Impact of stocked Atlantic salmon (Salmo salar L.) on habitat use by the wild population

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Abstract – We investigated the summer habitat occupied by populations of young-of-the-year wild and stocked (farmed populations released into the native range) Atlantic salmon under allopatric and sympatric conditions. Under allopatric conditions, farmed and wild salmon occupied habitats with the same characteristics. The salmon preferentially occupied the riffle areas. However, under sympatric conditions, the fish occupied meso- and micro-habitats with different characteristics. Wild salmon avoided habitats used by farmed salmon and preferred glide areas with considerable vegetation cover. This study suggests that differences in the pattern of habitats used by young Atlantic salmon were both size- and origin-dependent and may result from intra-species competition between farmed and wild populations. Given that stocking with farmed Atlantic salmon is carried out intensively to enhance recreational angling or to conserve salmon populations, this study warns that this can have a negative impact on the extant wild Atlantic salmon population.

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Introduction

The distribution of salmon (*Salmo salar* L.) populations in Europe and North America indicates that in many rivers that have historically supported Atlantic salmon populations, these populations have been the exterminated or suffered a severe decline. Consequently, the Atlantic salmon is now considered to be a threatened species in some regions. In many cases, this can be attributed to a number of factors, such as dam construction, pollution, overfishing, changing ocean conditions, introduction of non-native fish and aquaculture (Parrish et al. 1998). As well as additional marine research (Klemetsen et al. 2003), there is also a need for a better understanding of the factors that influence the production of salmon in freshwater habitats (Heggenes et al. 1999), and especially the interactions between farmed, stocked salmon and wild populations. In fact, large numbers of farmed fish are invading salmon habitats, by escaping or as a result of stocking throughout the North Atlantic to conserve and restore salmon populations (Hansen et al. 1991; Gross 1998) even if a wild salmon population seems to subsist. For example, it is the case in France in the Loire (Descroix et al. 2009) or in the Aulne (Croze 2008) basins.

Although it is usually difficult to predict the specific impacts of biological introductions (e.g., Leprieur et al. 2009), we do know that introduced fish can have profound effects on wild fish, particularly in the case of salmonids (e.g., Fausch 1998; Levin et al. 2002; Scott et al. 2005; Blanchet et al. 2007). For example, there is a large literature about the potential complex interactions between stocked and wild salmons (Gross 1998; Youngson & Verspoor 1998; Hutchinson 2006; Ford & Myers 2008). However, these effects are either too subtle or not sufficiently clearly identified to make it possible to definitely attribute the patterns of extermination and decline of Atlantic salmon populations to them. This concern arises from the potentially deleterious effects of ecological interactions between stocked and wild salmon, and especially fish originated from wild spawning salmon caught in the river and reared in specific salmon hatchery before stocked in the same river. In fact, little is known about direct effects of stocked salmon in modifying the use of specific habitats by wild salmon. The aim of this study was to investigate the meso- and micro-habitats used

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by stocked salmon and the wild population in a small stream during summer low-flow conditions under allopatric and sympatric conditions.

Materials and methods

The Aulne is a 145-km-long river, with a 1495-km^2 catchment area, characteristic of Brittany (France) rivers (see Croze 2008 for more details). The indices of the abundance of juveniles in this river indicate a low average density (5.5 ind. per 5 min of electrofishing), which is well below the average level for Brittany (21 ind. per 5 min). This low density of juvenile salmon produced naturally by the river confirmed the threat to the stock of wild salmon in the Aulne. In response to the major decline in the wild population of salmon, between 70,000 and 100,000 parr have been stocked every year since 1986. The fish stocked originated from wild spawning salmon caught each autumn in the river. Juveniles were reared from the egg stage in a specific salmon hatchery and fed commercial pellets. In June, young-of-the-year (0+ parr, fork length ranging from 40 to 50 mm) were released into various different river sections (the number of fry released ranging between 0.5 and 1 salmon·m^2 of habitat area suitable for parr). Because parr–smolt transformation takes place at the age of 1+ in most fish, 0+ parr were virtually the only age group in the river during the summer months. Consequently, only results for 0+ parr were used. Stocked and wild salmon were identified by observing the adipose fin. Indeed, all stocked fish have been finclipped before release.

