

## Reproductive strategies in Atlantic salmon, *Salmo salar* L.

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**Abstract.** Life-history strategies are means by which animals solve the problems of successful reproduction in varying environments. Their development patterns are consequences of responses to the opportunities the environment offers them. Understanding them requires an understanding of the way they evolved, their ontogenetic development, their physiological control, and their adaptive value. The present paper views the salmonids as marine fishes, which have radiated into fresh water through using river beds as protected spawning grounds. It also takes the view that the maturation process has priority over somatic growth in fish, and that it has already been initiated by the time of first feeding. Its completion is environmentally dependent, and can be arrested annually. Whether or not it will be arrested depends on the status of the energy stores of the individual at particular critical times of year. This mechanism has adaptive value both for immediate reproductive success—adequate energy to provision the next generation—and for later overwinter survival, ensuring that if energy stores are inadequate for reproduction they are spared. Atlantic salmon show variation in their reproductive patterns, and examples are given from laboratory and aquaculture experiments to demonstrate some environmental controls which result in these variations. A hypothetical model is presented to account for the operation of these controls.

### Introduction

Life-history strategies are means by which animals solve the problems of successful reproduction in varying environments. Such formulations are classifications by biologists of different patterns of development exhibited by individual animals. They can be approached in a variety of ways, for example in the context of population genetics, or of evolutionary theory. The naturally selected pattern in any given population is assumed to be the optimal solution for the species in that particular environment. It is the consequence of a continuing natural experiment in which those individuals whose collective responses throughout life result in maximal reproductive success are those whose genotypes determine the future pattern of life-history tactics. Hence observed strategies depend on individual behaviour (that is, proximate factors) as well as on the genetic structure of the stock (ultimate factors). Individual development patterns are the consequences of responses by those individuals to the opportunities that the environment offers them. The variation of response within a species is a measure of the range of its physiological ability, which in turn is a reflection of the variety of genetic blueprint for development.

Tinbergen (1963) defined a framework of investigation for understanding the patterns of an animal's behaviour. He posed four principal questions:

- (1) How did the species evolve?
- (2) What is the ontogeny of the behaviour pattern within the individual?

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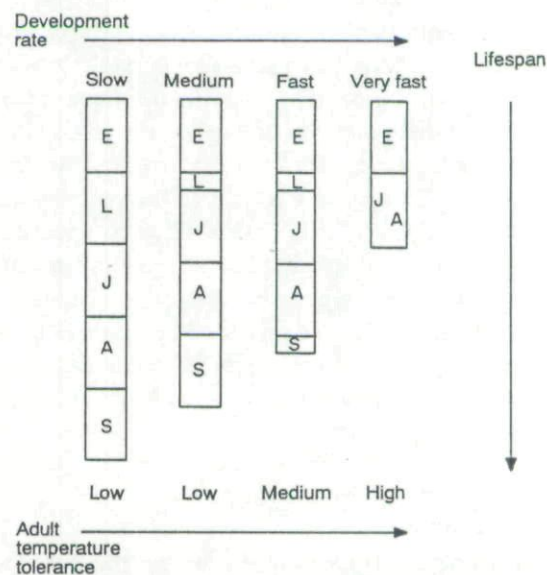
- (3) What are the mechanisms controlling that pattern? and
- (4) What is the adaptive value of the behaviour?

I shall consider the reproductive behaviour of Atlantic salmon, *Salmo salar* L., in such a framework, and lead on to discussing its different modes of expression, otherwise spoken of as its reproductive strategies.

