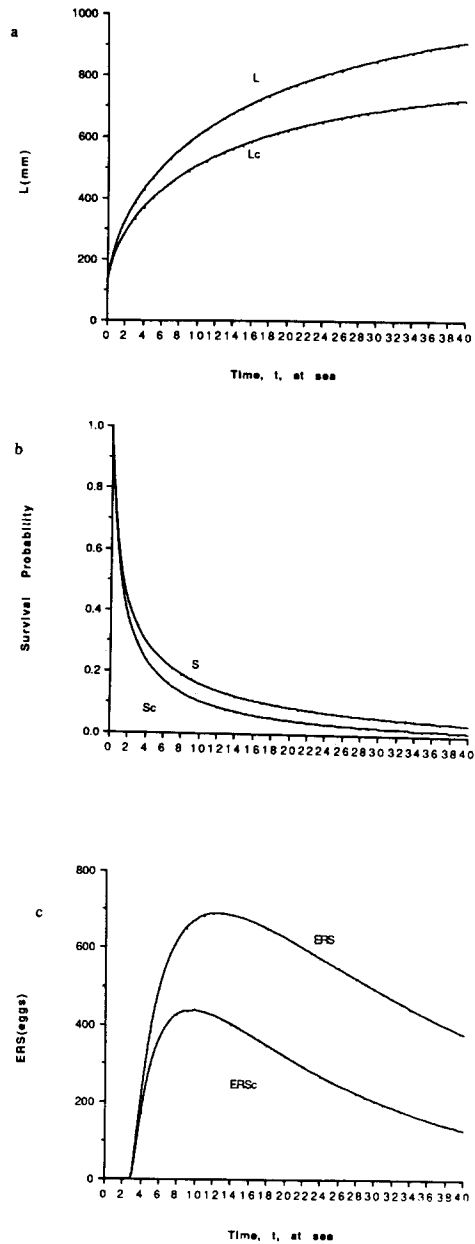
Fig. 4.   (a) The length of a fish, which migrates to sea with $W(0) = 25$ g, $L(0) = 124$ mm, as a function of time at sea under the base case ($L(t)$) and changed climate ($L_c(t)$) scenario in which k_2 is reduced by 20%. (b) The survival of the fish under the base case (S) and changed (S_c) scenarios. (c) The expected reproductive success of fish under the two scenarios. Successful reproduction can occur only at the windows corresponding to times 8, 20, 32, etc. Results are shown for $f_{ue} = 2$, i.e. for a fast growing fish.
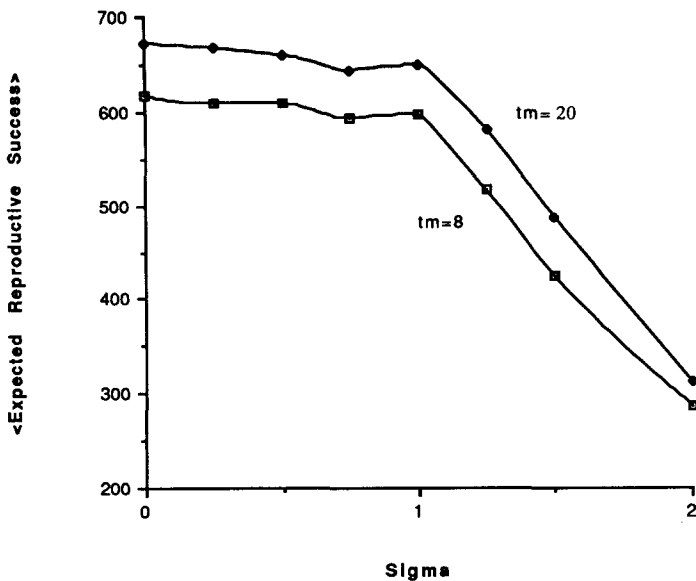
Fig. 5. The average expected reproductive success (averaged over realizations of the growth parameter k_2) for the case in which the changed growth parameter k_{2c} is log-normally distributed with mean 0 and standard deviation σ. The values $tm = 8$ and $tm = 20$ correspond to the times at which the fish mature. As the variance increases, the range of expected reproductive success widens, but note that the mean decreases only slightly until σ crosses 1.

existing stocks could be caused by the differing responses to fluctuations in the growth parameter k_2.

