

Behavioural influences on life-history variation in juvenile Atlantic salmon, *Salmo salar**

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Synopsis

Juvenile Atlantic salmon emigrate from the river in a given year as a consequence of a physiological decision influencing appetite and growth during the previous summer. The direction of the decision depends on developmental performance exceeding a genetically determined threshold at that time, and that performance is governed by environmental opportunity. The animal's foraging efficiency (ability to avoid predators, and to compete) determines how well that opportunity is used. Those fish which maintained relatively high growth after July preferred higher stream flows, and were more likely to hide than to flee from a predator. Predator vigilance reduced intake, and ability to discriminate edible particles. Early competitive ability depended on fierceness rather than size, and ultimate large size was a consequence of dominant status. Initial status among high ranking individuals (but not among low ones) predicted the likelihood of maintaining growth in late summer. Size by July was the better predictor for low ranked fish. The influence of high status on life-history variation depends on how much it suppresses the growth of those lower in the hierarchy.

Introduction

Atlantic salmon, *Salmo salar* L., spawn relatively few large yolky eggs in the gravel of stream beds in the cool temperate North Atlantic drainage of America and Europe. The juvenile fish emerge at first feeding in the spring weighing about 150 mg, spend 1–7 years in freshwater before entering the sea, and then return to their natal river to spawn after a further 1 or more years. Alternatively, some may mature without leaving freshwater, forming partially or wholly landlocked populations.

As with other salmonids, their life-history patterns are characteristically flexible (Thorpe 1989).

That flexibility depends on two principal physiological decisions made by juveniles in any given year: firstly, whether or not to emigrate to sea, and secondly, whether or not to mature sexually. The present paper deals with the first decision, which has been formulated as a simple developmental model (Thorpe 1986). In mid- to late summer the growth trajectories of potential emigrant and potential resident individuals in a population diverge (Thorpe et al. 1980, Wright et al. 1990, Nicieza et al. 1991). By November this results in a clearly defined bimodal length frequency distribution (Fig. 1). The upper modal group (UMG) represents individuals which have maintained relatively

