Ann. Zool. Fennici 27:139–147
Helsinki 26 September 1990

ISSN 0003-455X

Large or small at maturity — theories on the choice of alternative male strategies in anadromous salmonids

Torgny Bohlin, Claes Dellefors & Ulo Faremo

Department of Zoology, Animal Ecology, University of Gothenburg, PO Box 25059, S-400 31 Gothenburg, Sweden

Received 3 October 1989, accepted 4 January 1990

Precocious maturation (parr maturation) of salmonid males is treated as a conditional mixed ESS, and cues for the choice of life-history tactic discussed. Growth rate seems to affect the timing of the choice but not necessarily the choice of tactic. Unpredictable environmental conditions affecting potential fertility rather than survival would select for parr maturation. The temporal and regional variation of parr male frequency in wild sea trout suggests that populations are adapted to population specific parr male frequencies and that a state correlated with individual growth, e.g. nutritional state, is used as a cue.

1. Introduction

Some species and populations of salmonids are migratory (anadromous), and the life history for such forms of the genus *Salmo* is essentially the following. After hatching in fresh water in spring, the juveniles, called parr, often remain in the nursery stream for one year or more before smolting and seaward migration during spring. Rapid growth is often associated with migration early in life; this holds for within- as well as between-population variation (Randall et al. 1986). The fish grow in the sea for one season or more, and return for spawning in autumn. Stream length and sea survival seems to be associated with delayed age at maturity (Schaffer & Elson 1975), but the reasons for the large variation in age at maturity for anadromous salmonids are still largely obscure (Dempson et al. 1986). In addition to anadromous adults, there is also, in many populations, a fraction of males starting sexual maturation (precocious maturation) while still in the pre-migratory parr stage, usually during the autumn prior to main age/size at smolting. This leads to a physiological conflict (Thorpe 1986). In the sea trout *Salmo trutta* L., the result of this is that precocious maturation inhibits smolting/migration, and the parr males remain small and resident throughout their lives (Bohlin et al. 1986, Dellefors & Faremo 1988).

When monitoring the parr male frequency in wild populations of sea trout in SW Sweden

(Dellefors & Faremo 1988), we noticed that the parr male frequency varied annually and that this variation was related to growth rate — good growth, high frequency of parr males — suggesting some kind of causal relation between growth and the probability of sexual maturation in the parr stage. When comparing populations, however, we did not discover such a pattern; the population with the lowest growth rate was that with the highest incidence of parr males. Myers et al. (1985) arrived at similar conclusions concerning parr maturation in wild Atlantic salmon *S. salar* L. in North America; the individual or annual variation in growth rate partly explained the intra-population variation in parr male incidence but not the variation among populations. In hatchery reared stocks of Atlantic salmon, the incidence of parr males appears to be population specific but affected by variation in growth rate (Glebe & Saunders 1986).

The patterns observed raise two interrelated but different questions. One is: What determines and regulates the long-term average of parr male frequency? Another concerns the individual choice: What makes one male become mature at a small size while still in the nursery stream, and another at a considerably larger size following growth in the sea?

Our main object is to discuss the latter question, specifically how environmental heterogeneity or phenotypic variation among juveniles in a population would be expected to affect the choice of alternative life-histories for salmonid males.

The following notation is used:

a-male	Anadromous male, a male with first maturity after migration and growth in the sea.
p-male	Precocious male or parr male, a male starting sexual maturation in the pre-migratory stage.
P	The proportion of a male cohort programmed to become *p-males*.
Q	The proportion of all eggs fertilized by *p-males*.
p	The proportion of an individual's male offspring programmed to become *p-males*.
λ_a	Malthusian fitness of an *a-male*.
λ_p	Malthusian fitness of a *p-male*.