### Salmonid evolution

The origin of salmonids as a group has been debated for centuries, and the scarcity of fossil material offers wide opportunity for unsubstantiated theorizing. On the basis that the salmonid design is very ancient (probably about 100 000 000 years), relatively simple, and well suited to life as a pelagic oceanic predator, I shall adopt the following working hypothesis (Thorpe 1982, 1984):

- (1) the proto-salmonid was a marine fish;
- (2) it reproduced by hiding its eggs in gravel on the shoreline, as do some modern capelin (*Mallotus villosus*);
- (3) by a sophistication of this burying behaviour, the group has evolved through radiation upstream to spawn in gravel beds of rivers and streams;
- (4) further radiation has occurred through heterochrony, allowing the use of freshwater habitats for progressively extended periods of the life-cycle;
- (5) this has resulted in the development of some wholly freshwater forms, in which sexual maturation and reproduction have become possible before reaching the senescent stage (Fig. 1); and



**Figure 1.** Evolution of life history strategies in salmonids. Developmental periods are: E, embryonic; L, larval; J, juvenile; A, adult; and S, senescent. With increasing development rate, life-span is shortened, and first the larval, and then the senescent periods are shortened and disappear (from Thorpe 1987, modified after Balon 1980).

(6) the Atlantic salmon is intermediate in this evolutionary progression within the Salmonidae, in that the majority of its populations are anadromous — that is, usually the species uses both the freshwater and the marine environments for completion of its life-cycle.

### Ontogeny

Policansky (1983) argued that fish with access to abundant food and stable conditions for development mature at their earliest opportunity. The important implications of this argument are, first, that maturation has developmental priority over somatic growth, and second, that the maturation process is continuous from the differentiation of gonadal tissue but its completion is environmentally dependent, and regulated through physiological inhibition. The gonads of Atlantic salmon are differentiated clearly by the time of first feeding — that is when the fish weigh about 150 mg, and are about 25 mm long. Maturation represents the further development of gametes. The sequence of biochemical steps in this process is evidently very complex, but the facilitation of these steps (that is, their release from inhibition) depends on responsiveness to external cues at particular seasons. Ripening occurs in the autumn, and spawning usually during autumn or early winter. However, the age at which sexual maturity is achieved varies strikingly both between and within populations, emphasizing the regulation by inhibition.

### Mechanisms regulating maturation

Since the 1930s it has been known that the time of spawning can be modified by manipulating the animal's experience of photoperiod, and more recently it has been shown that aspects of photoperiod also influence the rate of gonad ripening (Eriksson & Lundqvist 1980; Munro, Scott & Lam 1990; also papers in Scott, Sumpter, Kime & Rolfe 1991). Scott & Sumpter (1983) showed that the physiological decision about whether or not to mature (that is, continuation of the maturation process, or its inhibition) in a given year was taken under conditions of increasing daylength in the spring, although recently we have found that the annual cycle of gonad growth starts in the autumn (Fig. 2), at a time before endocrine change appears to be detectable.

Traditionally, fish biologists have categorized species by an 'age of first maturity'. But if maturation is dependent upon a series of seasonal light signals, the opportunity to mature occurs annually. Hence the more interesting question is why do salmon not mature every year from age 0? What inhibits them? Thorpe (1986) suggested that the internal response to the external signal depends upon some genetically determined performance threshold, and the maturation process will continue to develop if performance exceeds a set point at this critical time, or it will be postponed for a year if that quantitative criterion is not reached.

It has been customary to describe such criteria in terms of body size — if an animal has reached a certain size by a specific date it will mature, if not, it will not. But how does a salmon know how big it is? Size is a historical statement — it represents the resultant of all the processes that have affected the animal up to the instant of measurement. If a developmental decision is critical at a specific season, it is more credible that the physiological assessment of the appropriate direction of that decision will relate to a dynamic characteristic of the animal at that critical time. What is the nature of this dynamic characteristic?

