



Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon

F. A. HUNTINGFORD AND C. GARCIA DE LEANIZ

Fish Behaviour and Ecology Group, Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, U.K.

(Received 6 February 1997, Accepted 16 June 1997)

Twelve groups of 10 Atlantic salmon *Salmo salar* parr were screened for dominance in small tanks with a single localized food source using a serial removal method and the top, middle and bottom two fish in each group were classified as high, medium and low social status, respectively. These 72 ranked fish were weighed and formed into four groups or waves, each consisting of six fish of each status category. The fish were given dye marks according to status and wave and were then introduced into an artificial stream in four waves over a 12-day period. Patterns of settlement/emigration were recorded over a 2-month period, at the end of which the fish were removed from the stream, identified and reweighed, and daily specific growth rates calculated. Fifty-one fish established feeding stations in the flume, the remainder emigrating via a downstream trap. The average growth rate over the 2-month period was 0.87% day⁻¹. Probability of settlement and growth rates following settlement were significantly higher in fish from the earlier waves. In contrast, salmon that were dominant in the initial trial were less likely than subordinate fish to settle in the experimental stream and showed lower post-settlement growth rates. The possibility that fish have individually consistent behavioural profiles that promote success in different competitive environments is discussed with reference to published literature for other groups. A small-scale trial at the end of the main experiment confirmed the prior residence effect and demonstrated that 1 day was sufficient for such an effect to be evident.

© 1997 The Fisheries Society of the British Isles

Key words: dominance; prior residence; settlement; *Salmo salar*.

INTRODUCTION

The effects of competitive ability and prior residence on an animal's ability to acquire a high-quality home range have been well documented (Archer, 1987; Huntingford & Turner, 1987), but little is known of how these two influences interact. This paper describes a study designed to examine the interactions between these two factors as determinants of territory establishment, performance and growth in juvenile Atlantic salmon *Salmo salar* L., held under semi-natural conditions.

Juvenile salmon are sit-and-wait predators that have well-defined feeding stations from which they emerge at variable intervals to intercept passing food items (Stradmeyer & Thorpe, 1987). Competition for both space and food can be intense (Keenleyside & Yamamoto, 1962), and individuals differ in their ability to acquire these resources. As part of a study of the effects of such individual differences in competitive ability on subsequent performance, Metcalfe *et al.* (1989) quantified social status in juvenile salmon in small groups (two to 10 individuals) in simple observation tanks and fed at predictable intervals from a single, localized food source. Dominant fish that monopolized

favourable feeding stations and gained most of the food in these conditions also performed well when transferred to high-density holding tanks with a regular, localized food supply; the converse was true for subordinate fish (Metcalfe *et al.*, 1989). Thus the behavioural traits that promote success in competition for a localized food supply at moderate densities are favoured also in the different competitive environment prevailing in high-density holding tanks. In contrast, Adams & Huntingford (1996) failed to find such an association between performance at high and low densities in Arctic charr *Salvelinus alpinus* L., and suggested that an individual's relative ability to acquire resources may depend on social conditions. One aim of the present study was to examine this possibility further in Atlantic salmon by determining whether individuals that are successful in competition for localized food at moderate densities also perform well in more natural conditions where density is lower and food supply widely dispersed and unpredictable.

The prior residence effect, whereby an animal that arrives first at a specific area gains a competitive advantage over subsequently arriving rivals, has been documented in a number of animal groups (Archer, 1987; Huntingford & Turner, 1987; Krebs & Davies, 1987). Experimental demonstrations of a competitive advantage to prior residents have been conducted mostly under rather restricted conditions in the laboratory, although Brännäs (1995) showed that in stream channels early emerging Atlantic salmon fry have a better chance of establishing a feeding territory than do late-emerging fry. This could be the result of a prior residence effect, but could also arise because good-quality fish both disperse early and fight well. Therefore, a second aim of the study reported here was to study the prior residence effect in juvenile Atlantic salmon experimentally but under semi-natural conditions. A final aim was to see how the effects of prior residence and competitive ability interact to determine the acquisition of feeding sites.