2. ESS for parr male frequency

We base our views on the notion that the system of parr males and anadromous males basically is a game between two size classes employing different reproductive behaviour, and that the reproductive success associated with these tactics or strategies is frequency dependent. The reason is the specific male-male interaction. Big anadromous males (*a-males*), attempt to monopolize a female by aggressive behaviour against both other *a-males* and the small parr males (*p-males*). The *p-males* take advantage of their small size using a cryptic, 'sneaking' behaviour by hiding in the vicinity of the courting pair and making a quick approach to the egg-laying female to fertilize eggs (Jones & King 1950). In addition, *p-males* are able to function as independent males in the absence of *a-males* (Myers & Hutchings 1987). In such a system, the reproductive success for individuals of either form is likely to be better when it is rare than when it is common, i.e. the fitnesses are negatively frequency dependent. This might lead to a stable coexistence at a population specific equilibrium frequency P^* in which the fitness for the two forms is equal, and which is determined by factors affecting the reproductive success and survival for the two forms (Gross 1984, Bohlin et al. 1986, Myers 1986).

The condition for this kind of coexistence can be illustrated in the following way (Fig. 1) (Bohlin et al. 1986). In a non-growing population with stable age structure, a proportion P of the male cohort is programmed to become *p-males*, and $(1-P)$ to become *a-males*. The *p-males* manage to fertilize the proportion Q of all eggs in the population, and the *a-males* $(1-Q)$. By definition, Q/P is the net reproductive rate of *p-males*, and $(1-Q)/(1-P)$ the net reproductive rate of *a-males*. If there is a frequency $P = P^*$ where the two forms are of equal fitness, then, in this case,

$$Q/P^* = (1-Q)/(1-P^*)$$

or

$$P^* = Q$$

In Fig. 1, the equilibrium frequency P^* is where the function $Q(P)$ crosses the diagonal from the origin. This is a stable equilibrium frequency, if the slope of $Q(P)$ in this point is < 1. P^* depends thus on the population specific shape of $Q(P)$,

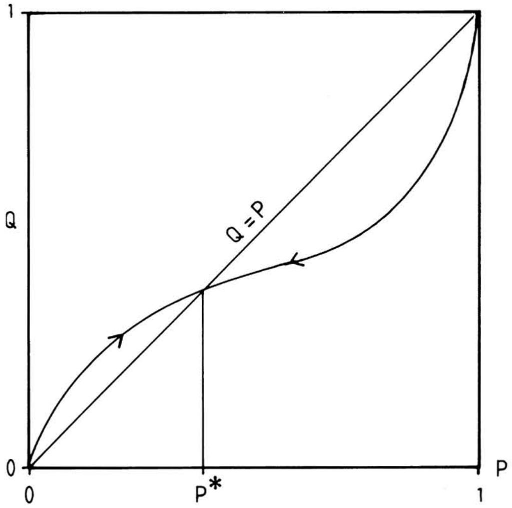

Fig. 1. *Q*, the proportion of all eggs which are fertilized by parr males, as a function of *P*, the proportion of a cohort programmed to become parr males. The population specific equilibrium frequency P^* is that at which $P = Q$, and P^* thus determined by environmental factors affecting the shape of $Q(P)$. By definition, Q/P is the net reproductive rate of parr males.

which is determined both by factors affecting fecundity (relative gonadal size, 'sneaking' opportunities etc.) and survival of the two forms (Bohlin et al. 1986, Myers 1986).

Theoretically, a system with two types of males is similar to a population with two sexes. In both cases, the frequency equilibrium P^* could be maintained by a genetic dimorphism leading to two pure strategies (*p-males* with only *p-male* offspring, *a-males* with only *a-male* offspring). Another alternative is a genetically homogeneous population with each parent programmed for one mixed strategy composed of two tactics, *viz.* to produce offspring of both kinds. In the case of one mixed strategy, the choice of tactic may be random (e.g. like the 'choice' of sex by meiosis), or conditional. In a conditional programme the individual utilizes environmental cues to determine the best choice in relation to its state or other conditions (e.g. like using body size or number of females present as cues to determine the optimal time for sex-changing in the case of protandric hermaphroditism, Charnov & Bergström 1987). Some general considerations concerning the type of system that will emerge are the following (Maynard Smith 1982, 1988), disregarding genetic or other constraints:

