A framework for understanding Atlantic salmon (*Salmo salar*) life history

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Abstract: We took a hierarchical approach to understanding Atlantic salmon (*Salmo salar*) life history patterns by first comparing salmonids to other teleosts, next comparing Atlantic salmon to other salmonids, and finally, mapping correlations among individual life history traits within Atlantic salmon. The combination of anadromy, large eggs, nest construction and egg burial by females, and large size at maturity differentiates salmonids from most other teleosts. Within the family Salmonidae, there is considerable variation in all traits but Atlantic salmon are generally in the middle of the range. Within Atlantic salmon, we were able to map correlations among individual life history traits, but we found that we still lacked an understanding comprehensive and quantitative enough to allow us to predict how the entire life history should respond to environmental changes. Thus, we proposed several general courses of action: (*i*) use models to synthesize complex patterns and relationships, (*ii*) collect long time series of data in individual systems, and (*iii*) design experiments to assess phenotypic plasticity and how environmental influences differ from genetic effects and constraints.

Résumé : Nous avons adopté une démarche hiérarchique pour comprendre les patrons du cycle biologique du saumon de l'Atlantique (*Salmo salar*) en comparant tout d'abord les salmonidés à d'autres téléostéens, puis le saumon atlantique à d'autres salmonidés, et enfin en cartographiant les corrélations ente les traits individuels du développement chez le saumon atlantique. La combinaison de l'anadromie, de la grande taille des oeufs, du creusement du nid et de l'enfouissement des oeufs par la femelle et de la grande taille à la maturité différencie les salmonidés de la plupart des autres téléostéens. Au sein de la famille des Salmonidae, on note une variation considérable dans tous les traits, mais le saumon atlantique se situe généralement au milieu de la fourchette. Chez le saumon atlantique, nous avons pu cartographier les corrélations entre certains traits individuels, mais nous avons constaté que notre compréhension n'était pas encore assez détaillée et quantitative pour nous permettre de prédire comment l'ensemble du cycle biologique devrait réagir aux changements environnementaux. Nous proposons en conséquence diverses approches générales (*i*) avoir recours à des modèles pour faire la synthèse des patrons et relations complexes, (*ii*) recueillir des séries de données dans des systèmes individuels sur une longue période, (*iii*) concevoir des expériences visant à évaluer la plasticité phénotypique et la façon dont les influences environnementales diffèrent des effets et contraintes d'ordre génétique.

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Introduction

Atlantic salmon, *Salmo salar*, have been the subject of much research owing to their great commercial and recreational importance on two continents, a very large Atlantic salmon aquaculture industry, and their suitability as models for studies of behavior, ecology, and evolution, among other disciplines. However, we still do not fully understand what drives patterns of variation in their life histories. Researchers have concentrated their studies on specific stages of Atlantic salmon life history or on life history patterns in specific geographic locations. Our objective is to draw together research from these disparate fields to construct a framework within which we can begin to develop a broader understanding of Atlantic salmon life history.

A first step in understanding what drives life history patterns in any taxon is to separate patterns and traits that

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distinguish that taxon from those in related taxa. We begin by describing how salmonid life histories differ from those of other teleost fishes, then we discuss how Atlantic salmon differ from salmonids in general, and finally, we look closely at patterns of variation within Atlantic salmon. Although there are some robust correlations between individual life history traits (e.g., female size is positively correlated with egg number), we are unable to make confident predictions about how changes at one stage translate into changes more than one or two direct links away (e.g., how does a change in female size affect parr size at maturity?). Thus, we suggest avenues of research, both model-based and empirical, that will lead to greater understanding of how changes at one life stage translate to changes at other life stages. Only through this depth of understanding can we predict life history responses by Atlantic salmon to changes in their environment and to future management actions.

Life history patterns: salmonids versus other teleosts

We compared salmonid life history traits (parental care, egg size, spawning and emergence dates, age and size at maturation, anadromy, and iteroparity) to those of teleosts in general and then compared life history traits of Atlantic salmon to those of salmonids in general (regarding the genera *Salmo*, *Salvelinus* (char), and *Oncorhynchus* (Pacific salmon) as representative of the family Salmonidae). Fish in general, and salmonids in particular, are genetically variable and phenotypically flexible in their life history traits. Thus, our generalizations about salmonids have exceptions within and among groups.