* Invited review

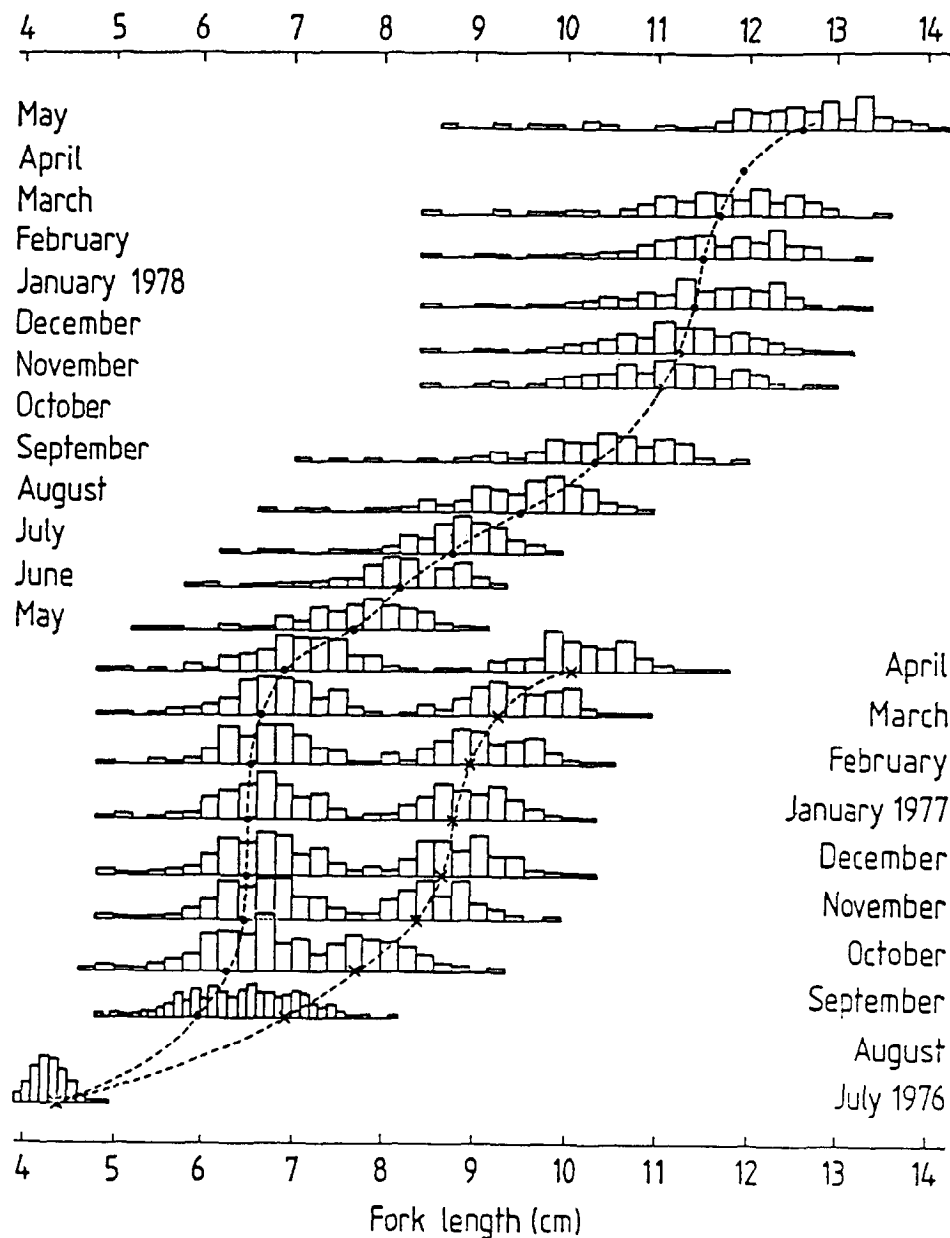


Fig. 1. Monthly length frequency distributions in a sibling salmon population held under laboratory conditions (from Thorpe 1987).

high metabolic and growth rates, and which will emigrate the following May (Thorpe 1977, 1987, Higgins 1985, Nicieza et al. 1991). The lower modal group (LMG) consists of individuals which have reduced metabolic and growth rates, and which will remain in freshwater for at least one more year.

The reduced growth of LMG fish is a consequence of a sharp reduction in food intake from

July onwards, independent of food availability and water temperature (Higgins 1985, Higgins & Talbot 1985). This implies that the decision functions by either maintaining appetite or reducing it, but the precise physiological mechanisms are unknown.

While the developmental programme is genetically fixed, it runs under environmental instruc-

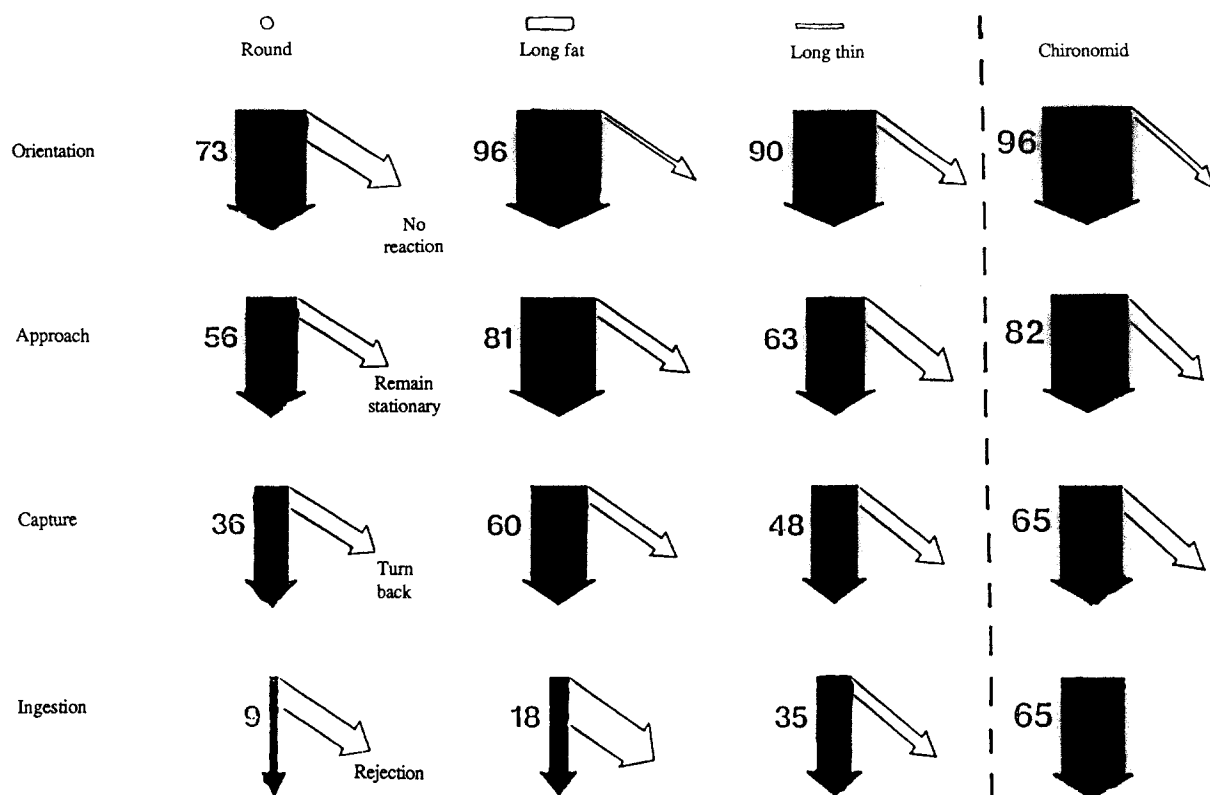


Fig. 2. The feeding responses of salmon parr towards round, long fat, and long thin pellets, and to chironomid larvae. The thickness of the arrows represents the percentage of fish responding as indicated (e.g. parr oriented to 73% of round pellets, but subsequently ingested only 9% of them) (modified from Stradmeyer et al. 1988).

tion. In the present case, some feature of photoperiod determines the season at which the decision is taken (Thorpe 1986, Villarreal et al. 1988), but its direction depends on individual performance at that time (Thorpe et al. 1989). The proportion of a sibling group that forms the ultimate UMG is influenced genetically (Thorpe & Morgan 1978, Thorpe et al. 1983), but we suggest that what is inherited is a particular threshold level of performance which must be exceeded at the critical time in July/August for appetite and growth to be maintained (Thorpe 1986).