1) In a large population where P^* is stable (no random variation), and in which environmental conditions have no differential influence on the individual performances (pay-offs) under the two options, systems with two pure strategies and systems with one mixed strategy appear equally probable.
2) If P^* fluctuates at random, e.g. due to climatic variation, individuals adopting a mixed strategy will generally perform better than either pure strategists.
3) If environmental conditions affect the individual pay-off under the two options differentially, individuals using a mixed conditional programme are favoured over both individuals choosing a tactic at random and individuals using pure strategies.

The *p-male/a-male* system is mixed; a parent generally has both kind of offspring, and the proportion eventually reaching maturity in the parr stage under artificial conditions depending on the treatment (Lundquist & Fridberg 1982). Furthermore, juvenile salmonids vary with respect to growth rate, condition, nutritional state, etc., at least partly as a result of a heterogeneous environment. This variation is not likely to be neutral in the sense that it is irrelevant for the individual performance under the two options. We will therefore treat the *p-male/a-male* system as a population of individuals utilizing a mixed strategy with a conditional choice of reproductive tactic.

3. Conditional response to environmentally determined cues

The simplest type of conditional choice would be the following. An environmentally determined phenotypic character *y* has a stable distribution in the population. In a mixed strategy, each offspring of an individual is equipped with the genetic programme: If *y* is larger than a threshold value *K*, the individual becomes a *p-male*, otherwise it becomes an *a-male*. In a population consisting of such individuals, natural selection would favour individuals happening to choose a value of K that divides its male offspring into the fraction $p^* = P^*$ above the threshold, and $(1-P^*)$ below.

This kind of system is similar to the simplest kind of sex ratio games (Hamilton 1967, Maynard Smith 1982), in which the only single stable sex ratio among offspring (p^*) is the same as the stable primary sex ratio in the population (P^*). As the cue variable y in this case is utilized merely as an aid (like tossing a coin), the 'choice' of tactic is random. Such a system would thus be possible if the frequency P is the only factor affecting the fitnesses differentially, which is not very probable.

If there is also an environmentally determined phenotypic variable x that does affect the fitness relations, then individuals using x as a cue rather than the neutral variable y would be favoured. Some environmentally determined characters or environmental conditions may strongly affect the fitness, but to the same extent for both tactics. These would not be more useful as cues than the variable y. Natural selection would rather favour the use of a variable x related to λ_p/λ_a for the individual male offspring. For an individual with an x value corresponding to $\lambda_p/\lambda_a > 1$, the p-tactic is the best, and if $\lambda_p/\lambda_a < 1$, the a-tactic should be chosen. An example is shown in Fig. 2 where x represents an arbitrary, environmentally determined, phenotypic variable, of which λ_p/λ_a is an increasing function. If x for an individual is large, it would perform better under the p-tactic, and if low the a-tactic is the better. Due to frequency dependence, this function will be large for a low value of P and successively depressed with increasing P, and thus the intersection with the line $\lambda_p/\lambda_a = 1$ (equal fitness) will also change with P. This simply means that if there are many individuals competing under the p-tactic, then only those with the very largest values of x would perform better as *p-males* than as *a-males*. In Fig. 2, this function is superimposed on the actual distribution of the cue variable x in the population. The equilibrium frequency P^* is reached when an area under the x-distribution to the right of the x-value for $\lambda_p/\lambda_a = 1$ equals Q. This value of x would then become the population specific threshold K selected for. If the relation is positive, as in Fig. 2, the conditional programme would be: If $x > K$, become a parr male, otherwise become an *a-male*.