The freshwater stage

The freshwater model requires specification of more detail than the seawater model. The temperature profile (Fig. 6) is based on data from the River Almond in Scotland (HIGGINS and TALBOT, 1985). I assume that food availability is high for months 1–5 and low for months 6–12 and use (18b) to compute the accumulated mortality. We predict that all fish will smolt after either one year ($S1$) or two years ($S2$), depending upon initial weight and food utilization efficiency (Table 6).

If we focus on the interaction of initial weight $W(0)$ and food utilization efficiency f_{ue}, it is possible to divide the $W(0) - f_{ue}$ plane into regions in which the optimal strategy is $S1$ and in which the optimal strategy is $S2$ (Fig. 7). Repeating this calculation under a scenario of climate change in which stream temperature is assumed to rise by 2°C uniformly leads to a second boundary curve. Perhaps the most interesting prediction in this case is that there are combinations of initial weight and food utilization efficiency that lead to $S2$ strategies in the base case but to $S1$ in the case of warming. The ultimate reproductive success of the fish, of course, would have to be tied to how warming effects the pattern of growth and survival in the ocean. This intermediate region provides a means of testing the theory, for example by increasing the water temperatue of fish growing in tanks. Although it is well known that fish smolt sooner in warmer water, the theory now allows a detailed set of predictions about the role of metabolic rate and size in the determination of smolting.
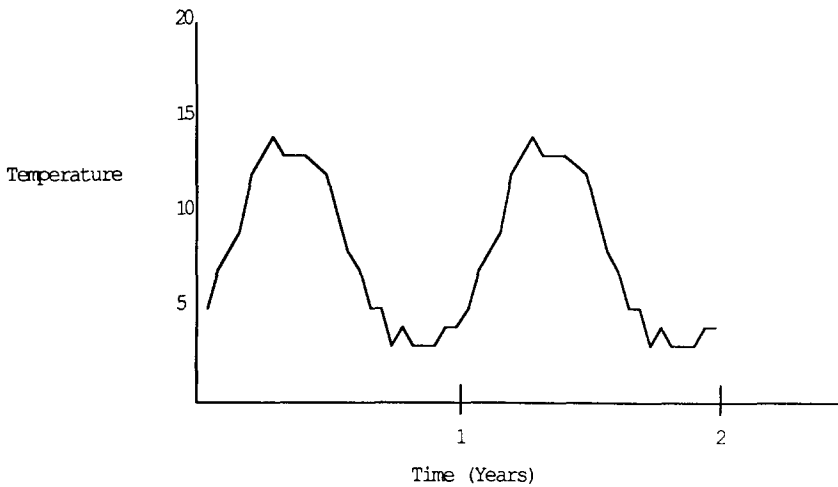
Fig. 6.   The temperature profile used in the freshwater model. This profile is based on data from
the River Almond in Scotland.

Table 6.   *Predicted developmental pattern (S1—smolt after 1
year in the river or S2—smolt after 2 years in the river) and length
at smolting as a function of initial weight and food utilization
efficiency*

$W(0)$	f_{ue}	S1 or S2?	Length at Smolting (mm)
0.1	0.8	S2	134.0
	0.9	S2	143.1
	1.0	S2	151.4
	1.1	S1	121.5
	1.2	S1	129.4
0.175	0.8	S2	137.7
	0.9	S2	146.4
	1.0	S1	118.7
	1.1	S1	126.4
	1.2	S1	133.3

DISCUSSION

Sissenwine (1983) argued that:

"Modeling should be an integral part of research on ...marine living resources. It is the process
of formalizing thought. Mathematical models express ideas in concise and universal language
...Like thinking, modeling is an ongoing process which is stimulated by observations (i.e. data).
Models in turn stimulate additional data collection, usually followed by modeling.