Performance implies acquisition and storage of energy, and so it depends on environmental opportunity (Thorpe et al. 1989). The fish's foraging efficiency (ability to avoid predation, and to cope with competitors) determines how well it uses that opportunity. The present paper summarises the results of a range of experiments designed to deter-

mine the influence of such activities on the outcome of this physiological decision process.

Foraging behaviour

Juvenile Atlantic salmon are sit-and-wait predators, feeding mainly on particulate drifting prey, captured from defended territories close to the bed of streams (Kalleberg 1958, Keenleyside & Yamamoto 1962, Wankowski 1981, Stradmeyer & Thorpe 1987a). They prefer and select prey items whose maximum width is equivalent to about 2.5% of their own body length (Wankowski 1979, Wankowski & Thorpe 1979b), on which their subsequent growth is maximal.

The appearance of the prey is important. In experiments in a large flume tank, salmon parr showed an increased preference for wriggling wild prey (chi-

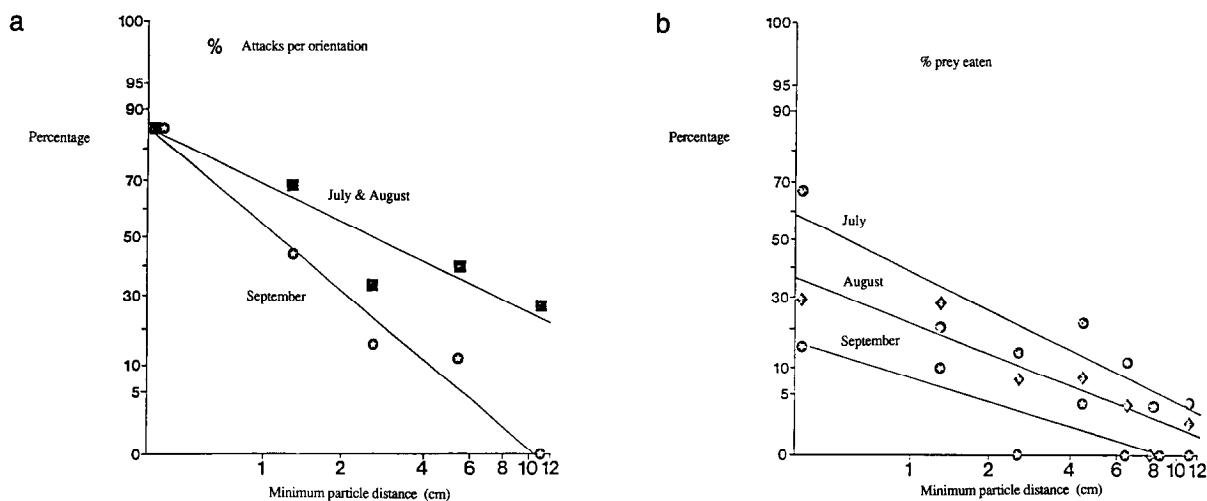


Fig. 3. a – The percentage of orientations of LMG fish that resulted in attacks, in relation to minimum particle distance and season. The elevation of the September regression is significantly lower than that for July and August ($p < 0.05$) (from Metcalfe et al. 1986). b – The percentage of food particles eaten by LMG fish in relation to minimum particle distance and season. The elevations of the three lines differ significantly ($p < 0.05$) (from Metcalfe et al. 1986).

ronomid larvae, ephemeropteran nymphs, and trichopteran larvae) over pellets of the same width (Stradmeyer & Thorpe 1987b). In further experiments they consumed twice as many long thin pellets as long fat ones, and four times as many as round ones (Stradmeyer et al. 1988) (Fig. 2). The texture of prey influenced its acceptance: soft pellets were ingested twice as often as hard ones.

Using these features of feeding behaviour, Metcalfe et al. (1986, 1988) examined the feeding motivation (appetite) of young salmon experimentally from July to October. Fishes were tested individually in a tank that allowed fine control over food presentation. They were offered EWOS salmon pellets of the optimal diameter (Wankowski & Thorpe 1979b) through feed pipes which terminated directly above three water inlets. The extent of the fish's movement from its sheltered holding station towards the food particle, and the degree of completion of the feeding sequence were indices of appetite.

Appetite declined from July to September, in both modal groups, but more in the LMG than in the UMG. This was evident at each stage in the sequence of prey capture: orientation was less likely to lead to attack, which was less likely to result in the food being captured and consumed (Fig. 3).

These experiments confirmed Higgins' (1985) findings from food intake estimates. However, in October the UMG showed a brief sharp increase in appetite, sufficient to fuel a growth spurt (cf. Kristinsson et al. 1985) even though temperatures were falling, and growth rate of the LMG was decreasing.