Egg stage

Salmonids differ from most teleosts in several traits associated with the egg stage. Like the great majority of fishes, salmonids lay eggs rather than produce live young, though the selection (Kondolf and Wolman 1993), modification (Kondolf et al. 1993), and guarding of a nest that generally characterizes salmonids (Groot and Margolis 1991) places them in the distinct minority of fish families. Parental care is found in only about 21% of teleost families and is more common among freshwater than marine fishes (Blumer 1982; Gross and Sargent 1985). Among the fishes that practice uni-parental care, the male is more often the care-giver than the female (61%), again distinguishing salmonids, in which only the female builds and guards the nest (Gross and Sargent 1985). The burial of eggs that is characteristic of salmonids (DeVries 1997) (though lake trout, *Salvelinus namaycush,* are an exception) is an uncommon form of parental care (Blumer 1982). Most fishes that do bury their eggs have comparatively small eggs and short incubation periods (e.g., Osmeridae and Cyprinidae), the latter perhaps related to the risk of deterioration of the nest environment during a protracted period of incubation (see Peterson and Quinn 1996*a*, 1996*b* for evidence of the changes in the environment of salmon embryos during incubation).

Despite the risk of deterioration of the nest, salmonids often have long incubation periods as many species spawn in the fall and fry do not emerge until in the spring. Canadian freshwater fishes (which may be taken to represent species spawning in the same general environment as salmonids) show a bimodal distribution of spawning periods (Wootton 1984). Most spawn in the spring or early summer and a smaller number, including many salmonids and coregonids, spawn in fall or winter and incubate during the coldest months of the year. The bimodal distribution of spawning periods converges into a unimodal distribution of emergence–hatching dates, however, as virtually all North American freshwater fish larvae, including salmonids, complete yolk absorption and initiate exogenous feeding in spring–early summer.

The long incubation period typical of salmonids is associated with unusually large eggs, even among the spring-spawning species (Hutchings and Morris 1985). Egg size generally increases with body size within salmonid populations but varies among species and populations (Beacham and Murray 1993; Fleming 1996; Hutchings 1998). Fecundity of salmonids is comparatively low for their body size; most teleosts have much smaller, more numerous eggs (Elgar 1990; Winemiller and Rose 1993; Chambers and Leggett 1996). The connection between large eggs, nest construction, and a protracted incubation period is a defining feature of salmonid life histories, as embryos are maintained on endogenous food reserves for several months. During these prefeeding stages, the embryos incubate in stream or lake gravels for a period of time that is negatively correlated with water temperature (Beacham and Murray 1990). The salmonid pattern contrasts with the high egg number, small eggs, brief incubation period, and dependence on food-rich environments typical of most fish species (Hutchings and Morris 1985; Winemiller and Rose 1992, 1993). It should be noted that the coregonids (whitefish and cisco), which are close relatives of the salmonids, spawn in fall and winter but produce smaller eggs than the salmonids and also apparently do not provide parental care (Scott and Crossman 1973).

Age at maturation

Despite a great range in age at maturation, Canadian freshwater fishes exhibit a distinct size-at-maturation mode at 50–100 mm (Wootton 1984). Salmonids vary greatly in size at maturation, chiefly because of the differences in growing opportunities in streams, lakes, and marine environments. Although some populations of salmonids mature at very small sizes (e.g., brook trout, *Salvelinus fontinalis*: Hutchings 1994; landlocked Atlantic salmon: Gibson et al. 1996) and some males may mature as parr at a small size (notably Atlantic salmon, which may mature at sizes as small as 10 cm in freshwater: Fleming 1996), the family as a whole is much larger at maturation than the modal size of other freshwater fishes (Hutchings and Morris 1985). Anadromous Pacific salmonids are often 500–800 mm at the time of first spawning (Groot and Margolis 1991). The modal lifespan of Canadian freshwater fishes is 4–9 yr and in this regard the salmonids are not atypical (though lake trout and representatives of other iteroparous species can live to be quite old). Salmonids are thus large for their age, compared to freshwater fishes, in part due to their anadromous behavior and rapid growth rates at sea. This is reflected in the unusually high salmonid catch:biomass ratio sustainable in the North Pacific Ocean, relative to other

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production domains and fish species (Ware and McFarlane 1989).

Anadromy

The capacity to exploit marine food resources results from the anadromous life cycle displayed in most salmonids and this is an essential feature of the family. McDowall (1987) concluded that there are about 160 diadromous fish species, or about 0.65% of the estimated total of 24 618 fish species (Nelson 1994). Of the diadromous species, 54% are anadromous, the others being catadromous or amphidromous. Thus, anadromy is not unique to salmonids but this life history pattern makes them very unusual among fishes. Salmonids are not only anadromous but show a strong tendency to return to spawn at their natal site. Although the literature on homing in fishes is dominated by work on salmonids, it seems that some form of homing may be common among fishes in general (Quinn and Dittman 1992). Homing results in reproductive isolation of salmonid populations but straying, especially by anadromous individuals, permits gene flow among populations. Analyses of patterns of genetic diversity among fish species have indicated that freshwater fish populations are more differentiated than those of marine fishes and anadromous fishes show intermediate levels of differentiation (Gyllensten 1985; Ward et al. 1994).