MATERIALS AND METHODS

MAIN EXPERIMENT

The subjects were 0+ Atlantic salmon parr from a single cross between wild-run adult salmon from the Girnock burn, Deeside, Aberdeenshire, U.K. reared under hatchery conditions. In August 1991, 12 groups of 10 parr (mean length 60 mm) were marked individually with blue dye on their lateral surface and placed in small (45 × 40 × 15 cm) tanks with a single food inlet supplying pellets at a rate of *c.* 1 min⁻¹. Light and temperature were ambient for 56°N and the flow of water through the tank was 1 l min⁻¹. After 1 day for settling, fish were assessed for dominance as described in Metcalfe *et al.* (1989). Briefly, on each day the fish were screened on six separate occasions, the positions of all fish with respect to the food inlet being recorded, together with the identity of the fish that ate each of six food pellets. In addition, the initiator and recipient of any aggressive acts (Keenleyside & Yamamoto, 1962) were noted, though overt aggression was relatively rare. On the basis of these behaviour patterns, a clear despot was identified in all groups. This fish was given a rank of 1, removed from the observation tank and placed in a holding tank. Similar observations were conducted on the following day, with the new despot being given a rank of 2, and so on until only three fish remained, by which time it was usually impossible to differentiate between them.

When all these behavioural observations were complete, after a period of 1 week in which all fish were housed together in the holding tank, the two top-ranking fish in each group were designated as dominants (prior social status=1), two fish from the middle of

the distribution were designated as of intermediate rank (prior social status=2) and two of the low-ranking fish were designated subordinates (prior social rank=3); the rest of the fish were discarded from the experiment and returned to their natal river system. The selected fish were given alcian blue dye marks on the sides of their dorsal surface according to these prior status categories. The fish were weighed (g) and photographed for subsequent identification. Dominant, intermediate and subordinate parr did not differ significantly in weight at this point ($F_{2,70}=0.64$, NS).

The 72 fish were divided into four groups of 18, comprising six fish from each prior status category. These groups were introduced into a semi-natural competitive arena (see below) at different times and so were referred to as 'waves'. Fish in the four waves (which were given an additional identifying dye mark on the dorso-lateral surface) did not differ significantly in size at this point ($F_{3,69}=1.26$, NS). The fish were released one wave at a time over a 12-day period into an artificial stream (0.60×14.5 m) in which water was circulated by means of a submerged motor. The stream was landscaped as a single long stretch providing areas of different substrate, depth and current velocity, offering a range of habitat quality (Garcia de Leaniz, 1990). Light and temperature were ambient for the latitude and flow ranged from 1 to 42 cm s^{-1} , depending on depth. The fish were fed twice daily on frozen *Daphnia* and bloodworm in quantities sufficient to maximize average growth (3.5% total initial body weight day^{-1} , increased to 5% of initial by the end of the study to allow for growth), introduced at the upstream end of the stream. A trap at the downstream end allowed the fish to leave the stream at will (or emigrate); fish that did so were released into their natal river system.

The stream was screened daily for a minimum of 2 h during the 12-day introduction period and for shorter daily periods (minimum 30 min) over a further 2-month period to determine patterns of settlement and subsequent behaviour. After 2 months, the fish remaining from the original 72 were captured, re-photographed and re-weighed. Individually distinct colour parr markings were used to match up the photographs taken before and after the experiment, so that individual fish could be identified (Garcia de Leaniz *et al.*, 1994) even though some of their dye marks had faded. In this way growth rates and behaviour in the flume could be related to prior status rank and wave number.