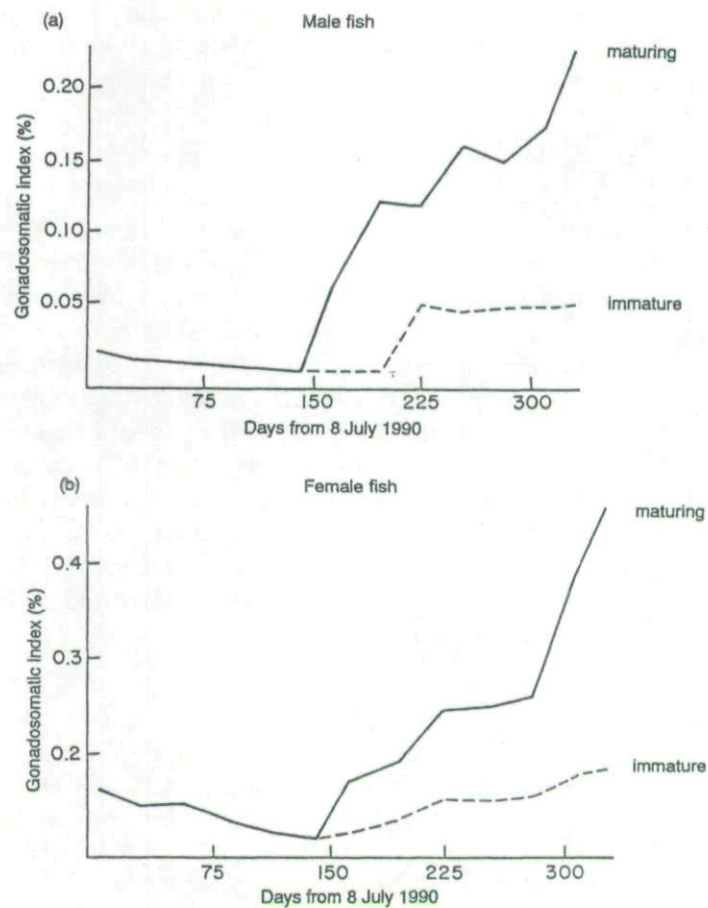
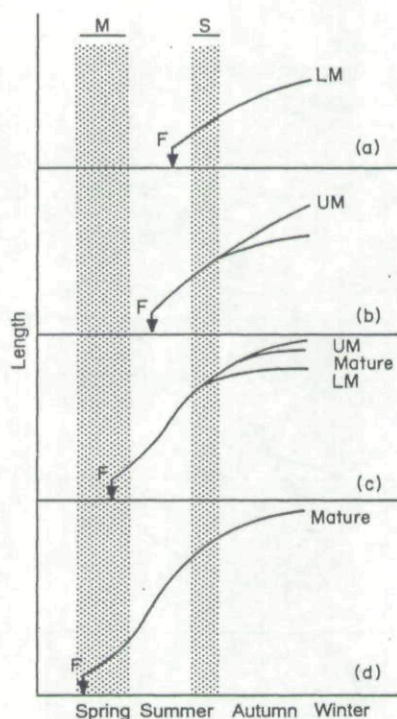


Figure 2. Gonadosomatic index of maturing and immature salmon in sea cages: aged 1+ in July 1990; (a) male fish; (b) female fish.

The maturation process is energetically expensive. This is reflected in the general finding that female fishes mature later than males do. It requires a relatively greater energy accumulation to develop ovaries and eggs than to develop testes and sperm. Hence rate of energy accumulation at the critical decision time has been suggested as a probable criterion on which the decision to mature or to postpone maturation can be taken.

Following this line of argument, some years ago my colleagues and I tested a simple model (Fig. 3) (Thorpe 1986) of the process, by offering different groups of first-feeding sibling Atlantic salmon different development opportunities in the spring, at the supposed time critical for the maturation decision (Adams & Thorpe 1989). Normally wild Atlantic salmon in Scotland would feed first in early May. By raising the incubation temperatures in winter we accelerated the early development of part of a sibling population, so that these treated fish were feeding by February. In summary, we found that individual males matured at age 0 only if they had experienced enhanced temperatures (i.e. better feeding opportunities) under the changing photoperiods characteristic of February–April: if they experienced only one of