In summer, parr tend to occupy feeding stations close to fast current (Wankowski & Thorpe 1979a, Stradmeyer & Thorpe 1987a). In laboratory flume tanks between August and December, in which

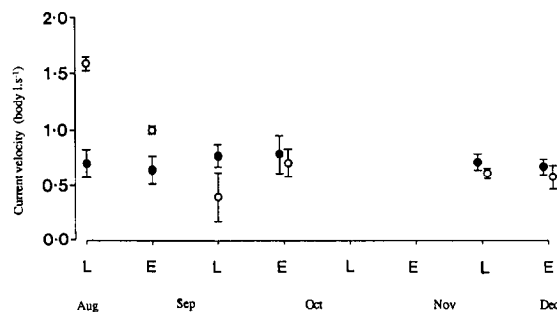


Fig. 4. Chosen current speed (mean \pm S.E.) for UMG (○) and LMG (●) salmon parr in the absence of a predator. L: late; E: early half of month. Current speed declined significantly with date for UMG fish ($p < 0.01$), but there was no trend for LMG fish (from Huntingford et al. 1988b).

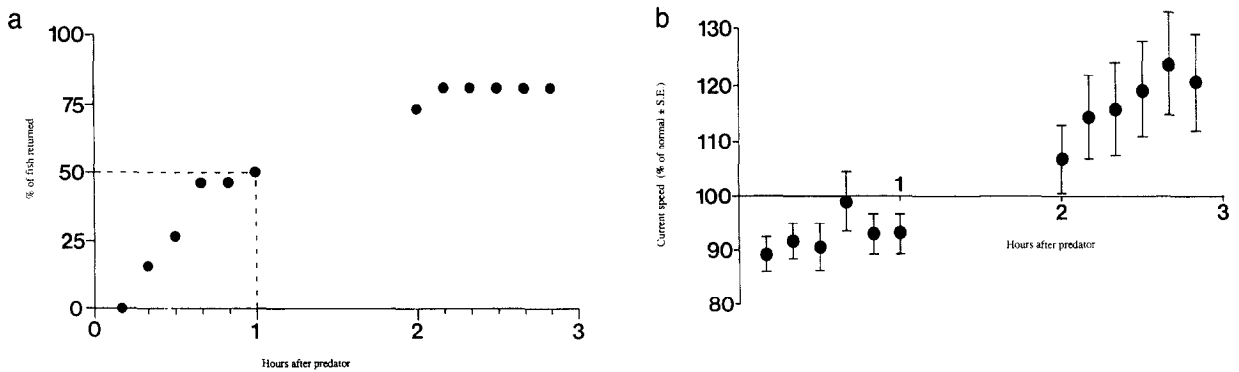


Fig. 5. The time course of the effect of exposure to a predator: a – cumulative percentage of parr returning to within 5 cm of their feeding station after flight from a predator, b – changes in mean current speed (as % of previously chosen speed) adopted by parr after seeing a predator (from Huntingford et al. 1988b).

individual parr could choose a preferred current speed, those that eventually became LMG fish consistently held station at low current speeds ($0.5\text{--}1.0$ body lengths sec^{-1}), and thus in areas with little food. Those that eventually became UMG fish held station at significantly higher flows in August (up to 1.5 bl s^{-1}) than did LMG fish ($p < 0.02$), but preferred flows in the UMG declined with both temperature and date (Huntingford et al. 1988b) (Fig. 4).

Predator avoidance

While high flow areas imply high food rewards, they are also more exposed and therefore imply higher risks of predation (Donnelly & Dill 1984). In the flow choice experiments the parr were also exposed for 30 sec to a model brown trout, *Salmo trutta* L., behind a transparent panel. 68% of UMG fish reduced their conspicuousness by flattening their bodies against the substrate, reducing tail-beat frequency and staying still, 21% moved less than 5 cm to cover and lower flows, and 11% moved more than 5 cm. By contrast LMG fish moved signif-

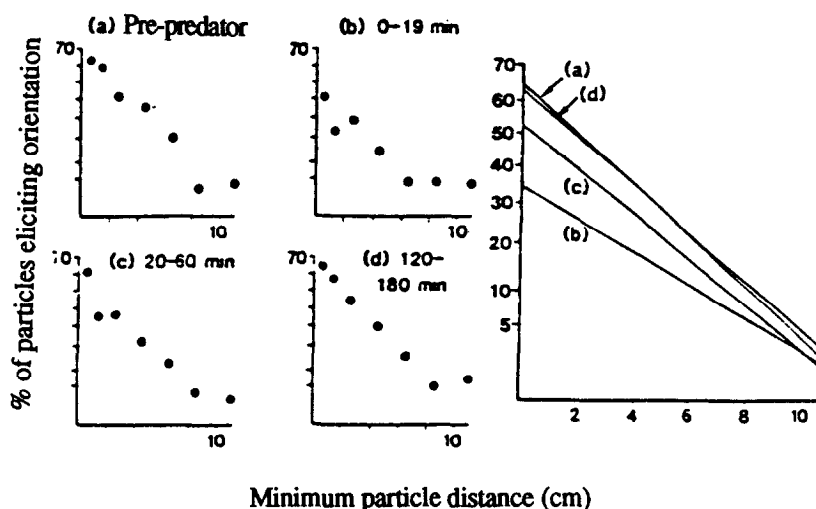


Fig. 6. The decrease and recovery in readiness of parr to orient to food particles, with time after exposure to a predator. The regressions are all significant ($p < 0.001$), and differ only in elevation ($p < 0.01$) (from Metcalfe et al. 1987a).