SUBSIDIARY STUDY

As an additional small-scale study of the effects of prior residence, just before the subjects of the main experiment (for this purpose called residents) were removed, a further 45 batch-marked parr with a similar length size distribution to the residents were introduced into the artificial stream (hence called intruders) and settlement/emigration monitored over 2 days. The intruders were all removed from the tank when the fish in the main experiment were captured, but were then reintroduced into the stream on their own and allowed to settle for 1 day, thus becoming short-term residents. Finally, a further 55 naive fish with no previous experience of the artificial stream were introduced and settlement/emigration monitored for 2 days.

RESULTS

A total of 51 of the original 72 fish established feeding stations in the artificial stream, the remainder leaving through the downstream trap. Fish settled throughout the stream from the start, with the shallow sections and small pools being favoured. All but three fish gained weight during the main experiment, the mean growth rate over the whole study period being $0.87\% \text{ day}^{-1}$ (ranging from -0.36 to $+3.46\%$) (Fig. 1).

The proportion of fish that established feeding stations in the stream decreased steadily with wave number [Fig. 1(a)]. In addition, the fish in wave 1 sustained significantly higher growth rates than those in later waves ($F_{3,47}=3.43$, $P<0.05$). In contrast, the proportion of fish settling increased from rank 1 to rank 3, as did

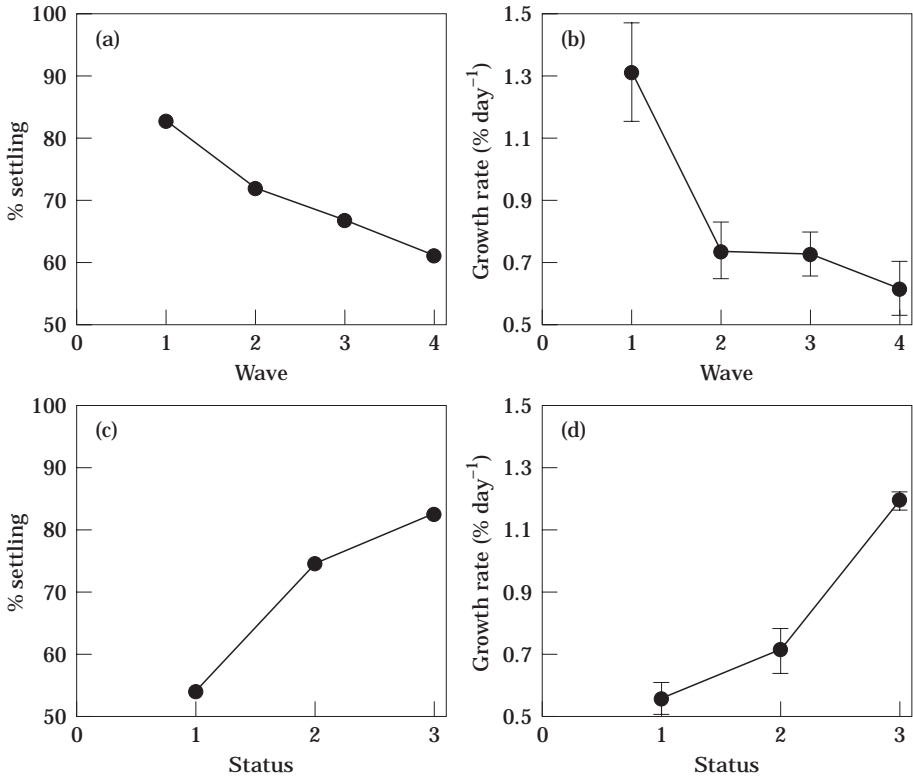


FIG. 1. Performance in the experimental stream in relation to wave number and prior social status. (a) Percentage of fish settling in the stream in relation to wave number; (b) growth rates (mean \pm s.e.) in relation to wave number; (c) percentage of fish settling in the stream in relation to prior status; (d) growth rate (mean \pm s.e.) in relation to prior status.

growth rates ($F_{2,48}=4.73$, $P<0.05$). There was no interaction between the effects of wave number and prior status ($F_{6,39}=1.10$, $P=0.34$).