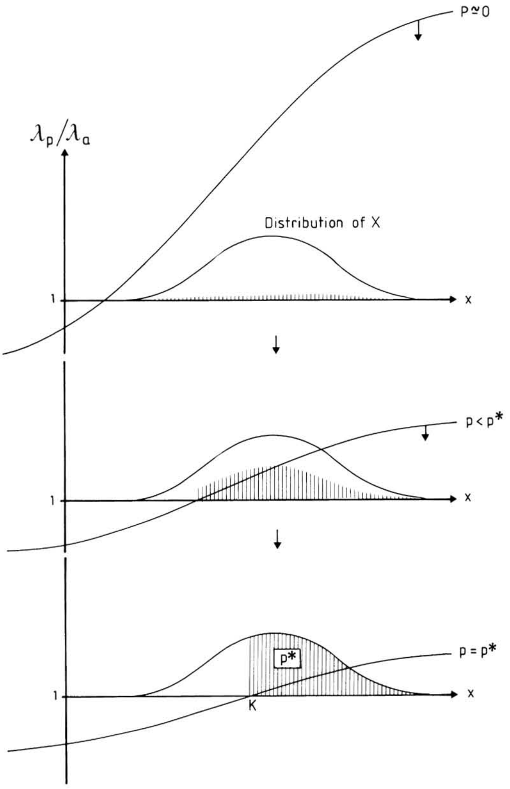

Fig. 2. Graphic representation of a continuous phenotypic variable x affecting the relative fitness (λ_p/λ_a) of parr males positively. Due to frequency dependence, the function will be successively depressed with increasing frequency P of parr males in the population. Superimposed is the distribution of x in the population. If the frequency P of parr males is low (top), all males in this specific population would perform best as parr males regardless of their phenotype. With an increasing parr male frequency (middle), individuals with a low x value would perform better as anadromous males. The equilibrium frequency is reached (bottom) when the parr male frequency (shaded) equals the area under the x distribution to the right of the intersection. Natural selection would favour the intersection K as a threshold.

The conditional model above would suggest an all or none response to the cue variable (all above K would employ the p-tactic). If, however, the variable x is only one of many characters

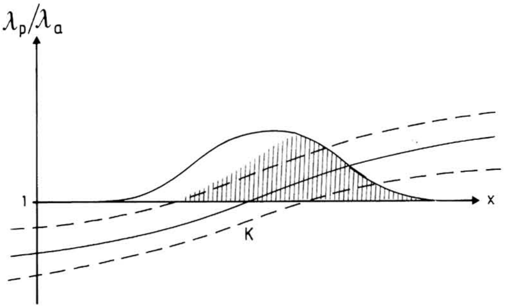

Fig. 3. If the relative fitness λ_p/λ_a is affected by other variables in addition to x, there will be a distribution around the λ_p/λ_a function (broken lines), resulting in a tendency rather than an all-or-none response. Notation as in Fig. 2.

affecting the relative fitnesses, this will lead to some kind of distribution around the λ_p/λ_a function (Fig. 3), and the result will be a tendency rather than an all or none response. In this case, λ_p/λ_a is a two- or multidimensional function rather than determined by one environmental variable.

The conditional mechanism is based on the assumption that an individual tends to make the best of its situation in terms of fitness. This does not necessarily mean, or lead to, equal average fitness for the two tactics. One of the tactics may be an emergency solution for a phenotype doomed to a lower fitness by its environment ('making the best of a bad job', Maynard Smith 1982). Whether the two tactics will yield the same average fitness depends basically on the shape of $Q(P)$ (Fig. 1).

4. If choice is conditional, which cues are selected for?

The question is to find environmental conditions or environmentally determined states affecting the individual performance under the two reproductive tactics differentially. Such conditions or states may be used as cues in the choice (e.g. a nutritional state or growth rate affected by the food available). States associated with a tactic may also be parts of that tactic and may have nothing to do with the choice (e.g. a nutritional state or growth rate which is the result of precocious maturation). Furthermore, choice of tactic has to be made in advance, so the cues selected for should also be reliable predictors of future states.

