Influence of habitat structure and fish density on Atlantic salmon *Salmo salar* L. territorial behaviour

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A laboratory stream experiment was performed to test the influence of young-of-the-year Atlantic salmon *Salmo Salar* density on habitat selection (*i.e.* pools and riffles) and the combined effect of habitat and density on territoriality. Pools were preferred at low and medium fish density. At higher density, the saturation of the riffles led to an equal fish repartition in both habitats. Aggressive interactions increased according to fish density, and the level of aggression was significantly higher in the pools than in the riffles.   © 2006 The Fisheries Society of the British Isles

Competition is a common phenomenon that occurs in most animal communities. Both intra- and interspecific competition reduces individual fitness, thereby affecting the dynamics of the population (Connell, 1983; Schoener, 1983). For freshwater fishes, and particularly salmonids, intraspecific competition is usually considered as a density-dependent process leading to modification in such life-history characteristics as growth rate (Deverill *et al.*, 1999; Jenkins *et al.*, 1999; Bohlin *et al.*, 2002; Sundström *et al.*, 2004), mortality and emigration (Elliott, 1994; Keeley, 2001; Einum & Nislow, 2005). Young-of-the-year (YOY) salmonids are strongly territorial. Each individual attempts to acquire a territory providing the best balance between energy gain from the environment and energy required for metabolism, growth and reproduction (Fausch, 1984). They actively compete to monopolize and defend a favourable territory (Grant & Kramer, 1990). Such intraspecific interactions increase interference between individuals, by way of aggression (Deverill *et al.*, 1999). In addition, territory defence can be affected by habitat complexity (Basquill & Grant, 1998) and population density (Cole & Noakes, 1980). In the same way, habitat preference increases the level of territorial defence (Johnsson *et al.*, 2000). Although

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Kalleberg (1958) and Cole & Noakes (1980) described YOY salmonid behavioural characteristics according to fish density under different current velocities, more comprehensive studies on the combined effect of habitat complexity and population density on territorial defence have never been conducted (Maher & Lott, 2000).

To fill this gap, an experimental design, using artificial laboratory streams, was created involving three different densities of YOY Atlantic salmon *Salmo salar,* L. and two contrasting habitat types (pools and riffles). The goals of this study were: 1) to evaluate the relationships between habitat use and Atlantic salmon density and 2) to measure the combined effect of population density and habitat type on aggression (as a measure of territoriality).

Experiments were conducted in three artificial channels fitted with a re-circulating water system. Each channel measured 1·90 m long, 0·30 m wide and 0·30 m deep. It was made of clear Plexiglas to permit direct visual observation. One riffle and pool succession was shaped using small pebbles (2–3 cm diameter). The water in each pool was 12–16 cm deep, and the velocity was 5–10 cm s^{-1}. The riffles were 3–6 cm deep with a water velocity of 4–35 cm s^{-1}. These channel characteristics were consistent with the natural habitat conditions of YOY Atlantic salmon (Klemetsen *et al.*, 2003) and the current velocity was set in a range of values sufficiently low to avoid downstream displacement of fish. Three large pebbles (7–10 cm diameter) were added in each riffle to make current refuges and increase visual isolation. Two 60 W lights above each channel provided illumination during the day (80% of the available intensity), dawn and dusk, and night (7% of the available intensity). The photoperiod was 9L : 14D plus 30 min each of dawn and dusk. Water temperature was maintained constant at 14° C, range ± 1° C. Water chemistry was kept constant by re-circulation through a series of biological and physical filters. Fish were hatchery 0+ year Atlantic salmon produced from a single cross between wild spawners [one female and two males caught from the River Malbaie, Québec, Canada, (47° 67′ N; 70° 16′ W) during the reproductive migration in summer 2003]. Prior to experiments, fish were reared in a circular tank where they were fed *ad libitum* on commercial fish feed pellets (grade size 0).

A full factorial experiment was conducted with density (*i.e.* 6, 12 and 18 individuals m^{-2}) and habitat type (i.e. pool and riffle) as fixed-factors. A channel haphazardly received three, six or nine individuals (corresponding to the low, medium and high density levels, respectively) and sampling was conducted over 2 days after an acclimatation period of 24 h. This design constitutes a block experiment and was replicated three times as time blocks within an 11 day period. Atlantic salmon were visually chosen from the rearing tank to limit size variability within and between treatments and replicates. Each individual was used only once and was weighed at the end of each experiment. Mean ± S.E. body mass was 3·46 ± 0·06 g and individual fish mass did not vary between treatments nor replicates (two-way ANOVA, d.f. = 4, 45, P = 0·86). In addition, the fish were not fed during the experiment to avoid potential biases due to competition for a point food source.