Summary

Salmonids differ in many notable aspects from other fishes. However, their freshwater habitat requirements seem to be quite adaptable. The best evidence for this is the numerous successful transplants throughout the world. Populations of nonnative salmonids (especially brown trout, *Salmo trutta*; rainbow trout, *O. mykiss*; brook trout, and Atlantic salmon) have been established in all continents except Antarctica (MacCrimmon and Marshall 1968; MacCrimmon and Campbell 1969; MacCrimmon 1971; MacCrimmon and Gots 1979). The paucity of successful transplants of anadromous populations, even within the native range of the species, however, indicates that this is a highly specialized feature of their biology (McDowall 1988).

Life history patterns: Atlantic salmon versus salmonids

Spawning

Although salmonids as a group differ from most teleosts in many respects, Atlantic salmon life history patterns are generally representative of the family. They spawn in autumn–winter (Heggberget 1988), in keeping with many species but differing from others, notably rainbow trout, cutthroat trout (*Oncorhynchus clarki*), and grayling (in the related family Thymallidae) that spawn in the spring. They spawn mostly in streams, as is typical of the family (with the exception of lake trout). The mechanics of nest construction, courtship, and spawning are quite similar within the family and Atlantic salmon seem to be no exception (Groot and Margolis 1991; Fleming 1996).

Egg size

Atlantic salmon have smaller eggs for a given body size than Pacific salmon (Beacham and Murray 1993; Fleming

1996) and their fecundity is somewhat higher. Incubation time is within the range of Pacific salmon but shorter than most (days from fertilization to 50% hatching at 8°C: Atlantic salmon = 63; coho, *O. kisutch* = 63; chinook, *O. tshawytscha* = 67; chum, *O. keta* = 67; pink, *O. gorbuscha* = 72; sockeye, *O. nerka* = 77; Crisp 1988; Murray and McPhail 1988). The main source of variation within the family seems to be the slower temperature-specific incubation rate of fall-spawning compared with spring-spawning species (Brannon 1987). Leitritz and Lewis (1980) listed 41, 44, and 49 days to hatch at 10°C for brown, brook, and lake trout (fall spawners), respectively, compared with only 31 for spring-spawning rainbow trout.

Freshwater rearing habitat

Most juvenile Atlantic salmon spend their first year or more (1–8) residing in stream habitats (Metcalfe and Thorpe 1990; Gibson 1993). In this regard they are like most salmonids but unlike lacustrine species such as lake trout and sockeye salmon and species that migrate directly to sea such as pink, chum, and some populations of chinook salmon. Rearing habitat in streams varies among populations and also changes as the fish age, but Atlantic salmon parr tend to occupy territories with relatively high water velocities (see review by McCormick et al. 1998). However, some populations of Atlantic salmon rear in lakes (Berg 1985) rather than streams. Such flexibility with respect to rearing habitat is quite common within the family. Swain and Holtby (1989) documented distinct stream- and lake-rearing coho salmon populations. Most sockeye salmon populations rear in lakes but others rear in rivers or migrate directly to sea (Wood et al. 1987) and brown trout also occupy a range of freshwater habitats. Atlantic salmon are thus quite typical of the salmonids, having a "characteristic" habitat but also having populations that occupy distinctly different habitats.

Anadromy

Most Atlantic salmon are anadromous, but freshwater populations exist and males commonly mature as parr in streams (Berg 1985). The degree of anadromy displayed by Atlantic salmon is intermediate within a family that ranges from chum and pink salmon (always anadromous in their native range) to lake trout (never anadromous; Rounsefell 1958; McDowall 1988). Rounsefell (1958) considered Atlantic salmon to be less anadromous than sockeye salmon and more so than rainbow trout. One life history trait linked to anadromy is the occurrence of sexually mature male parr. Such parr are common in Atlantic salmon (Fleming 1996) but are not typical of Pacific salmon in North America. However, mature parr have long been known in some populations of chinook salmon (e.g., Snyder 1931) and are common in brown trout (Bohlin et al. 1994) and masu salmon, *O. masou* (Kato 1991; Tsiger et al. 1994).

Atlantic salmon are large at seaward migration (Hutchings 1998) comparable to steelhead trout but larger than most Pacific salmon. The marine migration patterns of Atlantic salmon most closely resemble those of steelhead trout (except the Asian coastal populations; Burgner et al. 1992), sockeye salmon, or stream-type chinook salmon (Groot and Margolis 1991). These species apparently make only limited use of estuaries, move rapidly to the open ocean, and feed

there for a year or more. Most Atlantic salmon returning from the ocean are maturing and will spawn before migrating back to sea, unlike some salmonids which often migrate back to freshwater but do not spawn that season, such as Dolly Varden char, *Salvelinus malma* (Armstrong 1981), brown trout (Jonsson 1985), steelhead trout (Burgner et al. 1992), brown trout (Jonsson 1985), and Arctic char (Nordeng 1983). The relationship between the date of river entry and the date of spawning varies greatly, however, and in some stocks of Atlantic salmon, individuals return nearly a year before they spawn, arriving in the rivers in late autumn and not spawning until the following autumn (Berg 1964; Saunders 1981).