those environmental characteristics, or neither, they failed to mature at age 0. (Females did not mature, but the accelerated individuals committed more resources to reproductive tissue.) Conversely, restricting the energy intake of 1-year-old fish in different months, the proportion of the population that matured in the following autumn was least if the restriction occurred in March and April (Rowe & Thorpe 1990b). When we studied the seasonal lipid reserves of such fish, we found that maturation was maintained only in those individuals which refilled their lipid stores in April (Rowe, Thorpe & Shanks 1991). If they continued to deplete these stores during April, and delayed until May before replenishing them, they failed to mature that year. Hence, either the absolute quantity of fats remaining in April, or their rate of increase, governed the direction of the maturity decision at that time of year. This pattern is also visible in the data of Hunt, Simpson & Wright (1982) from cage-cultured salmon, and in those of Johnston, Gray, McLennan & Paterson (1987) among recovering kelts, as discussed by Rowe & Thorpe (1990a).



**Figure 3.** Hypothetical model of development in Atlantic salmon (from Thorpe 1986). M, sensitive period for maturation decision; S, sensitive period for smolting decision; F, first feeding; UM, upper modal group (smolting at age 1+); LM, lower modal group (smolting at ages >1+). (a) Poor development conditions: F late, growth slow during S-period, and whole population arrests growth. (b) Moderate development conditions: F early summer, growth rate higher during S-period, part of population maintains growth. (c) Good development conditions: F late spring, growth rates in both S- and M-periods high, part of population maintains growth, then the fastest males slow down as they mature. (d) Exceptionally good development conditions: F early spring, growth rate of whole population high during both sensitive periods, all males mature, and females mature one year later.

Applying some of these ideas in culture, we have shown that the proportion of a caged population of Atlantic salmon that matures can be reduced by restricting food intake over the previous winter (Fig. 4) (Thorpe, Talbot, Miles & Keay 1990). We infer that control operates through the level of depletion of energy reserves over winter. Similar dependence of gonad maturation on fatty tissue has been demonstrated in the newt, *Triturus (diemyctylus) viridescens*, in which surgical removal of the fat body associated with an individual gonad prevented development of that gonad, while the 'control' gonad developed normally (Adams & Rae 1929). Subsequently a similar energy dependence of maturation was shown to occur regularly in amphibians (Fitzpatrick 1976) and reptiles (Derickson 1976).

Gonad development is stimulated and regulated by the output of gonadotrophins (GTH) from the pituitary, which in turn is prompted by releasing hormones (GnRH) from the hypothalamus. The production of GnRH is dependent on stimulation of the hypothalamus by oestrogens, which in the immature fish are produced by aromatization of androgens from the head kidney. In higher vertebrates the aromatase enzymes which catalyse this conversion are found in fatty tissue (Frisch 1988). While their presence has yet to be demonstrated in the fat