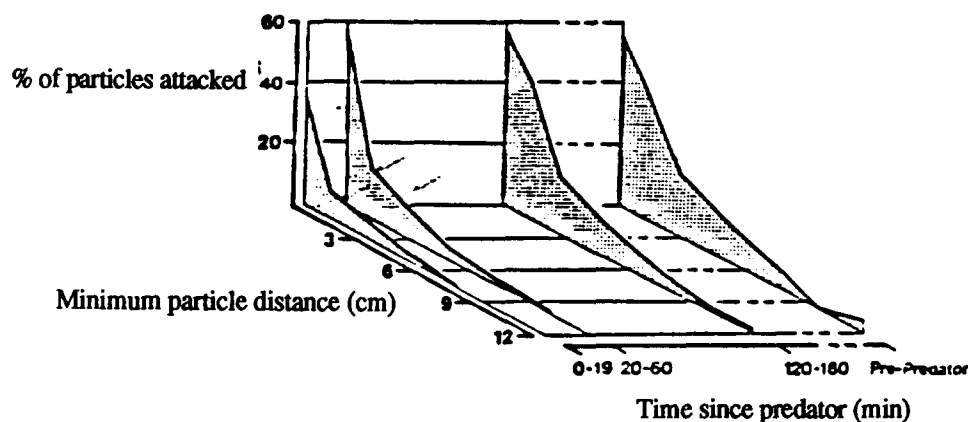


Fig. 7. The percentage of particles attacked by parr, in relation to time after exposure to a predator, and minimum particle distance (from Metcalfe et al. 1987a).

icantly more readily ($p < 0.05$): only 42% stayed still, 30% moved less than 5 cm, and 28% more than 5 cm. Thereafter there was a median time lag of 1 h before those that had fled returned to their stations, but by 3 h these individuals occupied stations at significantly higher flows than formerly ($p < 0.05$), possibly compensating for the period of reduced food intake (Fig. 5).

Under constant flow conditions, Metcalfe et al. (1987a) showed that after predator exposure the parr were less likely to orient to passing food particles (Fig. 6), and having oriented, were less likely to attack them (Fig. 7). They moved less, and so delayed attacks until the particles were closest to them. The outcome of attacks didn't change, so reduced intake was not caused by reduced appetite. Predator avoidance behaviour gradually lost priority, so that while intake rates in the 20 min after predator sighting were only 33% of the earlier level, they rose to 57% in the next 40 min, and had completely recovered after 2 h. Feeding intensity decreased by a constant amount in both UMG and LMG fish, whatever its level before the predator was seen, implying no difference in risk taking between fish of the two modal groups (Huntingford et al. 1988a) (Fig. 8).

However, concentrating part of their attention on predators, the salmon parr were less able to discriminate between profitable and unprofitable prey. Metcalfe et al. (1987b) offered individual fish a pellet every 10 min for 1 h; 3 pellets of the opti-

mum size (Wankowski & Thorpe 1979b) and 3 which were too big to swallow, in an unpredictable sequence. In the absence of a predator (low risk) only 25% of the attacks were on inedible pellets, but after sighting the trout model (high risk) the 'mistake' rate rose to 50% (Fig. 9a). This reduction in efficiency of discrimination also applied at the constituent phases of the feeding sequence (orientation, through to pellet capture) (Fig. 9b).

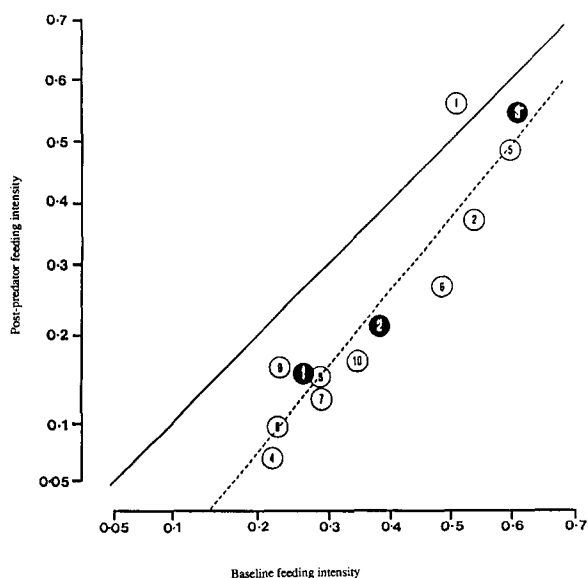


Fig. 8. The depression of salmon feeding intensities after seeing a predator. (●) UMG fish; (○) LMG fish. The solid line is that of equal intensities before and after sighting the predator (from Huntingford et al. 1988a).