The process of modeling forces consistent thinking. This process is particularly important for
multi-disciplinary, multi-national situations where observations are made and ideas evolve
independently. A model is a synthesis of these observations and ideas".
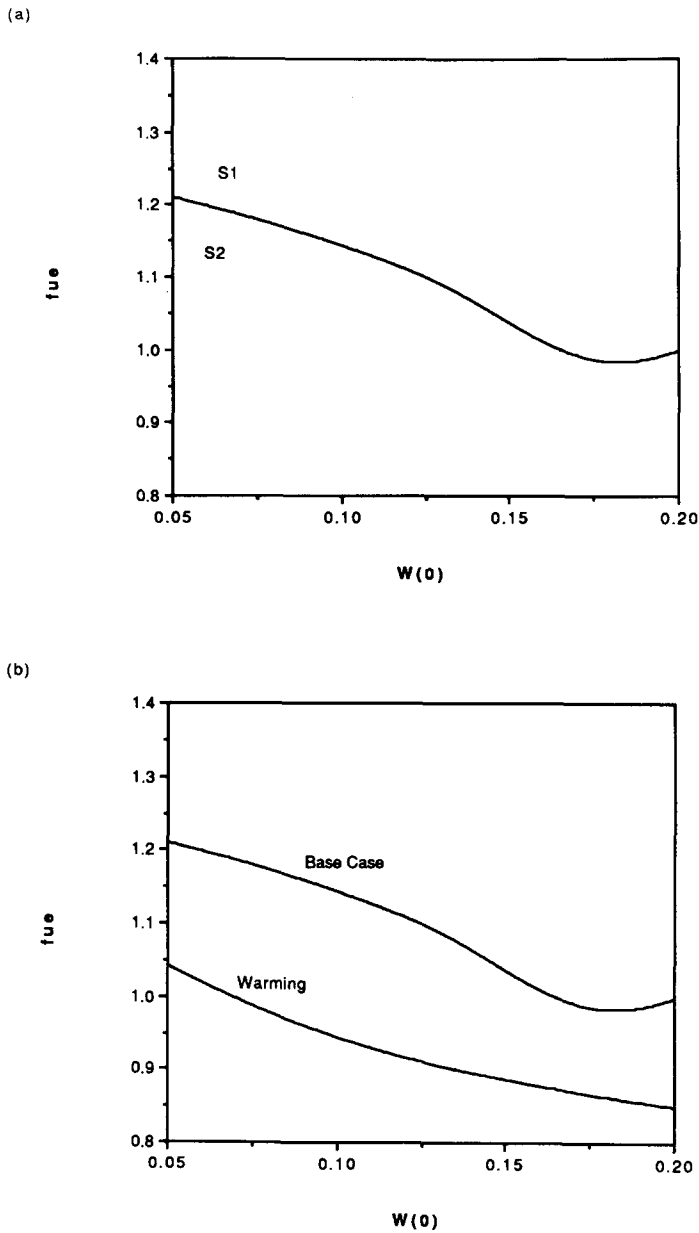
(a)

W(0)

(b)

W(0)

Fig. 7. (a) Separation of the $W(0)-f_{ue}$ plane into regions in which the strategy of development and behavior is $S1$ (smolt after 1 year in the river) or $S2$ (smolt after 2 years in the river). (b) The pattern of behavior and development will change in response to warming in the stream. In particular, fish will follow the $S1$ pattern at smaller initial size and food utilization efficiency. The region between the two curves represents those combinations of initial weight and food utilization efficiency which lead to $S2$ in the base case but $S1$ in the case of climate change.

In fact, there is considerable merit to the argument that the more difficult it is to collect data, the more imperative it is to have modeling go hand-in-hand with empirical work.

The model described in this paper is an attempt to formalize broad knowledge of the physiology, development and behaviour of Atlantic salmon in a way that can be used to investigate potential effects of climate change and to suggest potential experiments. The model is in good agreement with available data, but as Sissenwine suggests, the process of modeling is more than simply describing in another way what is known about the salmon. We should not ask, however, if the model and data are in agreement, but how each of a number of models fare in confrontation with the data (HILBORN and MANGEL, in press). Thus, we begin with the work of ELSON (1957) who developed the model that fish larger than 10 cm at a critical time would initiate the parr–smolt transformation. This model fares poorly on two accounts. The first is variability in smolt sizes and the second is the role of growth rate. Variability in smolt sizes, when a single critical size is predicted, can be dealt with by adopting the approach of quantitative genetics (FALCONER, 1971) and assuming that the 10 cm critical value is the phenotypic mean of the population but that there is some source of variance around this value.

The role of growth rate in the transformation has been stressed by Thorpe and his colleagues. The work presented here is, in large part, a formalization of the conceptual models of Thorpe to include size and growth rate as components of the parr–smolt transformation. This model, successful in incorporating growth rate, fails when confronted with the additional information that older fish of a fixed size and growth rate will smolt whereas younger fish of the same size and growth rate will not. This requires a modification of the model. In fact, we find that including population growth effects (e.g. MANGEL and LUDWIG, 1992) does not lead to such a prediction, but extending the model by assuming that the chance of successful smolting depends upon river age does lead to such a prediction.