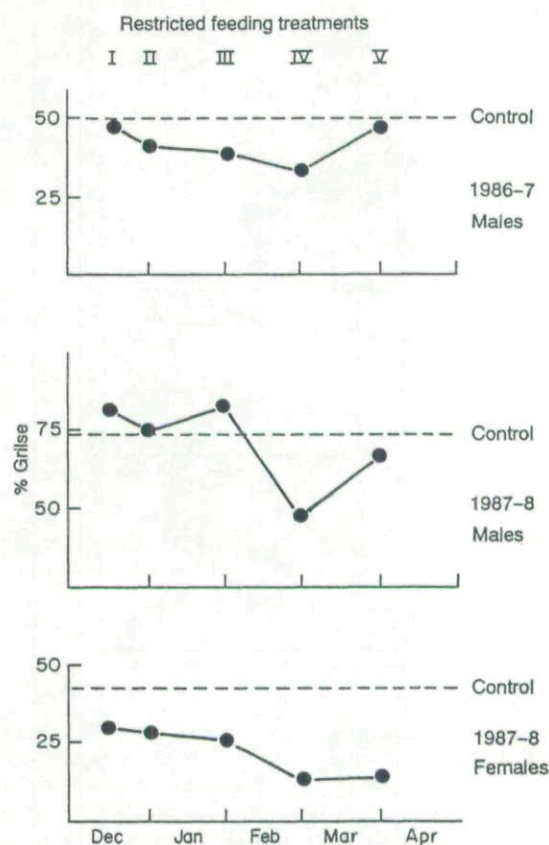
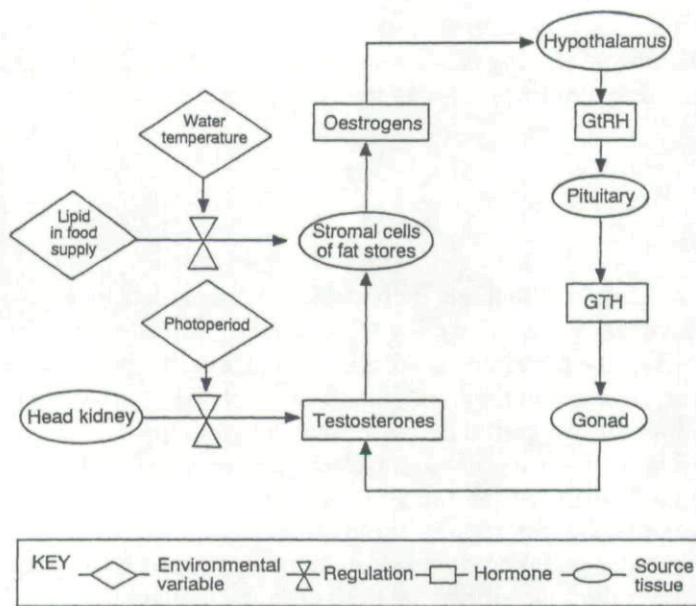


Figure 4. Percentages of salmon maturing as grilse, in relation to months in which food was restricted (from Thorpe *et al.* 1990).



**Figure 5.** Hypothetical systems model for the environmental regulation of the positive hormonal feedback loop controlling maturation in Atlantic salmon (GtRH = gonadotrophin releasing hormone, GTH = gonadotrophin) (from Rowe *et al.* 1991).

of salmon, such enzymes are present in the brain (Andersson, Borg, Lambert, Granneman & van Oordt 1988). It seems probable, then, that the control process for gonad growth is similar in salmon to that established for higher vertebrates, and we have postulated a hypothetical model for this (Fig. 5) (Rowe *et al.* 1991).

So if the timing of maturation is determined by the fat dynamics (energy balance) of the individual in the previous winter and spring, what is the adaptive value of such an arrangement?

### Adaptation

Fat stores permit overwinter survival, but are depleted by salmon during maturation and spawning in autumn. In the wild, Thurow (1966) suggested that Baltic salmon needed more than 12% lipid content at the end of winter if they were to spawn that year. Among anadromous fish, besides having to meet the costs of gonad ripening, the fat is needed to support the costs of up-river migration, development of secondary sexual characteristics, and spawning behaviour itself. Although Atlantic salmon are iteroparous, the proportion of repeat spawners in anadromous populations is generally low (often not more than 10%, Ducharme 1969), which suggests that mortality after spawning is high and implies a precarious balance between stored energy and that spent on reproduction. Likewise among mature parr, maturation without sufficient lipid stores would increase probability of post-spawning mortality, and so reduce the individual's total reproductive fitness. A physiological switch which suppresses maturation at spring-time fat levels below a threshold

value would act as a safeguard against such risks (Rowe *et al.* 1991). Since under relatively poor conditions slowly developing fishes will eventually mature, this would suggest that the level of the threshold that must be overcome to ensure maturation occurs must decrease as the fish ages.

#### Variations of strategy

In summary, it is suggested that an individual will reproduce in a given year only if environmental opportunity has allowed it to accumulate sufficient lipid reserves that the turnover rate of the residue remaining is still above its genetically specified threshold level for maturation at a critical decision time, and that it can increase those reserves from then on. Such a restriction would suggest that the probability of a particular proportion of the population maturing would vary naturally from year to year, and that relatively good opportunities would lead to earlier and relatively bad opportunities to later maturation. There are many examples which support these predictions.