Anadromous Atlantic salmon are large at maturity (Hutchings 1998), exceeding all but chinook among the Pacific salmon. Although less numerous than the Pacific salmon species that use streams only for spawning (pink, sockeye, and chum), their abundance is comparable to large-bodied species that have extended rearing periods in freshwater (e.g., chinook salmon and steelhead trout). With respect to iteroparity, the life history pattern of Atlantic salmon is intermediate within the family. The five North American species of Pacific salmon are semelparous (though under certain controlled conditions chinook salmon can survive after maturation and reproduce again; Bernier et al. 1993). Atlantic salmon are iteroparous, having the capacity to spawn many times (Hutchings and Morris 1985). Populations vary considerably in iteroparity and in the proportion of annual and biennial spawners (Jonsson et al. 1991). In many Atlantic salmon populations, most anadromous individuals do not survive to spawn a second time (Fleming 1996); however, other populations are characterized by high proportions of repeat spawners (Ducharme 1969; Saunders and Schom 1985).

Summary

Salmonids as a family differ in many obvious respects from most fishes, notably their patterns of female parental care, burial and lengthy incubation of large eggs, rapid growth and large size at maturity associated with anadromy, and tendency toward semelparity. Despite these specialized patterns, freshwater populations have been readily transplanted around the world, hence they can successfully compete in ecosystems in which they have not evolved. Within the family, there is considerable variation in all traits but Atlantic salmon are generally in the middle of the range, not being extreme in the major traits (e.g., anadromy, iteroparity, size and age, habitat). They are thus generally suitable as a "model" for salmonid studies.

Life history patterns: correlations within Atlantic salmon

We used information from this workshop, from our own research, and from the literature to specify directions of correlations between pairs of life history traits in Atlantic salmon (Fig. 1). In some cases, we used knowledge from similar species to infer relationships in Atlantic salmon. We were interested in the relationships between life history traits within populations rather than correlations obtained from studies comparing different populations. The latter studies

Fig. 1. Directions of correlations between Atlantic salmon life history traits.
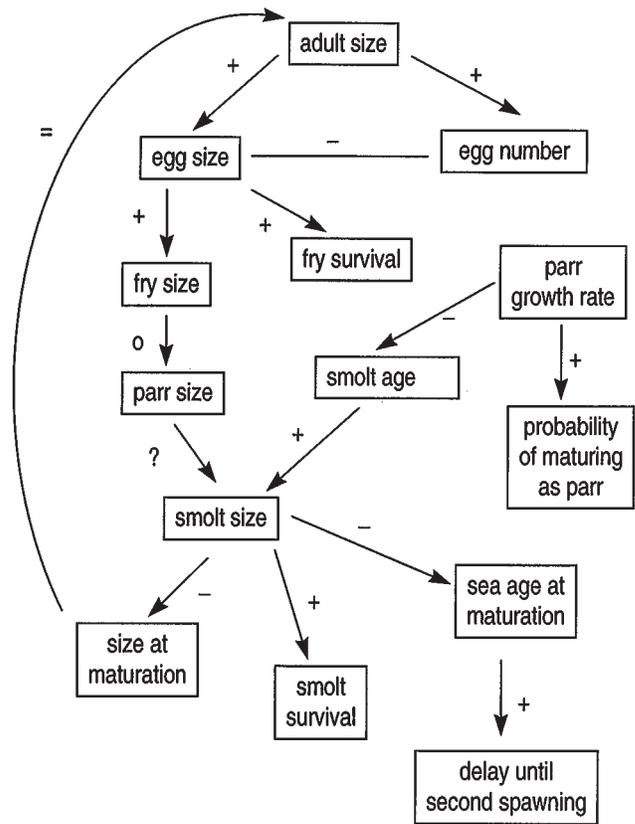
are important in showing the range of evolutionary responses but can give misleading information with respect to the within-population trajectories. For example, analysis among populations shows no significant relationship between smolt size and survival at sea (Hutchings 1998), whereas studies within a population have demonstrated a positive correlation between these two variables (e.g., Lundqvist et al. 1994).

Certain relationships are fairly predictable; for example, total ovary weight, fecundity, and egg size increase with female body size (Fleming 1996; Jonsson et al. 1996). Although this might seem to imply that egg number and egg size should be positively correlated, in fact, just the opposite is true. Egg number and egg size show a negative correlation among females of similar size (Fleming 1996). The foregoing example illustrates the need for empirical data and the care required in constructing a life history model.