Over the 2 days, each channel was observed three times a day (1000, 1300 and 1700 hours) for 10 min. During each observation session, habitat use as the harmonic mean of fish abundance in pools and riffles was evaluated using the

following formula: $n_j = \sum\limits_{i=1} (n_{ij} \cdot t_i) t_t^{-1}$, where n_j is the mean number of fish observed in the habitat j during 10 min, n_{ij} is the number of fish observed in the habitat j during the period i, t_i is the duration of the period i (s) and t_t is the total duration of an observation session (*i.e.* 600 s). The six harmonic means obtained after 2 days of observations for each habitat type (riffle and pool) were averaged as one datum before statistical treatment. The distribution of the fish (dependent variable) was compared according to fish density (*i.e.* low, medium and high) and habitat (pools and riffles), using a two-way ANOVA (Underwood, 1997; Zar, 1999). Fish habitat selection was significantly linked to the interaction between habitat and fish density (ANOVA, d.f. = 2, 12, $P < 0.01$) (Fig. 1). In addition, the Student-Newman-Keuls (SNK) multiple comparisons tests (Underwood, 1997) showed that the number of fish increased in riffles between low and high (SNK test, $P < 0.001$) and low and medium (SNK test, $P < 0.001$) density trials but remained constant between medium and high density treatments (SNK test, $P = 0.09$). The number of fish in pools remained stable between the low and medium density trials (SNK test, $P = 0.71$) but significantly increased at high fish density (SNK test, low *v.* high density, $P < 0.001$ and medium *v.* high, $P < 0.001$) (Fig. 1). The comparison between pools and riffles showed a significant tendency to prefer pools when fish density was low (SNK test, $P < 0.05$) whereas riffles were preferred at medium density (SNK test, $P < 0.001$). At higher density habitat preference did not significantly differ between pools and riffles (SNK test, $P = 0.07$) (Fig. 1).

Aggression was measured in the two habitat types (pools and riffles) as the number of aggressive encounters [*i.e.* intentional movements, nips, chases and displays (Kalleberg, 1958; Mason, 1969)] for each 10 min observation. Although increasing fish abundance could interfere with the ability of an observer to
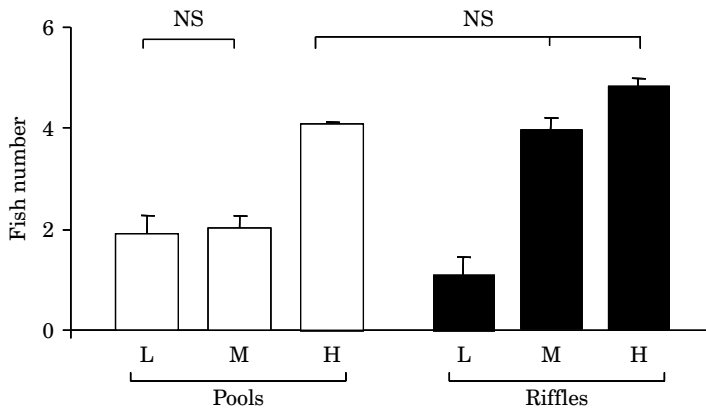

FIG. 1. Young-of-the-year Atlantic salmon distribution according to the two habitat types (□, pools and ■, riffles) under three different density treatments. Fish number was the harmonic mean of fish density observed during the 10 min observation session (mean + s.e.). L, M and H correspond to low (3 individuals m^{-2}), medium (6 individuals m^{-2}) and high (9 individuals m^{-2}) fish density treatments, respectively. Differences in fish distribution among treatments were tested using ANOVA and SNK multiple comparison tests. Only non-significant differences are indicated.