When the 45 new fish were introduced [Fig. 2(a)], in spite of a doubling of population density, all the residents remained in the stream. In contrast, 56% of the intruders left, driven out by the attacks of the resident fish ($\chi_2=38.3$, d.f. = 1, $P<0.001$). When the same group of fish were subsequently reintroduced into the empty flume, only 11% (41 of 45) left ($\chi_2=22.4$, d.f. = 1, $P<0.001$), so they were clearly physically capable of and motivated to remain there. Finally, when the further 55 intruders were added just 1 day later [Fig. 2(b)], all the new residents stayed while 24% of the new intruders left the flume ($\chi_2=9.20$, d.f. = 1, $P<0.01$).

DISCUSSION

This experiment demonstrated that differential success in competition among juvenile salmon for favoured sites within an artificial stream depends on time of arrival and on prior social status and that these two influences act independently. The main study showed that experimentally induced differences in time of arrival in a previously empty habitat had a clear effect on the probability of settlement of juvenile salmon and also influenced growth rates among those fish that did

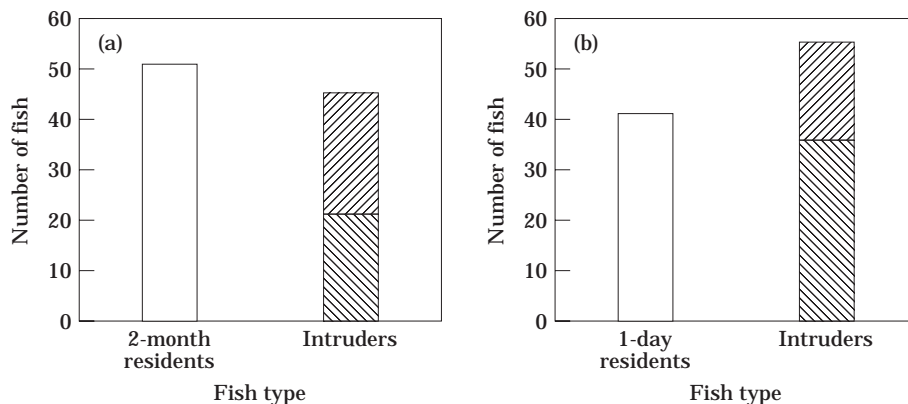


FIG. 2. The number of juvenile salmon in the stream on first introducing additional fish in the subsidiary experiment and one day later. (a) Two-month residents plus intruders; (b) 1-day residents plus intruders. □, the number of residents on the day intruders were added; ▨, number of intruders leaving the stream; ▩, number of intruders staying in the stream.

establish feeding stations within the stream, with fish arriving earlier doing better in both respects. The introductions at the end of the main experiment provided an additional demonstration of the advantage conferred by even a brief period of residence. Egglisshaw & Shackley (1973) found that prior residence ensured interspecific competitive advantage between salmon and trout fry *S. trutta* L., in an experimentally planted stream. This agrees with Brännäs' (1995) finding that in stream channels early emerging fry have a better chance of establishing a feeding territory than their late-emerging siblings. It also agrees with the extensive literature on prior residence effects in other animal groups (Archer, 1987; Huntingford & Turner, 1987).

The negative relationship between prior social status and performance in the stream might, in principle, have resulted from the fact that the subordinate fish in the tanks were removed last and so had more recent experience of holding the top position within a small group. This is considered unlikely since all the fish were housed together in groups for a week between the two phases of the study, but it remains a possibility to be tested. Our data suggest, therefore, that the behavioural traits that promote success at moderate densities during competition for localized food may not be the same as those promoting success at low densities in a more complex and unpredictable environment. In nature, parr often defend their feeding sites and consequently are dispersed over relatively wide areas, but they are also sometimes seen at high densities in particularly favourable feeding sites at which they fight for access to food (García de Leaniz, 1990). Different competitive environments may exist therefore in which individuals having particular behavioural profiles perform differentially.