As we might expect, fry size increases with egg size (Fleming 1998) and large size gives fry a survival advantage (Fig. 1). Large fry, however, do not necessarily become large parr. Rapidly growing parr smolt at a younger age (Metcalfe et al. 1989; Økland et al. 1993; Hutchings 1998; Metcalfe 1998) and a smaller size (Økland et al. 1993) than more slowly growing parr. The fastest growing parr either migrate to sea as smolts or mature as parr (Thorpe 1977, 1986; Myers et al. 1986; Bohlin et al. 1994). The incidence of smoltification and maturity among the fastest growing parr undoubtedly varies among populations and may primarily

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depend upon the age at which individuals get large enough to overcome size-biased marine mortality patterns. In Scotland, the fastest growing parr appear to be those that migrate to sea (Thorpe 1977, 1986), whereas in Canadian populations, the fastest growing males mature as parr. There is a positive correlation between growth rate (or condition factor) and likelihood of maturing as parr (Thorpe 1986; Simpson 1992; Bohlin et al. 1994; Metcalfe 1998). Smolt size is positively related to smolt survival during their migration downstream. Large smolts seem to be less vulnerable to predators (White 1957; Reitan et al. 1987; Kennedy and Greer 1988; Feltham 1990), disease (Cusack 1986; Jansen and Bakke 1993a, 1993b), and osmoregulatory stress (Bjerknes et al. 1992; Thorpe and Metcalfe 1998) than smaller smolts. Large smolts also have higher marine survival rates (Lundqvist et al. 1994). Individuals that smolt at a young age tend to be small and thus have poorer survival than larger, older smolts.

The paradoxical pattern of fast-growing parr becoming small smolts is similar to the pattern of smolt size and size at maturity. Large smolts tend to retain their size advantage over small smolts, even after a year at sea (Nicieza and Braña 1993), and tend to mature after fewer winters at sea and at smaller sizes than individuals that were smaller as smolts (Carrière and Roff 1996). Both sea-age at maturity and adult size are positively correlated with the delay until a second spawning attempt (Jonsson et al. 1991). Large (>90 cm), late-maturing (sea-age at maturity >2 yr) salmon tended to spawn biennially rather than annually in Norway (Jonsson et al. 1991).

Population or cohort density affects some of the life history parameter values described above in Atlantic salmon, particularly growth and survival during the riverine life stages. Survival from egg through fry and growth rate of parr are both inversely density dependent (Talbot 1994; Crozier and Kennedy 1995). In addition to density dependence, frequency dependence may also affect some life history traits. For example, reproductive success associated with maturing as a parr may depend on both the density and frequency of anadromous males spawning that year. When anadromous males predominate, maturing as a parr provides a way to avoid the intense competition for mates that occurs between anadromous males, although the success of this alternative strategy is of course itself frequency dependent (Hutchings and Myers 1988, 1994; Fleming 1996).

In some cases it may be tempting to use our understanding of directions of correlations among life history traits (i.e., Fig. 1) to predict how changes in one life history trait affect other life history traits, but the complexity of relationships and density or frequency dependence of rates requires a more quantitative approach. For example, we might ask how increased river temperature might affect life history characteristics such as the return age and size of Atlantic salmon (Roff and Carrière 1996). A slight increase in stream temperature produces higher growth rates (assuming adequate ration) and leads to a change in smolt size. Individuals that are large as smolts mature at smaller sizes than those that are small as smolts (see Fig. 1) and thus produce fewer eggs per female. However, these individuals that are large as smolts mature at a younger age than those that are smaller as smolts, so although they produce fewer eggs per female,

they produce them in fewer years. Thus, the actual outcome for the population as a whole cannot be predicted from qualitative correlation alone.

The situation is made even more complex and the outcome more difficult to predict when we recognize that many of these life history traits are heritable and many are genetically correlated with other traits (Jonsson et al. 1991). For example, an individual's size at smoltification is at least partially determined genetically by its parents and an individual's size at age at sea is genetically correlated with its size at smoltification. We also know that size at maturity is heritable. However, genetics only partially determine these traits; the rest is influenced by environment. Thus, we have a complex set of phenotypic and genetic relationships between smolt size and size at maturity, which makes prediction of the actual response to changes in selective factors and growing conditions difficult to predict without explicit mathematical models and knowledge of the relative contribution of the environment and genetics in the expression of these life history traits.

The outcome of a sequence of events is not predictable by simple examination of the direction of correlation of pairs of traits as illustrated in the flow chart shown in Fig. 1. This analysis is not atypical of analyses of life history variation; they generally involve the interaction of several functions, frequently nonlinear, and prediction is not possible without explicit solution of the equations using numerical methods. To use our current understanding to predict outcomes of environmental changes successfully, it must be enhanced either with specific empirical information or with quantitative models. Below, we first address modeling approaches and then empirical approaches that we believe will lead to a more comprehensive understanding of Atlantic salmon life histories.