Fifty-eight river sections corresponding to all the different tributaries were selected randomly (one section for each small tributaries and two for large ones), without taking the resettlement areas into account, to represent the range of habitat conditions available for young-of-the-year Atlantic salmon in the Aulne streams. Backpack electrofishing equipment was used to catch fish late in the summers of 2002 and 2003, using a point abundance sampling by electrofishing (PASE) technique (Laffaille et al. 2005). Salmon were caught during one electrofishing pass at the different sampling points at each river section. As soon as each point was reached, the anode was immediately placed on the bottom of the stream and was kept turning in an area of 1 m^2 for at least 30 s. Fish were then collected with several fine-mesh dipnets (50 mm mesh size). Electrofishing was conducted in an upstream direction and always with systematically a distance of 3 m between sampling points to prevent possible contamination of the salmon by downstream samples. The total number of sampling points in the experiment was 1540 (averaging 27 per river section, depending on the sampling points available in each river section). Approximately 1⁄3 of the total habitat area was point-sampled in each river section.

The salmon were measured (fork length, to the nearest mm). After a log ($X + 1$) transformation to ensure the normality of the distribution, the sizes of the salmon were compared using Student's *t*-test (*t*-test). The correlation between salmon density (number of fish per sampling point) for the different river sections and the origin of the salmon was tested using Pearson's correlation.

Several parameters were measured to analyse salmon distribution *vs*. habitat conditions according to Bardonnet & Baglinière (2000). At each sampling point, the general habitat type (meso-habitat) was defined as a pool (slow <50 cm·s^{-1} and deep >30 cm), glide (slow to fast, nonturbulent), riffle (shallow <30 cm, fast >50 cm·s^{-1} and turbulent) according to the definitions of Delacoste et al. (1995). We measured five micro-scale habitat parameters that are known to influence the spatial organisation of salmonid communities. These micro-scale parameters were estimated at each sampling point to assess the salmon micro-habitat:

- three topographical variables: depth (in cm), the presence or absence of fish shelter and distance from the bank (described as sampling from the bank or as sampling in the middle of the river);
- one biotic variable: the aquatic vegetation expressed as the cover index (from minimum 0 to maximum 5) calculated for the whole area covered by all the sampling points; and
- one substratum composition expressed as the dominant type: sand, gravel or boulders.

Atlantic salmon habitats (the spatial distribution of salmon densities according to the environmental variables, the origin of the salmon and salmon size classes) were analysed in greater detail using ecological profiles. The influence of each variable was visualised independently. To test the origin effect, we used data from allopatric and sympatric conditions. To test the salmon size effect, we used four size classes (total salmon, <75, 75–85 and >85 mm). Finally, each matrix (i.e., one for salmon from each origin in allopatric and sympatric conditions, from each size class and with or without presence of *Salmo trutta* – the most abundant salmonid) was used to develop habitat preference indices for each environmental variable as a measurement of the habitat used by salmon *vs*. habitat availability, based on the method of Brosse et al. (2001). The habitat used was calculated as a normalised ratio of utilisation to availability for different modality of each environmental variable. Indices of the habitat used were obtained after dividing each variable into several modalities. Their number was defined according to

the range of variation of each variable. The following formula was used:

$$I = [(\mathrm{Ob}/\mathrm{Ex})/(\mathrm{Ob}/\mathrm{Ex})_{\max}] - 0.5$$

where Ob is the density of fish observed for each modality of each environmental variable, Ex is the expected density for a theoretical random distribution and $(\mathrm{Ob}/\mathrm{Ex})_{\max}$ is the maximum value of (Ob/Ex) for each modality. I varies between −0.5 and +0.5. Positive values indicate habitat use, and negative values indicate habitat avoidance for a given variable. Therefore, values between −0.1 and +0.1 can taken to reveal indifference; those from −0.3 to −0.1 and from +0.1 to +0.3 indicate slight avoidance and slight use, respectively; and those from −0.5 to −0.3 and +0.3 to +0.5 reveal strong avoidance and use, respectively. Ecological profiles were compared using Wilcoxon's nonparametric test (Z-test).