Aquaculture provides individuals with feeding opportunities far in excess of what they normally experience in the wild, since food need never be limiting. The whole development cycle is then accelerated, the proportion of males which mature as parr is very often 100% at age 1+, and under heated conditions may even be high at age 0+. Since the bulk of farm production is based on fish transferred to sea at age 1, then at whatever age they mature they are usually at least one year younger than comparable wild fish. From the sea cages, high proportions maturing after one year at sea (i.e. a total age of 2+), have been a regular feature especially after warm winters. Further, a supposedly late maturing stock from Norway, when reared in Brittany, produced 30–50% mature individuals after one sea winter.

Transplantation of stocks to more favourable environments can show similar responses. In Norway, salmon from the River Neva (Russia) that were reared at Ims smolted at age 1+, and returned from the sea at age 2+ (Hansen & Jonsson 1989). In their home river the age at smolting was 3+ and 4+, and at return from the Gulf of Finland 6+ to 8+. Relatively improved opportunities may arise in other ways. In lacustrine environments in Newfoundland, O'Connell & Ash (1993) found that salmon grew faster, matured earlier and had a shorter generation time than those in fluvial environments. Heavy exploitation of adult salmon in the north-west Atlantic has been suggested as the cause of the numerical decline of populations in the rivers draining into the north shore of the St Lawrence River, Canada. Caswell, Naiman & Morin (1984) noted a concomitant increase in the number of males maturing as parr in those rivers, suggesting that the decreased competition at the juvenile stage had resulted in increased individual opportunity, and increased numbers maturing early before smolting.

Conversely, Saunders, Henderson, Glebe & Loudenslager (1983) found that under sub-zero winter temperatures in cages in the Bay of Fundy, Canada, almost no fish matured after one winter, whereas moderate proportions of fish of the same population at large in the Atlantic matured in that time. Scarnecchia, Isaksson & White (1989) found that the proportion of fish in some wild Icelandic populations which matured as grilse was positively correlated with April–May sea temperatures, and attributed earlier maturity to improved development opportunities at the higher spring temperatures. In Norway, Naevald (1983) noted lower proportions of maturing salmon after cold winters. Such a correlation is



consistent with an adaptive springtime switch which arrests maturation in years with late springs — and thus potentially short growing seasons — when the probability of acquiring sufficient lipid reserve for reproduction and continued survival is relatively low.

### Between-population differences in strategy

There is evidence that different groups of salmon differ in their maturation responses to the same developmental opportunities (Thorpe 1975, 1986; Naevdal 1983; Thorpe, Morgan, Talbot & Miles 1983; Gjerde & Refstie 1984; Glebe & Saunders 1986), thereby implying that there is genetic regulation of the biochemical thresholds which must be overcome to release inhibition to further maturation. Thorpe (1993) has suggested that these are the processes which underlie what is usually called inheritance of age at first maturity.

Besides proximate regulators of reproductive strategy, selection may create genetically distinct strategies. The Atlantic salmon exists as a large set of discontinuous populations, more or less totally discrete, with very high homing precision — straying levels between populations usually of only some 2–3%. As genetic migration rates are even smaller, the gene-flow between these populations is very little indeed (Ståhl 1981). The degree of adaptive differences between these populations is actively debated, but evidence does exist for such differences, and in some very long, or very rugged, rivers probably only large adult fish can succeed in reaching the spawning grounds. Such conditions would favour slower developing fish, with high thresholds for maintaining maturation, maturing late at a large size, and such genetically based developmental characteristics would be expected to prevail in these populations.

Finally, the interplay of a genetically based spectrum of development rates, and heterogeneity of habitat within the nursery rivers, results in a range of cohorts within year-classes, leaving the rivers at different smolt ages, and hence returning to those rivers to breed in different years. This results in a wide mixture of age-classes in spawning populations, which has two implications. The first is that the effective number of spawners in the breeding population is much larger than is present in any one breeding season. The second is that, even though homing precision is very high, the population has temporal insurance against extinction in the event of a catastrophe within the river, since all members of that population (of any year class) are not present there at the same time after their first year.