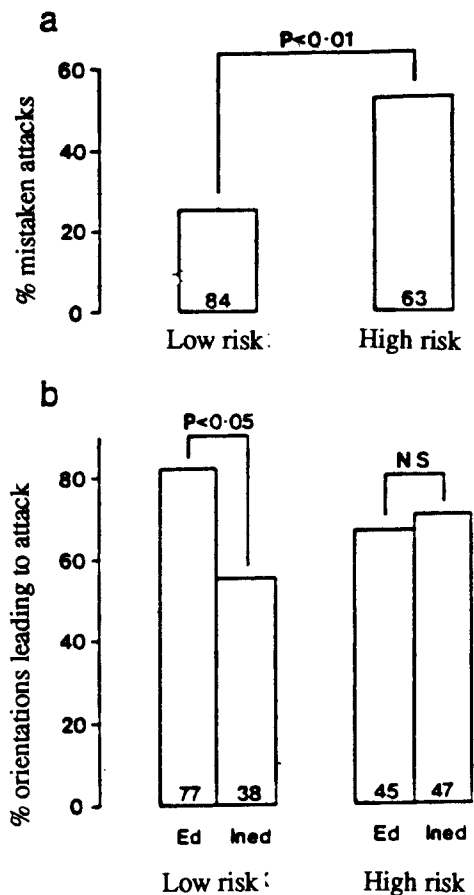


Fig. 9. Attacks on inedible pellets as a percentage of all attacks by salmon: a – the proportion of mistaken attacks increased significantly with an increase in predation risk, b – the percentage of orientations to edible and inedible pellets that led to attacks (from Metcalfe et al. 1987b).

Coping with competitors

As noted already, juvenile salmon defend feeding territories against competitors. Several studies have shown that relative size determines which fish wins a fight with a competitor, and how intense the fight is (Frey & Miller 1972, Abbott et al. 1985, Turner & Huntingford 1986). In pairwise comparisons, the dominant salmon parr was identified as the one which was most often in front of its companion in a narrow flume, and which obtained most food (Metcalfe et al. 1991). From these and from serial removal tests in which the dominance hierarchies of groups of 6–10 individuals were determined, larger ones were dominant in 56% of pairs

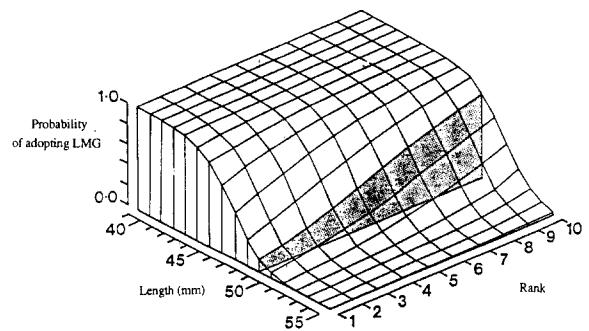


Fig. 10. Dominance rank, length in July, and the probability of a fish subsequently adopting the LMG developmental style. The shaded section illustrates the effect of rank (1 = most dominant) on probable style for fish of 49 mm (close to the mean length of the stock) (from Metcalfe et al. 1989).

in June/July (after 2–3 months of feeding), increasing to 72% in September (Huntingford et al. 1990). Among the LMG fish in the following April, the larger ones were dominant in only 48% of pairwise tests. This suggests that status in early social interactions depends on readiness to attack an opponent (fierceness) (Bakker 1986) rather than size. Since dominants obtain preferential access to food, they are likely to grow faster (Fausch 1984, Metcalfe 1986), and so larger size is initially a consequence rather than a cause of dominance in salmon.

Status and length by mid-July were good predictors (84% accurate) of which fish would form the UMG subsequently (Metcalfe et al. 1989) (Fig. 10). However, size and dominance rank at this time were only weakly correlated, emphasising that ultimate large size is a consequence of high status. To test this further, the absolute status of individual fish was established in paired encounters during the first two weeks of feeding, and relative status was manipulated by dividing the population into one half containing fish of the highest absolute status (High Ranking), and the other half the lowest status (Low Ranking) (Metcalfe et al. 1991). The status and growth rates of individually marked fish were then determined within the two populations until segregation into modal groups was clear. The sizes of subsequent UMG and LMG parr overlapped completely in early June, but from late June UMG fish grew faster (Fig. 11). The High and Low Ranking groups did not differ either in mean

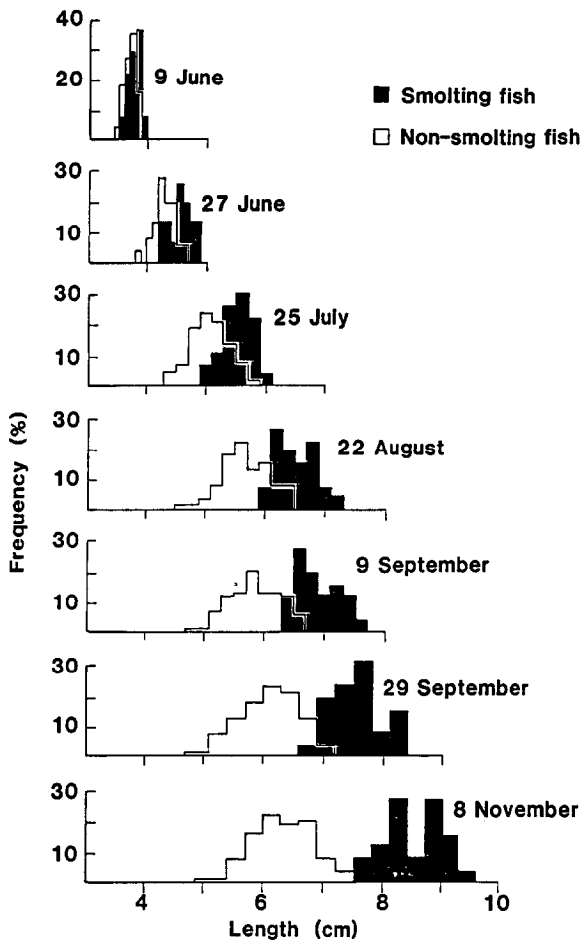


Fig. 11. Progressive segregation of UMG (■) from LMG (□) individuals in a sibling salmon stock. Histograms plotted as percentages of each modal group (from Metcalfe et al. 1991).