In the *p-male/a-male* system, there are two major differences between the two behavioural tactics that may affect the type of cue selected for. One is body size, and the other is the difference in time lapse between choice of tactic and reproduction for *a-males* and *p-males*. For the *p*-tactic, the question is to predict one's reproductive success some months later and for the *a*-tactic one's survival and reproductive success some years later.

4.1. Growth and size as affected by the environment

It is tempting to see an environmentally determined growth rate as a cue for choice of tactic. The first reason is based on life-history theory. With a growth curve (growth in fertility), where the potential fertility is continuously approaching a fixed upper limit, one would expect a rapid growth to be associated with early maturation, and a slower growth, caused by environmental stress, with later maturation, other variables constant. The second reason is that growth is correlated with the probability of parr maturation (e.g. Thorpe 1986, 1987), although this relation may also be more obscure (Lundquist 1980).

The predictions of current theory on phenotypic plasticity do not, however, agree well with the *a-male/p-male* system. Under reasonable mortality regimes, one would expect slow-growing individuals to mature later but at a *smaller* size than the more rapidly growing ones (Stearns & Koella 1986). Contrary to what is generally found, the small *p-males* should be old and the larger *a-males* young, and maturation at a large size is not expected to be associated with poor growth. Moreover, tagging experiments suggest a positive relation between sea survival and body length (e.g. Lundquist et al. 1988) and thereby also between growth and sea survival. Therefore, under this theory, it seems far from evident why poor growth would select for migratory *a-males*.

One reason for this discrepancy is that the model used is based on the assumption that fertility is proportional to body size (Stearns & Koella 1986). For salmonid males using 'sneaking' behaviour or fighting this is clearly an oversimplification. The game is essentially between two size classes. Parr males take advantage of their small size, whereas the anadromous males, fighting for spawning opportunities, are favoured by a large body size. Using proximity to the females as a measure of male reproductive success, Gross (1985) found that medium-sized males did less well than smaller and larger males in coho salmon. Therefore, Leonardsson & Lundberg (1986) hypothesized that body size is a cue variable x and used a dome-shaped relation between the reproductive success of parr males and their body size; being too small or too large would reduce the fertility of a *p-male*. The result is a population specific parr male size range, where the optimum parr male size is affected both by the size of the big male and the physical structure of the spawning area (type of substrate, etc.). At the time when the choice has to be made (at least some months before parr maturation), only male juveniles with certain combinations of body size and growth rate would be likely to hit the size window and therefore be selected to become parr males. If so, a rapid growth may or may not select for parr maturation.

The size-window theory is hard to test because of the difficulty of relating the size-window range to environmental factors. Meanwhile, with modern techniques, e.g. DNA-fingerprinting (Jeffreys et al. 1985), it might prove possible to assess the shape of the relation between the individual reproductive success and body size among competing parr males under reasonably realistic conditions. However, a qualitative prediction from the conditional model which it might be possible to test is that populations with a low P^* would be associated with a more narrow *p-male* size range (relative to the size range of all males) than populations with a higher P^*. In sea trout populations there seems to be no such tendency (Dellefors & Faremo 1988). In addition, there is an almost complete overlap in the size distributions of parr males and those of the same age which are still immature. Thus, although the assumption of a basic size-dependent game seems reasonable and supported by some evidence (Gross 1985), it appears that the size-window is wide and that individuals within the range use additional cues for the life-history choice (cf Fig. 3).

The effect of environmentally determined variation in growth rate on the *p-male*/*a-male* system is thus unclear. On the other hand, from general life-history theory one would expect a rapid growth to influence the system in one specific direction: towards an earlier *choice*, and, once this choice is made, an earlier maturation in *both* options. An earlier choice related to better growth is supported by the fact that faster growing salmon smolt emigrate earlier than more slowly growing ones (Chadwick 1981). In hatchery reared populations the general picture is that enhanced growth reduces age at smolting as well as age at parr maturation. Thus rapid growth is likely to be associated with rapid development and early maturation, but thereby not necessarily with the increased probability of choosing the *p*-tactic.