The model results suggest a number of interesting experiments, which can be used to test the fundamental assumptions in a manner not at all connected to the model itself. The ideas for the test are based on "phenotypic engineering" (KETTERSON and NOLAN, 1992) and "allometric engineering" (SINERVO et al., 1992). The boundary curve in Fig. 7 separates those combinations of initial weight and food utilization efficiency leading to $S1$ or $S2$ patterns of growth and feeding. Now, if initial weight could be reduced for an $S1$ fish—for example by the yolkectomy methods described by SINERVO et al. (1992)—we would predict that such a fish would shift from the $S1$ strategy to the $S2$ strategy (the "yolkectomy" arrow in Fig. 8). Similarly, if hormones can be used to increase the value of food utilization efficiency (e.g. KETTERSON and NOLAN, 1992), it should be possible to take fish which would normally follow the $S2$ pattern and "convert" them to the $S1$ pattern (the "hormone" arrow in Fig. 8). As described in the text, the modification for truly iteroparous fish is truly straightforward. Similarly, to focus on males we must allow maturation in the freshwater environment. The general approach taken here could clearly be applied to other species of fish, with appropriate modification.

The model described can be used to understand potentially enigmatic results such as the work of THORPE et al. (1984) on the relationship between river years, sea years and fecundity. It can be used to investigate the fitness consequences of life history patterns that are not observed (e.g. loss of appetite during a winter followed by smolting the following spring). Because of an explicit focus upon lifetime reproductive success, we can connect the individual processes described here to population processes (e.g. MANGEL and CLARK,
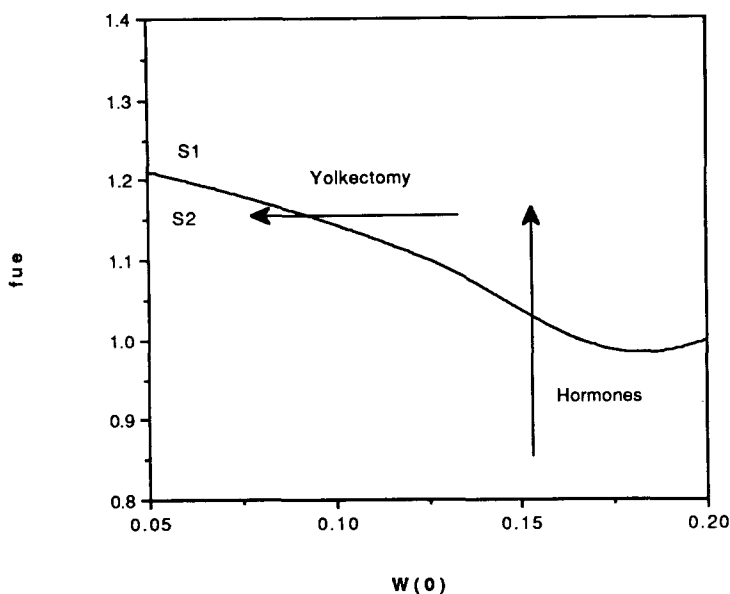
Fig. 8. The theory described here can possibly be tested by methods of "allometric" engineering. For example, yolk removal from eggs would decrease the value of $W(0)$, and possibly "convert" a $S1$ fish to a $S2$ fish. Similarly, hormonal modification of the food utilization efficiency might convert a $S2$ fish to a $S1$ fish.

1988, Chapter 7) and begin to focus on possible changes in abundance as a result of climate change.

This work also illustrates two broad principles for those concerned with connecting biological and physical oceanography and concerned with predictive biological ocean-ography. The first is that models can indicate the kinds of data that need to be collected and new experiments or empirical observations that should be made. We have seen this above, for example, in that certain kinds of data were not known and consequently particular assumptions had to be made in the process of the modeling. The second is the principle "know your organism": to construct the coupling between biological and physical oceanography and to make biological oceanography truly predictive we must focus in detail on particular species and situations. Then, of course, we lose the generality of models rooted in physical mathematics, but we gain the insight afforded by natural selection and models rooted in biological mathematics. The trade-off is worth it.

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