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### References

- Adams A.E. & Rae E.A. (1929) An experimental study of the fat bodies in *Triturus (diemyctylus) viridescens*. *Anatomical Record* **41**, 181–203.
- Adams C.E. & Thorpe J.E. (1989) Photoperiod and temperature effects on early development and reproductive investment in Atlantic salmon (*Salmo salar* L.). *Aquaculture* **79**, 403–409.
- Andersson E., Borg B., Lambert J.G.D., Granneman J.C.M. & van Oordt P.G.W.J. (1988) Aromatase activity in

- brain and pituitary of immature and mature Atlantic salmon (*Salmo salar* L.) parr. 14th Conference of European Endocrinologists, Salzburg. (Abstract.)
- Balon E.K. (1980) Early ontogeny of the lake charr, *Salvelinus (Cristivomer) namaycush*. In: *Charrs: salmonid fishes of the genus Salvelinus* (ed. by E.K. Balon), pp. 485–562. Dr W. Junk Publishers, The Hague.
- Caswell H., Naiman R.J. & Morin R. (1984) Evaluating the consequences of reproduction in complex salmonid life-cycles. *Aquaculture* **43**, 123–134.
- Derickson W.K. (1976) Lipid storage and utilization in reptiles. *American Zoologist* **16**, 711–723.
- Ducharme L.J.A. (1969) Atlantic salmon returning for their fifth and sixth consecutive spawning trips. *Journal of the Fisheries Research Board of Canada* **26**, 1661–1664.
- Eriksson L.-O. & Lundqvist H. (1980) Photoperiod entrains ripening by its differential effect in salmon. *Naturwissenschaften* **67**, 202–203.
- Fitzpatrick L.C. (1976) Life history patterns of storage and utilization of lipids for energy in Amphibians. *American Zoologist* **16**, 725–732.
- Frisch R. (1988) Fatness and fertility. *Scientific American March* **1988**, 70–77.
- Gjerde B. & Refstie T. (1984) Complete diallel cross between five strains of Atlantic salmon. *Livestock Production Science* **11**, 207–226.
- Glebe B. & Saunders R.L. (1986) Genetic factors in sexual maturity of cultured Atlantic salmon (*Salmo salar*) parr and adults reared in sea cages. *Canadian Special Publication in Fisheries & Aquatic Sciences* **89**, 24–29.
- Hansen L.P. & Jonsson B. (1989) Salmon ranching experiments in River Imsa: returns of different stocks to the fishery and to River Imsa. In: *Aquaculture: a Biotechnology in Progress* (ed. by N. De Pauw, E. Jaspers, H. Ackefors & N. Wilkins). European Aquaculture Society, Bredene.
- Hunt S.M.V., Simpson T.H. & Wright R.S. (1982) Seasonal changes in the levels of 11-oxotestosterone and testosterone in the serum of male salmon (*Salmo salar* L.) and their relationship to growth and maturation cycle. *Journal of Fish Biology* **20**, 105–119.
- Johnston C.E., Gray R.W., McLennan A. & Paterson A. (1987) Effects of photoperiod, temperature and diet on the reconditioning response, bloods chemistry and gonad maturation of Atlantic salmon (*Salmo salar*) kelts held in freshwater. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 702–711.
- Munro A.D., Scott A.P. & Lam T.J. (1990) *Reproductive Seasonality in Teleosts: Environmental Influences*. CRC Press, Boca Raton.
- Naevdal G. (1983) Genetic factors in connection with age at maturation. *Aquaculture* **33**, 97–106.
- O'Connell M.F. & Ash E.G.M. (1993) Size and growth of smolts in relation to age at first maturity of Atlantic salmon (*Salmo salar* L.): the role of lacustrine habitat. *Journal of Fish Biology* **42**, 551–569.
- Policansky D. (1983) Size, age and demography of metamorphosis and sexual maturation in fishes. *American Zoologist* **23**, 57–63.
- Rowe D.K. & Thorpe J.E. (1990a) Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L., parr. *Journal of Fish Biology* **36**, 643–658.
- Rowe D.K. & Thorpe J.E. (1990b) Suppression of maturation in male parr of Atlantic salmon (*Salmo salar* L.) by reduction in feeding and growth during spring months. *Aquaculture* **86**, 291–313.
- Rowe D.K., Thorpe J.E. & Shanks A.M. (1991) The role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 405–413.
- Saunders R.L., Henderson E.B., Glebe B.D. & Loudenslager E.J. (1983) Evidence of a major environmental component in the determination of the grilse:larger salmon ratio in Atlantic salmon (*Salmo salar*). *Aquaculture* **33**, 107–118.
- Scarnecchia D.L., Isaksson A. & White S.E. (1989) Effects of oceanic variations and the West Greenland fishery on age at maturity of Icelandic west coast stocks of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 16–27.
- Scott A.P. & Sumpter J.P. (1983) The control of trout reproduction: basic and applied research on hormones. In: *Control Processes in Fish Physiology* (ed. by J.C. Rankin, T.J. Pitcher & R.T. Duggan), pp. 200–220. Croom Helm, London.
- Scott A.P., Sumpter J.P., Kime D.E. & Rolfe M.S. (eds) (1991) *Proceedings of the Fourth International Symposium on the Reproductive Physiology of Fish*, pp. 338. Sheffield: FishSymp 91.
- Ståhl G. (1981) Genetic differentiation among natural populations of Atlantic salmon (*Salmo salar*) in northern Sweden. *Ecological Bulletin* **34**, 95–105.
- Thorpe J.E. (1975) Early maturation in male Atlantic salmon. *Scottish Fisheries Bulletin* **42**, 15–17.
- Thorpe J.E. (1982) Migration in salmonids with special reference to juvenile movements in freshwater. In: *Proceedings of the Salmon and Trout Migratory Behavior Symposium* (ed. by E.L. Brannon & E.O. Salo), pp. 86–97. University of Washington, Seattle.