4.2. Growth rate and survival

On the individual level there might be a trade-off between growth and survival. An individual could choose a risky way of increasing its growth, or a safer life at the cost of reduced growth. Without frequency dependent interaction, one would expect one optimal risk level (foraging effort, etc.) yielding the optimal growth under a given set of conditions. Under frequency dependence in a system with two optimal size classes, however, such a trade-off might lead to two strategies or tactics, one associated with good growth, lower survival and thereby early maturation at a small size (*p-males*?) and another with slower growth, better survival and thereby later maturation (*a-males*?). The adaptive variation in growth rate alternative is supported by Metcalfe (1989) and Metcalfe et al. (1989), juvenile salmon parr choosing the tactic of delayed smolting changed into a more prudent form of behaviour (in order to increase survival?) and a slower growth. This scenario would not necessarily explain the choice of tactic; the differential growth rates here are parts of the tactics and may have nothing to do with the actual choice. There are, however, environmental situations that might influence growth and survival differentially. In the field there may be, say, territories associated with safe but scarce food resources, and others with risky but abundant resources. If individuals are able to assess both the risk level and resource value, this might influence the choice of reproductive tactic.

4.3. 'State'

The over-lap in the size distributions of parr males and those still immature suggests cues other than size/growth, or additional cues, for the choice of life-history. It appears that the choice of parr maturation has to be made at least some months prior to the spawning time in autumn, and that the 'state' during this period is used as a cue (Thorpe 1986). In addition to body size, environmentally determined individual variation in condition, nutritional state, state of health, etc., will affect the individual performance, and the question is one of the differential effect of this variation on the fitnesses associated with the two life-history tactics. Fertility is affected by the nutritional/energetic surplus acquired by foraging, and is therefore likely to increase rapidly above a certain feeding level. Survival, on the other hand, may be more gradually favoured by the nutritional state, and variation in 'state' would therefore create larger variance in potential fertility than in survival. If (1) current 'state' affects immediate potential fertility rather than survival, and (2) future 'states' are unpredictable, then a 'good state' would select for reproduction soon (because future 'states' are likely to be worse), and a 'low state' for delayed maturation (because future states are likely to be better). If so, the conditional mechanism suggested (Fig. 2) might be tested by rearing fish from two or more wild populations with known average parr male frequencies and subjected them to a range of, say, feeding regimes in a hatchery during the critical period of strategy choice. The experimental populations are then followed until parr maturity. The threshold model predicts that the switch to precocious maturation should occur at different and population specific levels of feeding — those from populations with a low parr male frequency at higher levels of feeding. As far as we know, no such tests have been made.

5. The conditional model and temporal variation in parr male frequency

In the wild populations of sea trout (Dellefors & Faremo 1988), we may recall that the temporal variation of parr male frequency was related to growth rate, whereas the long-term population averages were not. One possible explanation is the following. The different populations are adapted to environments with different $Q(P)$ functions (Fig. 1) and have, as a result, different values of parr male frequency P^*. Nutritional state is a cue x, and individuals with a state above the population specific threshold K, corresponding to P^*, will become *p-males*. The distribution of x, however, varies from year to year due to variation in food availability, etc. If K is fixed to correspond to the long-term average P^*, this variation would lead to environmentally determined variation in parr male frequency around P^*. A positive correlation between nutritional state and growth would then lead to an annual variation with growth correlated to parr male frequency.

The reason why K is not adjusted upwards in 'good' years, which would seem to make sense, may simply be that an individual can assess its own state x but has limited information about the population, viz. the current distribution of x. An adaptive reason could be a combination of frequency and density dependence. x (nutritional state or growth) is likely to be negatively related to the density of a parr cohort (see e.g. Randall et al. 1986). If the number of returning *a-male* competitors varies at random, it would be safer to choose the p-tactic if a member of a poor parr cohort. This would automatically be achieved if K is fixed and x negatively density dependent.