A similar phenomenon has been described in several other species. For example, the results of genetic selection experiments on wild mice *Mus musculus* L., derived from a natural population suggest that two inherited behavioural modes exist. One is aggressive and relatively inflexible; the other is relatively unaggressive and able to respond flexibly to environmental contingencies (Benus *et al.*, 1987). Non-aggressive, flexible mice do better in the early stages of colony formation, but as population density rises the aggressive, inflexible mode is more

successful. Other studies indicate a similar divergence of behavioural profiles and suggest adaptive explanations for these (sticklebacks *Gasterosteus aculeatus* L., Huntingford, 1976; sunfish *Lepomis gibbosus* (L.), Wilson *et al.*, 1994; rats *Rattus norvegicus* Fischer, Bohus *et al.*, 1987; rhesus monkeys *Macaca mulatta* Lacépède, Suomi, 1987). Therefore, consistent differences in competitive style that yield differential advantages depending on the current competitive environment may be a widespread phenomenon.

This study was supported by grants from the NERC and SOAEFD. We thank John Thorpe for discussion of the experiments; Liz Denton for preparation of the figures; and two anonymous referees for comments on an earlier draft of this manuscript.

References

- Adams, C. E. & Huntingford, F. A. (1996). What is a successful fish? Determinants of competitive success in Arctic char (*Salvelinus alpinus*) in different social contexts. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 2446–2450.
- Archer, J. (1987). *The Biology of Aggression*. Cambridge: Cambridge University Press.
- Benus, R. F., Koolhaas, J. M. & Van Oortmerssen, G. A. (1987). Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour* **100**, 105–122.
- Bohus, B., Benus, R. F., Fokkema, J. M., Koolhaas, J. M., Nyakas, C. & Van Oortmerssen, G. A. (1987). Neuroendocrine states and behavioural and physiological stress responses. *Progress in Brain Research* **72**, 57–70.
- Brännäs, E. (1995). First access to territorial space and exposure to strong predation pressure: a conflict in early emerging Atlantic salmon (*Salmo salar* L.). *Evolutionary Ecology* **9**, 411–420.
- Egglishaw, H. J. & Shackley, P. E. (1973). An experiment on faster growth for salmon *Salmo salar* (L.) in a Scottish stream. *Journal of Fish Biology* **5**, 197–204.
- Garcia de Leaniz, C. (1990). Distribution, growth, movements and homing behaviour of juvenile Atlantic salmon and brown trout in the Girnock Burn, Aberdeenshire. PhD thesis, University of Aberdeen, U.K.
- Garcia de Leaniz, C., Fraser, N., Huntingford, F. A. & Mikheev, V. (1994). Individual recognition of juvenile salmonids using melanophore patterns. *Journal of Fish Biology* **45**, 417–422.
- Huntingford, F. A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* **24**, 245–260.
- Huntingford, F. A. & Turner, A. K. (1987). *Animal Conflict*. London: Chapman & Hall.
- Keenleyside, M. H. & Yamamoto, F. T. (1962). Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour* **19**, 139–169.
- Krebs, J. R. & Davies, N. B. (1987). *Introduction to Behavioural Ecology*, 2nd edn. Oxford: Blackwell Scientific Publications.
- 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. *Proceedings of the Royal Society of London B* **236**, 7–19.
- Stradmeyer, L. & Thorpe, J. E. (1987). Feeding behaviour of wild Atlantic salmon, *Salmo salar* L., parr in mid- to late-summer in a Scottish river. *Aquaculture and Fisheries Management* **18**, 33–49.
- Suomi, S. J. (1987). Genetic and maternal contributions to individual differences in rhesus monkey biobehavioural development. In *Perinatal Development: A Psychobiological Perspective* (Krasnegor, N. A., Blass, E. M., Hofer, M. A. & Smotherman, W. P., eds), pp. 6–18. New York: Academic Press.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. (1994). The shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology* **107**, 250–260.