Results

A total of 641 (385 stocked and 256 wilds) young-of-the-year (0+) salmons were collected. Stocked salmon fork lengths ranged from 43 to 108 mm (mean ± SD = 79.9 ± 12.5 mm) (Fig. 1) and were larger (t-test, $t = 7.984$, $P < 0.001$) than wild salmon length ranged from 43 to 101 mm (mean ± SD = 70.1 ± 12.2 mm).

The mean density of 0+ salmon was 0.42 ± 0.70 fish per sampling point. Half of the river sections studied (30) were found to contain 0+ salmon. When salmon were present, the mean density was 0.66 ± 0.69 fish per sampling point. Other salmonids (native *Salmo trutta* and non-native *Oncorhynchus mykiss*) were present under sympatric conditions, but comparatively in low numbers (mean density: 0.26 ± 0.23 and 0.09 ± 0.09 fish per sampling point, respectively). Nine river sections were colonised solely by wild salmon, with a mean density of 0.26 ± 0.29 fish per sampling point, and five river sections were colonised solely by stocked salmon, with a mean density of 0.70 ± 0.53 fish per sampling point. The density of wild salmon was negatively correlated (Pearson $r = -0.434$, $P = 0.017$) with that of stocked salmon (Fig. 2).

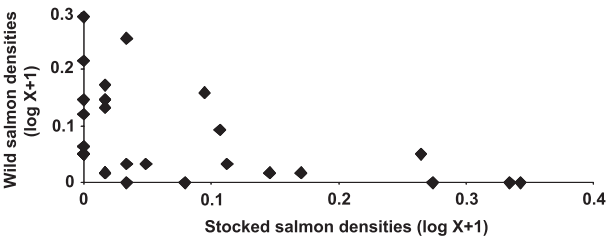

Fig. 2. Densities of wild *vs*. stocked salmon estimated from the 30 river sections in the Aulne River were found to contain 0+ salmon.

Under allopatric conditions, 0+ stocked and wild salmons (Fig. 3) used habitats with the same characteristics (Wilcoxon's test, $Z = -1.76$, $P = 0.07$). Moreover, Wilcoxon's nonparametric test showed nonsignificant difference between the ecological profiles of the different size classes and with or without the presence of *Salmo trutta* (Z between 0.28 and 0.94 and P between 0.77 and 0.35). At the meso-habitat scale, the salmon chose a riffle habitat (i.e., a shallow, fast-flowing turbulent stream) and avoided pools (slow flowing and deep) and glides (slow to fast and nonturbulent). At the micro-habitat scale, ecological profiles revealed no strong avoidance, and both stocked and wild salmons were ubiquitous. Salmon preferred shallow to intermediate depth streams (<50 cm) and coarse substrates (gravel and boulder). The minor differences concerned their use of aquatic vegetation and shelters. Wild salmon preferred micro-habitats with little aquatic vegetation cover (<3) or indeed no shelter, whereas stocked salmon preferred