6. Heritability of parr male frequency

Although the choice of life-history is likely to be conditional, there is, at least in hatchery reared populations, often some heritability of parr male frequency (Glebe et al. 1980, Thorpe & Morgan 1980, Thorpe et al. 1983, Glebe & Saunders 1986). In terms of the simple conditional programme suggested this means a genetically determined within-population variation in the threshold K. The mechanisms creating additive genetic variance, or reducing the rate at which it is drained by natural selection, is complex and only partly understood (Falconer 1981). Generally, one would expect a lower heritability for traits closely related to fitness than for more neutral traits (Mousseau & Roff 1987). How closely a threshold K is related to fitness depends on the slope of the λ_p/λ_a function in Fig. 2 (bottom); the lower the slope, the lower the difference in fitness between individuals with different K values and the weaker the selection. In the extreme case that the slope is zero (the cue x neutral), and if the population is large with no random variation in P^*, any combination of offspring frequencies p, and thereby of K values, is possible as long as the individual offspring frequencies add up to the population specific parr male frequency $P^* = Q$.

7. Final remarks

The general picture of environmentally determined factors influencing the choice of life-history for salmonid males is that conditional mechanisms are probable but the conditional programme complex. The basic system may be similar to that in Fig. 2, but including several variables as cues. The relative fitness *p-males/a-males* would then form a multidimensional space rather than a two-dimensional function. Growth is obviously involved, either as a cue or merely correlated to cues utilized. Rapid individual growth is likely to select for early choice of life-history, but its relevance as a cue for choice of tactic is obscure. Furthermore, if fertility is affected by an unpredictable 'state', e.g. nutritional state as influenced by climatic conditions, then a good state would select for immediate reproduction, e.g. parr maturation.

Most information on precocious maturation has come from hatchery reared populations. If the main object is to gain an understanding of adaptive mechanisms, one has to keep in mind the vast difference between the conditions in a hatchery and those in the environment to which the populations are adapted. Growth rates are often doubled or tripled, and population densities not comparable. Functional programmes may fail to deal with such conditions; the cues may be out of range. Further comparative studies of natural and artificial populations would therefore be interesting.

References

Bohlin, T., Dellefors, C. & Faremo, U. 1986: Early sexual maturation of male sea trout and salmon — an evolutionary model and some practical implications. — Rep. Inst. Freshw. Res. Drottningholm, No. 63:17–25.

Chadwick, E. M. P. 1981: Biological characteristics of Atlantic salmon smolts in Western Arm Brook, Newfoundland. — Can. Tech. Rep. Fish. Aquat. Sci. No. 1024. 45 p.

Charnov, E. L. & Bergström, B. 1987: Alternative life histories in sex changing shrimp: a phenotype limited ESS. — Evol. Ecol. 1:107–111.

Dellefors, C. & Faremo, U. 1988: Early sexual maturation in males of wild sea trout Salmo trutta L., inhibits smoltification. — J. Fish Biol. 33:741–749.

Dempson, J. B., Myers, R. A. & Reddin, D. G. 1986: Age at first maturity of Atlantic salmon (Salmo salar) — influences of the marine environment. — In: Meerburg, D. J. (ed.), Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89:79–89.

Falconer, D. S. 1981: Introduction to quantitative genetics. 2nd ed. — Longman. New York. 340 pp.

Glebe, B. D., Eddy, W. & Saunders, R. L. 1980: The influence of parental age at maturity and rearing practice on precocious maturation of hatchery reared Atlantic salmon parr. — ICES C.M. 19080/F:8.

Glebe, B. D. & Saunders, L. 1986: Genetic factors in sexual maturity of cultured Atlantic salmon (Salmo salar L.) parr and adults reared in sea cages. — In: Meerburg, D.J. (ed.), Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89:24–29.

Gross, M. R. 1985: Disruptive selection for alternative life histories in salmon. — Nature 313:47–49.

— 1984: Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. — In: Potts G. W. & Wootton, R. J. (eds.), Fish reproduction: strategies and tactics: 55–75. Academic Press. London.