- Thorpe J.E. (1984) Downstream movements of juvenile salmonids: a forward speculative view. In: *Mechanisms of Migration in Fishes* (ed. by J.D. McCleave, G.P. Arnold, J.J. Dodson & W. H. Neill), pp. 387–396. Plenum, New York.
- Thorpe J.E. (1986) Age at first maturity in Atlantic salmon, *Salmo salar* L.: freshwater period influences and conflicts with smolting. *Canadian Special Publication in Fisheries & Aquatic Sciences* **89**, 7–14.
- Thorpe J.E. (1987) Smolting versus residency: developmental conflict in salmonids. *American Fisheries Society Symposium* **1**, 244–252.
- Thorpe J.E. (1993) Impacts of fishing on genetic structure of salmonid populations. In: *Genetic Conservation of Salmonid Populations* (ed. by J.G. Cloud & G. Thorgaard), pp 67–80. Plenum, New York.
- Thorpe J.E., Morgan R.I.G., Talbot C. & Miles M.S. (1983) Inheritance of developmental rates in Atlantic salmon, *Salmo salar* L. *Aquaculture* **28**, 123–132.
- Thorpe J.E., Talbot C., Miles M.S. & Keay D.S. (1990) Control of maturation in cultured Atlantic salmon, *Salmo salar*, in pumped seawater tanks, by restricting food intake. *Aquaculture* **86**, 315–326.
- Thurow F. (1966) Beiträge zur Biologie und Bestandskunde des Atlantischen Lachses (*Salmo salar* L.) in der Ostsee. *Bericht der Deutschen Wissenschaftlichen Kommission für Meeresforschung* **18**, 223–379.
- Tinbergen N. (1963) On the aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433.

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