document all aggressive interactions, aggressive encounters were mainly due to a few dominant fish and were sufficiently spaced in time to ensure that all aggressive encounters were observed. A least-square linear regression was used to test the relationship between aggressive rate [$\log_{10} (x + 1)$ transformed to ensure homoscedasticity] and fish abundance according to habitat type. To evaluate this relation, each pseudoreplicated observation from the three replicates and the three density treatments were pooled according to habitat type, and the harmonic mean of fish abundance for each data point was used as the continuous factor. Records with only one fish (and therefore no aggression possible) were not considered as they could artificially influence the slope of the regression and hence bias the results. The relationship between fish abundance and aggression increased significantly in pools ($r^2 = 0.14$, ANOVA, d.f. = 1, 46, $P < 0.01$). In riffles, a positive trend was not significant ($r^2 = 0.03$, ANOVA, d.f. = 1, 40, $P = 0.27$) (Fig. 2). Differences in mean levels of aggression according to habitats (Underwood, 1997) were tested using ANCOVA with harmonic mean of density as covariate, habitat as the fixed factor and individual aggression rate as the dependent variable. Aggressive encounters were positively correlated to fish density (ANCOVA, effect of fish density, d.f. = 1, 59, $P < 0.01$; unpubl. data) and were significantly higher in pools (ANCOVA, comparison of regression slopes, d.f. = 1, 59, $P = 0.07$, effect of habitat, d.f. = 1, 60, $P < 0.01$), where the number of aggressive encounters was two times higher than in riffles. Because pseudoreplication can interfere with these results in such a model, the same analysis was performed using an averaged value for each replicate. A similar statistical outcome was found: ANCOVA, effect of fish density, d.f. = 1, 14, $P < 0.01$ comparison of regression slopes, d.f. = 1, 14, $P = 0.22$
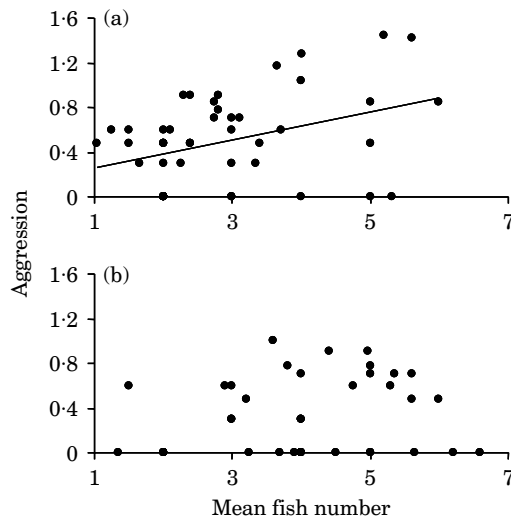

FIG. 2. Relationship between mean number of Atlantic salmon observed and number of aggressive encounters [$\log_{10} (x + 1)$ transformed] during each 10 min session in the (a) pool and (b) riffle. (a) The curve was fitted by: $y = 0.12 \, x + 0.14$ ($r = 0.37$, $P < 0.01$). (b) There was no significant relationships ($r = 0.17$, $P > 0.05$).

and effect of habitat, d.f. = 1,15, $P < 0.01$. It was concluded therefore that the results were not biased by pseudoreplication. The results indicated: (1) a modification of fish habitat use according to fish density and (2) different aggressive patterns between pools and riffles according to fish density.

The present work is consistent with the results of Cole & Noakes (1980) showing that high fish densities tend to increase agonistic interactions. In addition, the difference of aggression according to habitats can be related to differences in habitat complexity between pools and riffles. Indeed, aggression decreases with habitat complexity (Basquill & Grant, 1998), which promotes visual isolation and reduces territory size (Kalleberg, 1958; Imre *et al.*, 2002). These proximate factors probably explain the reduced fish aggression in the riffles compared to the pools (Basquill & Grant, 1998), but also the variation in habitat use. The increase of aggressive interactions in pools, due to higher density, tended to be compensated by a preferential use of riffles, where fish aggression and territory size are reduced due to the complexity of this kind of habitat (strongly structured by water velocity). This study also supports and adds weight to the hypothesis of Johnsson *et al.* (2000) stipulating that territory defence increases with habitat preference. Although pools are known as an energetically profitable habitat for YOY salmonids (Young, 2001; Blanchet, 2003), the selection of this habitat was beneficial only when the cost of fighting did not exceed the energy gain from this habitat (*i.e.* when fish density was low). Therefore, it can be hypothesized that the cost of density-dependent processes (*i.e.* aggressive interactions) exceeded the benefits the fish derive from the use of preferred habitats (*i.e.* pools). Under medium fish density, such phenomena may lead Atlantic salmon to preferentially use habitats that are less favourable from a physical point of view (*i.e.* riffles) to reduce competition. When density becomes higher, the number of fish observed in pools increased and Atlantic salmon tended to inhabit both pools and riffles without distinction. At this time, a carrying capacity was probably attained in riffles and supernumerary fish may have preferred to adopt a cryptic strategy in pools rather than facing current velocity in riffles (S. Blanchet, pers. obs.). Adopting this cryptic strategy permitted settlement in pools by reducing interactions with dominant fish.

These results support the hypothesis that the strength of territorial defence is heterogeneous among habitats, and therefore that density-dependent processes are highly dependent on habitat structure. In pools, where interference was higher, emigration to riffle habitats can be considered as the main density-dependent response. In contrast, for riffles, according to Imre *et al.* (2002), territory size decreases with fish density. This reduces the abundance of potential prey and probably leads to a reduction in growth rate and increased mortality. Accordingly, the present results could explain the discrepancy between studies identifying different responses to density dependence, such as variations in growth rate (Deverill *et al.*, 1999; Jenkins *et al.*, 1999; Bohlin *et al.*, 2002) or variations in mortality and emigration processes (Elliott, 1994; Keeley, 2001). Such discrepancies may be due to habitat structure which has a strong influence on the strength but also the outcome of density-dependent processes.

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