Hamilton, W. D. 1967: Extraordinary sex ratios. — Science 156:477–488.

Jeffreys, A. J., Wilson, V. & Thein, S. L. 1985: Hypervariable 'minisatellite' regions in human DNA. — Nature 314:67–73.

Jones, J. W. & King, G. M. 1950: Further experimental studies on the spawning of the Atlantic salmon (Salmo salar LINN.). — Proc. Zool. Soc. London 120:317–323.

Leonardsson, K. & Lundberg, P. 1986: The choice of reproductive tactics as a mixed evolutionary stable strategy: the case of male Atlantic salmon (Salmo salar L.). — Rep. Inst. Freshw. Res. Drottningholm, No. 63:69–76.

Lundquist, H. 1980: Influence of photoperiod on growth in Baltic salmon (Salmo salar L.) with special reference to the effect of precocious sexual maturation. — Can. J. Zool. 58:940–944.

Lundquist, H. & Fridberg, G. 1982: Sexual maturation versus immaturity: different tactics with adaptive values in Baltic salmon (Salmo salar L.) male smolts. — Can. J. Zool. 60:1822–1827.

Lundquist, H., Clarke, W. C. & Johansson, H. 1988: The influence of precocious sexual maturation on survival to adulthood of river stocked Baltic salmon, Salmo salar, smolts. — Holarct. Ecol. 11:60–69.

Maynard Smith, J. 1982: Evolution and the theory of games. — Cambridge University press. Cambridge. 224 pp.

— 1988: Can a mixed strategy be stable in a finite population? — J. Theor. Biol. 130:247–251.

Metcalfe, N. B. 1989: Differential response to a competitor by Atlantic salmon adopting alternative life-history strategies. — Proc. R. Soc. London B 236:21–27.

Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. E. 1989: Early social status and the development of life-history strategies in Atlantic salmon. — Proc. R. Soc. London B 236:7–19.

Mousseau, T. & Roff, D. A. 1987: Natural selection and the heritability of fitness components. — Heredity 59:181–197.

Myers, R. A. 1986: Game theory and the evolution of Atlantic salmon (Salmo salar L.) age at maturation. — In: Meerburg, D. J. (ed.), Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89:53–61.

Myers, R. A. & Hutchings, J. A. 1987: Mating of anadromous Atlantic salmon, Salmo salar, with mature male parr. — J. Fish Biol. 2:143–146.

Myers, R. A., Hutchings, J. A. & Gibson, R. J. 1985: Variation in precocious maturation within and among populations of Atlantic salmon. — I.C.E.S. C.M. 1985/M:9.

Randall, R. G., Thorpe, J. E., Gibson, R. J. & Reddin, D. G. 1986: Biological factors affecting age at maturity in Atlantic salmon (Salmo salar). — In: Meerburg, D. J. (ed.), Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89:90–96.

Schaffer, W. M. & Elson, P. F. 1975: The adaptive significance of variations in life history among local populations in North America. — Ecology 56:577–590.

Stearns, S. C. & Koella, J. C. 1986: The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. — Evolution 40:893–913.

Thorpe, J. E. 1986: Age at first maturity in Atlantic salmon Salmo trutta L.: freshwater period influences and conflicts with smolting. — In: Meerburg, D. J. (ed.), Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89:7–14.

— 1987: Environmental regulation of growth patterns in juvenile Atlantic salmon. — In: Summerfelt, R. C. & Hall, G. E. (eds.), Age and growth of fish: 463–474. Iowa State University Press.

Thorpe, J. E. & Morgan, R. I. G. 1980: Growth rate and smolting rate of progeny of male Atlantic salmon parr, Salmo salar L. — J. Fish Biol. 17:451–460.

Thorpe, J. E., Morgan, R. I. G., Talbot, C. & Miles, M. S. 1983: Inheritance of developmental rates in Atlantic salmon, Salmo salar L. — Aquaculture 33:119–128.