Approaches to new understanding: models

Regression models

Regression models are the simplest type of predictive models (Powers 1989). In principle they make no statement concerning the mechanism producing the regression between two traits. As an example, consider the following two regressions:

$$\text{Egg size} = c_0 + c_1(\text{Female spawner size})$$

$$\text{Female spawner size} = c_2 - c_3(\text{Smolt size})$$

where the c_0, c_1, c_2, and c_3 are fitted constants. To use these two equations for prediction we must assume that they can be chained together, i.e.,

$$\text{Egg size} = c_0 + c_1(c_2 - c_3(\text{Smolt size}))$$

which requires that the correlations be very large (>0.8), which is not typical for ecological data. Thus the separate regression of egg size on smolt size will not usually give the same constants as those from the above chaining (so, in general, the intercept will not equal $c_0 + c_1c_2$ and the slope will not equal $-c_1c_3$). Further, unless the correlations are very high, the equations cannot be algebraically manipulated to switch dependent and independent variables: thus the

Female spawner size on egg size regression is not Female spawner size = $(1/c_1)$(Egg size $- c_0$). A further complication is that equations may be nonlinear.

Given the above considerations, the regression approach will be of limited use in constructing a general life history model. This method should be used only where there are few variables (preferably only two) and prediction is to be made only within the range of the observed data. Its strength lies in the fact that very few assumptions are made. It does, however, form the basis of the approaches described below, because almost all relationships are ultimately based on a regression analysis. The contribution that regression (linear or nonlinear) analysis plays is to establish the sign of the correlation and a range within which parameter values are constrained to lie.

Mechanistic models

In contrast to the regression approach, mechanistic models are based on an assumed functional relationship between variables; for example, the relationship between egg size and egg number might be developed based on geometric constraints. Thus we might predict that

$$\log(\text{Egg number}) = c_4 - c_5 \log(\text{Egg size})$$

where c_4 and c_5 depend on the particular geometry of the body and the egg. In practice the two constants would generally be estimated by regression. It is quite possible that the simple linear regression

$$\text{Egg number} = c_6 - c_7(\text{Egg size})$$

will fit the data equally well (i.e., there would be no significant difference in the variance accounted for by the two regressions). From the linear regression approach there is no reason to prefer one to the other. As long as predictions remain within the range of the observed data, it would not matter which model is used, but predictions outside the range could be quite different and it is at this point that the argument of function becomes important. An incorrect mechanistic argument can lead to a predictive equation that can be made to fit the data but is in fact incorrect; a good example of this is the von Bertalanffy growth function. Although the resulting model can be fitted to the data, the underlying physiology is wrong (Knight 1968) and the fit comes about simply because the equation is flexible in shape and the three parameters are not determined independently from metabolic studies but estimated from the growth data itself (Roff 1980). It is important to keep in mind the assumptions of the model components and subject them to independent tests.

Mechanistic models are very important in predicting short-term responses to changes in conditions. An example is the "proximate model" of Thorpe et al. (1998), which predicts life-history pathways in salmonids from knowledge of how an individual fish's growth performance matches genetically determined thresholds. These thresholds must be surpassed by key times of year for smolting or sexual maturation to be triggered and once these developmental processes are in train, further thresholds must be attained for the process to be completed. This simple series of switch points is capable of generating the observed wide diversity of salmonid life histories both among and within populations, because threshold values will vary among fish and both the environment and the genotype of the fish create variation in growth rates. Metcalfe (1998) illustrates how a simplified form of this approach can be used to predict demographic responses to changes in mean growth rate.

Optimality models

Mechanistic models generally make no a priori assumption about the effect of selection on model components; they are taken as fixed. In contrast, optimality models assume that some fitness measure is maximized. As a consequence, evolution will sculpt a suite of characteristics that maximizes fitness. The central assumption of optimality models is that there are trade-offs that constrain the range of possible combinations. We can consider egg number and egg size to constitute a trade-off, with some limitation of the total egg mass that can be produced by a female of a given size. Then, rather than simply describing the relationship between egg number, egg size, and female size from data or as a geometric constraint of body size, we may believe that it is adaptive to have egg number and egg size change in response to maternal and environmental conditions. Thus, we would develop an optimality model. Model components may be derived from a regression model or from mechanistic considerations. Obviously the less "biology" there is in the model the greater the likelihood of producing erroneous predictions. When the value of a life history characteristic depends on characteristics of other individuals in the population (see "Life history patterns: correlations within Atlantic salmon"), we can use game theory models which allow us to consider frequency dependence in optimal life history strategies.