growth rates or in proportions of fish arresting growth (LMG). However, within the High Ranking group relative social status in June was a significant predictor of whether a fish would enter the LMG, while length was not; in the Low Ranking group size but not status predicted growth arrest (Fig. 12).

This implies that the influence of status on life-history variation in juvenile salmon depends on the extent to which fish of high status suppress the growth of those lower in the hierarchy.

Conclusions

These overall findings imply that individual varia-

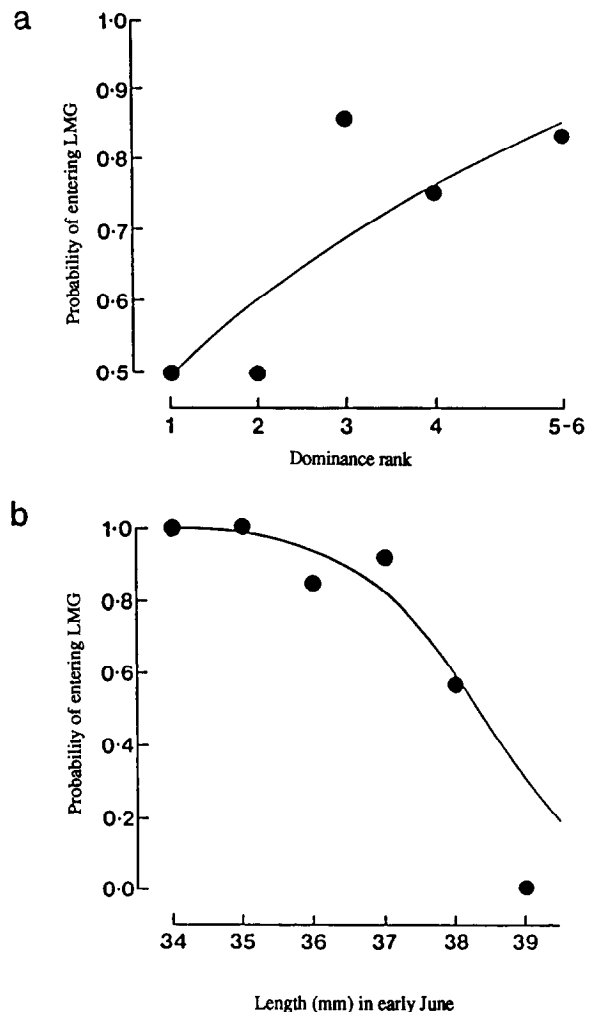


Fig. 12. a - High Ranking population of salmon: the relationship between relative status and probability of entering the LMG. b - Low Ranking population of salmon: the relationship between length on 9 June and probability of entering the LMG (from Metcalfe et al. 1991).

tion in feeding intensity, readiness to flee from predators, and readiness to attack opponents, influence developmental performance under given conditions of environmental opportunity. This in turn determines the outcome of a physiological decision in mid- to late-summer to maintain or decrease appetite. This decision, taken against a genetic reference threshold for performance, determines the life-history pattern for the individual salmon for at least the next year.