The criterion for validating an optimality model is that it predicts the observed field values when fitness is maximized. If the model fails in this regard it is assumed that a trade-off has been incorrectly specified or omitted. Mechanistic models may be able to predict the general form of a relationship, but they may not be able to specify parameter values. The principle of fitness maximization permits the estimation of parameter combinations. Hence it is possible to generate a set of possible suites of parameter values. Working with such combinations it is then possible to predict the outcome of changes in parameter values due to environmental change, for example. Two types of predictions are possible: first, those arising under the assumption that relationships (e.g., the amount of energy devoted to growth versus reproduction) remain constant, and second, those arising under the assumption that relationships change. The second type of prediction may be a consequence of phenotypic plasticity or of genetic change. In the former case the response will be immediate and the underlying assumption is that selection has molded the norm of reaction to maximize fitness. In the latter case the optimality model can predict only the final outcome, not the trajectory between the initial and final combinations. In this case short-term predictions likely will be most reliably made using the assumption of fixed relationships. To make a prediction of the trajectory between the two states, we must add another component, the genetic control of the traits.

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Genetic models

Optimality models predict equilibrium conditions but not the trajectory that led to them. As a consequence, novel perturbations which would not have molded a reaction norm cannot be dealt with by optimality models. A genetic model contains all the components of a mechanistic model plus the assumption that parameters are genetically variable. For a single trait X, the relevant equation is

$$R_X = h_X^2 S_X$$

where R_X is the response to selection (the change in the trait value X), h_X^2 is the heritability of trait X, and S_X is the selection differential (the difference between the population value and the parental value). For two traits, X and Y, we must also consider the correlated response of trait Y to selection on trait X, the genetic correlation between the two traits, the heritabilities of each trait, and the two phenotypic variances associated with each trait. Also, if selection acts on both traits, the equations become more complex but no additional genetic parameters are required. The important message is that a genetic model requires considerably more information than the previous modeling approaches. Each pair of traits requires the estimation of 6 (co)variances. If the changes in the environment are within the range normally experienced by the fish or we wish to predict equilibrium trait combinations, as in a geographic comparison, the optimality approach is preferred because it requires fewer data. On the other hand, if we wish to predict trajectories of changes in life history resulting from changes outside the normal range, then a genetic model is necessary.

Approach to comprehensive understanding: empirical studies

Long-term monitoring

Long-term monitoring programmes provide one means of obtaining data relevant to the construction of a general life history model of Atlantic salmon. Most importantly, long-term data provide estimates of the temporal variability associated with life history traits. Data collected concurrently on several life history traits would also permit direct and indirect estimates of the parameters required of a general life history model. In addition, one could use long-term baseline data to identify those traits most sensitive to unanticipated environmental or demographic change.

To minimize financial costs, long-term monitoring of life history traits could represent relatively small-scale projects that are constituent parts of existing research or stock assessment programmes. For example, temporal variation in the frequency of parr maturity, a parameter thought to increase with juvenile growth and adult fishing mortality, with consequences for population biomass (Myers 1984), could be obtained from random samples of parr taken over a period of a few days every autumn. These data could then be analyzed with reference to other life history data collected concurrently from the same population. Efforts should be made to maximize the information obtained from such monitoring programmes, including the archiving of samples (e.g., scales, adipose tissue) for future analysis.

Table 1. Number of Atlantic salmon populations for which life history data have been measured for a minimum of 10 years.

Life history data	Number of populations
Life history character	
Parr length	0
Incidence of parr maturity	1
Smolt length	2
Smolt age	7
Smolt-to-grilse survival	6
Seawinter:multiple seawinter salmon ratio	16
Grilse sex ratio	3
Grilse length	5
Fecundity	1
Egg size	0
Life history trait combination	
Smolt-to-grilse survival – fecundity	0
Smolt-to-grilse survival – smolt age	2
Smolt-to-grilse survival – smolt length	1
Smolt-to-grilse survival – grilse length	2
Smolt-to-grilse survival – incidence of parr maturity	0
Smolt-to-grilse survival – sex ratio	1

Note: Data collated from Appendix 2 in Hutchings 1998.

A minimum of 10 years of data is required to obtain reliable estimates of the variance associated with life history traits. There are at least 24 populations throughout the range of Atlantic salmon for which 10 or more years of data exist for at least 1 life history trait (see Appendix 2 of Hutchings (1998) for more details). Ranked by frequency of occurrence, life history characters for which long-term data are most readily available include grilse:multi-sea-winter salmon ratios, smolt age, smolt-to-grilse survival, and grilse length (Table 1). However, despite the apparently large number of populations for which long-term data have been collected, there are exceedingly few populations for which characters relevant to life history analyses have been measured concurrently for 10 or more years. Indeed, long-term data on a metric of survival and at least one additional life history character are available for only two populations, Western Arm Brook and Conne River (both in Newfoundland; Table 1). There are no populations for which long-term data are available on both survival and fecundity, or on both survival and incidence of parr maturity.