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References cited

- Abbott, J.C., R.L. Dunbrack & C.D. Orr. 1985. The interaction between size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). *Behaviour* 92: 241–253.
- Bakker, T.C.M. 1986. Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.): a behaviour-genetic study. *Behaviour* 98: 1–144.
- Donnelly, W.A. & L.M. Dill. 1984. Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preference and achromatic reflectance. *J. Fish Biol.* 25: 183–195.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* 62: 441–451.
- Frey, D.F. & R.J. Miller. 1972. The establishment of dominance relationships in the blue gourami, *Trichogaster trichopterus* (Pallas). *Behaviour* 42: 8–62.
- Higgins, P.J. 1985. Metabolic differences between Atlantic salmon (*Salmo salar*) parr and smolts. *Aquaculture* 45: 33–53.
- Higgins, P.J. & C. Talbot. 1985. Growth and feeding in juvenile Atlantic salmon. pp. 243–263. *In*: C.B. Cowey, A.M. MacKie & J.G. Bell (ed.) *Nutrition and Feeding in Fish*, Academic Press, London.
- Huntingford, F.A., N.B. Metcalfe & J.E. Thorpe. 1988a. Feeding motivation and response to predation risk in Atlantic salmon parr adopting different life history strategies. *J. Fish Biol.* 32: 777–782.
- Huntingford, F.A., N.B. Metcalfe & J.E. Thorpe. 1988b. Choice of feeding station in Atlantic salmon, *Salmo salar*, parr: effects of predation risk, season and life history strategy. *J. Fish Biol.* 33: 917–924.
- Huntingford, F.A., N.B. Metcalfe, J.E. Thorpe, W.D. Graham & C.E. Adams. 1990. Social dominance and body size in Atlantic salmon parr (*Salmo salar* L.). *J. Fish Biol.* 36: 877–881.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout. *Rep. Inst. Freshw. Res. Drottningholm* 39: 55–98.
- Keenleyside, M.H.A. & F.T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour* 19: 139–169.
- Kristinsson, J.B., R.L. Saunders & A.J. Wiggs. 1985. Growth dynamics during the development of bimodal length-frequency distribution in juvenile Atlantic salmon (*Salmo salar* L.). *Aquaculture* 45: 1–20.
- Metcalfe, N.B. 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *J. Fish Biol.* 28: 525–531.
- Metcalfe, N.B., F.A. Huntingford & J.E. Thorpe. 1986. Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.* 64: 2439–2446.
- Metcalfe, N.B., F.A. Huntingford & J.E. Thorpe. 1987a. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.* 35: 901–911.
- Metcalfe, N.B., F.A. Huntingford & J.E. Thorpe. 1987b. Predation risk impairs diet selection in juvenile salmon. *Anim. Behav.* 35: 931–933.
- Metcalfe, N.B., F.A. Huntingford & J.E. Thorpe. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* 57: 463–474.
- Metcalfe, N.B., F.A. Huntingford, W.D. Graham & J.E. Thorpe. 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proc. Roy. Soc. Lond. B* 236: 7–19.
- Metcalfe, N.B., F.A. Huntingford, J.E. Thorpe & C.E. Adams. 1991. The effects of social status on life history variation in juvenile salmon. *Can. J. Zool.* (in press).
- Nicieza, A.G., F. Brana & M.M. Toledo. 1991. Development of length bimodality and smolting in wild stocks of Atlantic salmon, *Salmo salar* L., under different growth conditions. *J. Fish Biol.* (in press).
- Stradmeyer, L. & J.E. Thorpe. 1987a. Feeding behaviour of wild Atlantic salmon, *Salmo salar* L., parr in mid- to late-summer in a Scottish river. *Aquac. Fish Manag.* 18: 33–49.
- Stradmeyer, L. & J.E. Thorpe. 1987b. The responses of hatchery-reared Atlantic salmon, *Salmo salar* L., parr to pelleted and wild prey. *Aquac. Fish Manag.* 18: 51–61.
- Stradmeyer, L., N.B. Metcalfe & J.E. Thorpe. 1988. Effect of food pellet shape and texture on the feeding response of juvenile Atlantic salmon. *Aquaculture* 73: 217–228.
- Thorpe, J.E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *J. Fish Biol.* 11: 175–184.
- Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. *Can. Spec. Publ. Fish Aquat. Sci.* 89: 7–14.
- Thorpe, J.E. 1987. Environmental regulation of growth patterns in juvenile Atlantic salmon. pp. 463–474. *In*: R.C. Summerfelt & G.E. Hall (ed.) *Age and Growth in Fishes*, Iowa State University Press, Ames.
- Thorpe, J.E. 1989. Developmental variation in salmonid populations. *J. Fish Biol.* 35 (Suppl. A): 295–303.
- Thorpe, J.E., C.E. Adams, M.S. Miles & D.S. Keay. 1989. Some photoperiod and temperature influences on growth opportunity in juvenile Atlantic salmon, *Salmo salar* L. *Aquaculture* 82: 119–126.
- Thorpe, J.E. & R.I.G. Morgan. 1978. Parental influence on

- growth rate, smolting rate and survival in hatchery reared juvenile Atlantic salmon, *Salmo salar* L. J. Fish Biol. 13: 549–556.
- Thorpe, J.E., R.I.G. Morgan, E.M. Ottaway & M.S. Miles. 1980. Time of divergence of growth groups between potential 1+ and 2+ smolts among sibling Atlantic salmon. J. Fish Biol. 17: 13–21.
- Thorpe, J.E., R.I.G. Morgan, C. Talbot & M.S. Miles. 1983. Inheritance of developmental rates in Atlantic salmon. Aquaculture 33: 123–132.
- Turner, G. & F.A. Huntingford. 1986. A problem for game theory analysis: assessment and intention in male mouth-brooder contests. Anim. Behav. 34: 961–970.
- Villarreal, C.A., J.E. Thorpe & M.S. Miles. 1988. Influence of photoperiod on growth changes in juvenile Atlantic salmon, *Salmo salar* L. J. Fish Biol. 33: 15–30.
- Wankowski, J.W.J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, *Salmo salar*. J. Fish Biol. 14: 89–100.
- Wankowski, J.W.J. 1981. Behavioural aspects of predation by juvenile Atlantic salmon (*Salmo salar* L.) on particulate drifting prey. Anim. Behav. 29: 557–571.
- Wankowski, J.W.J. & J.E. Thorpe. 1979a. Spatial distribution and feeding in Atlantic salmon, *Salmo salar* L., juveniles. J. Fish Biol. 14: 239–247.
- Wankowski, J.W.J. & J.E. Thorpe. 1979b. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). J. Fish Biol. 14: 351–370.
- Wright, P.J., N.B. Metcalfe & J.E. Thorpe. 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. J. Fish Biol. 36: 241–249.