The near absence of long-term data on relevant life history traits from the same population makes it extremely difficult to construct and test general life history models for Atlantic salmon. But, despite this deficiency of data, long-term monitoring programmes should not be entered into without careful consideration of the variables that warrant measurement and those that do not. In addition, when collecting long-term data, one must be aware that many rivers may contain more than one genetic stock of salmon (Saunders 1981). Thus, variation in measured traits may reflect temporal variation, variation among stocks, or temporal changes in relative abundance of different stocks. Data collection programmes must be sufficiently rigorous to allow
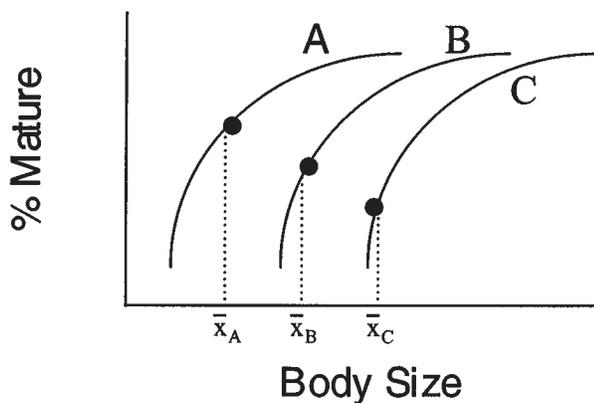
for discrimination among these different sources of variation.

Manipulative experiments

Much of the information for variation in life history strategies in salmonids comes from comparisons between populations (e.g., in the mean age at smolting, mean percentage maturing at different ages, etc.). Although such data can be instructive in revealing the phenotypic plasticity that can occur in life history traits, they are also misleading if used to predict how a single population might respond to environmental changes. This is a consequence of the fact that each population has its own composition of genotypes and hence its own average reaction norm (Stearns 1992). For example, the shape of the relationship between body size at a given age and probability of maturing may differ among populations (as a result of population differences in growth or mortality rates). If mean values for both body size and percent mature are obtained from these different populations, it is possible to obtain a negative relationship between size and likelihood of maturity across populations, even though the relationship is positive within each of them (Fig. 2). The among-population trends thus tell us nothing about the underlying causal mechanisms (e.g., the relative genetic and phenotypic contributions). Such information can be revealed only by manipulative experiments designed to test the life history responses of fish of different origin to a range of environmental conditions.

The simplest such experiments are so-called "common garden" trials, in which fish from two or more populations are reared in a common environment (e.g., Nicieza et al. 1994). If there is no difference in response between fish of different origin, this suggests that the reaction norms for the different populations are very similar and any geographical variation in the measured life history traits is of environmental rather than genetic origin. However, experiments that do reveal population differences in response to a common environment are more difficult to interpret, especially since many common garden trials are carried out in an environment (e.g., a hatchery) that is markedly different from that experienced by any of the source populations. A more satisfactory (but logistically more difficult) experimental design is to carry out reciprocal transplants, which monitor the response of two or more populations when reared in each other's natural environment. The reciprocal nature of the rearing environments means that information on reaction norms is obtained independently for each population and population differences in phenotypic plasticity are immediately apparent.

An alternative approach is to carry out phenotypic manipulations, where phenotypic variation is generated by appropriate manipulations of the environment. While the nature of some of the relationships shown in Fig. 1 has been tested by such manipulation experiments (e.g., the link between growth rate and smolt age (Thorpe et al. 1989)), these have inevitably mostly been carried out in the laboratory or hatchery. A challenge for the future is therefore to carry out phenotypic manipulation experiments in conditions that more clearly resemble the natural environment.

Summary

Due to their economic importance and wide geographic range, Atlantic salmon are particularly well studied. Because of this, we have been able to construct a diagram illustrating the correlations among individual life history traits. But despite this level of understanding, we still lack an understanding comprehensive and quantitative enough to allow us to predict how the entire life history should respond to environmental changes or to changes in specific parts of the life history. Thus, we propose several general courses of action designed to enhance our ability to predict how the life history of Atlantic salmon should respond to change. First, we must continue to collect data, especially long time series in individual systems. Next, we must synthesize the available information, using models to tie together complex patterns and relationships. Finally, we must design experiments that will allow us to assess phenotypic plasticity and how specific phenotypes arise from different environmental influences and separate this from genetic influences and constraints.

Fig. 2. Hypothetical relationships between the size of salmon at a given age in three different populations (A, B, and C) and their likelihood of becoming sexually mature that year. The solid lines show the reaction norm within each population, while the dots indicate the mean values for each of the populations that might have been obtained during a short-term study. An among-population comparison using these mean values would indicate a negative relationship, while the true causal relationship is always positive.

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