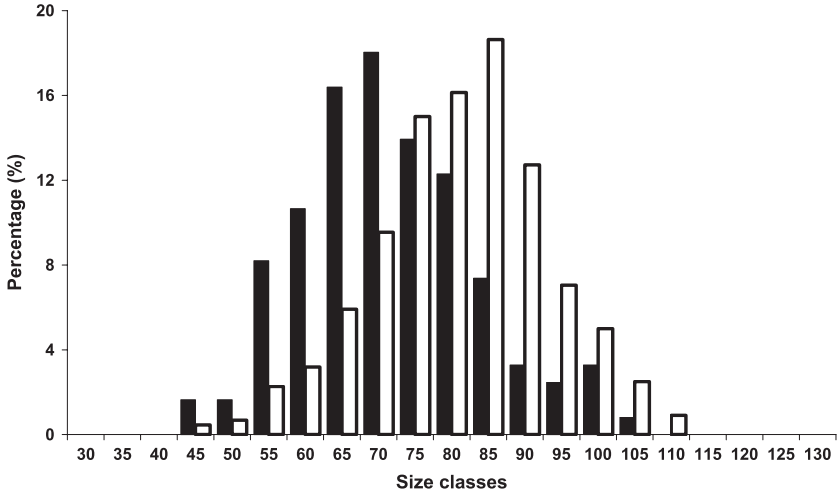

Fig. 1. Length histogram (mm) of stocked (in white) and wild (in black) salmon sampled in 58 sections of the Aulne river.

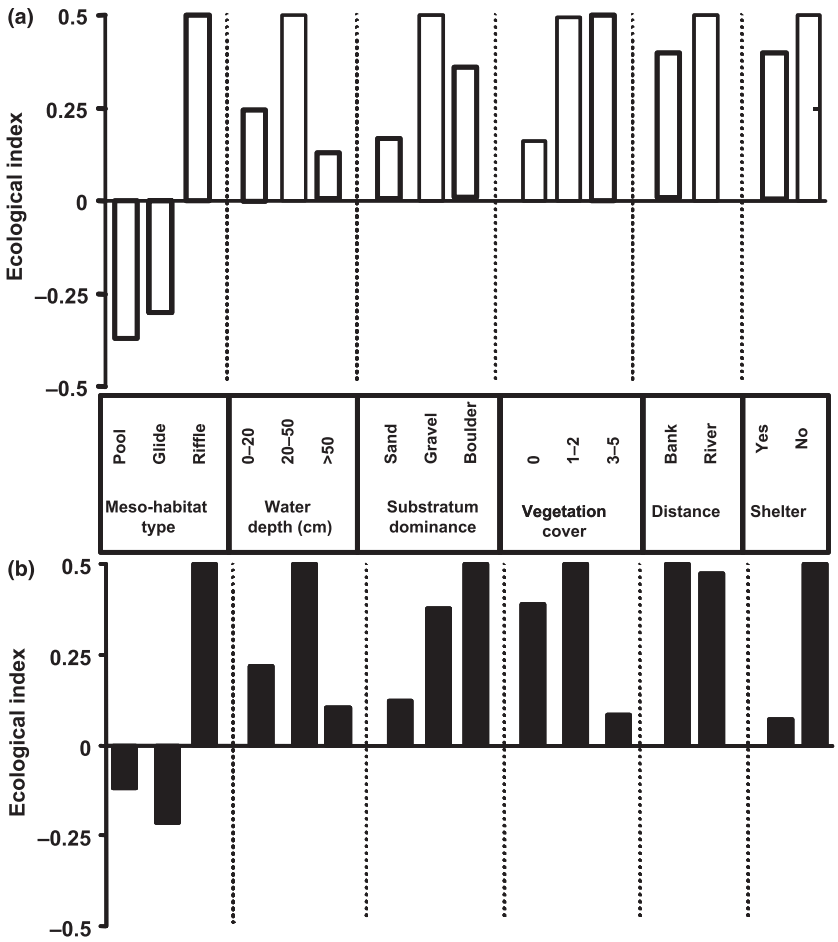

Fig. 3. Meso- and micro-habitat profile (*Y* axis) of (a) the total 0+ stocked salmon (in white) and (b) the total 0+ wild salmon (in black) under allopatric conditions calculated for each environmental variable (*X* axis – see text for detail).

micro-habitats with vegetation cover and at least some shelter. The distance from the bank was not a distinguishing spatial factor.

However, under sympatric conditions (Fig. 4), salmon from the two origins occupied markedly different habitats (Wilcoxon's test, $Z = -3.47$, $P < 0.01$). However, for each salmon origin, Wilcoxon's nonparametric test showed nonsignificant difference between the ecological profiles of the three size classes and with or without presence of *Salmo trutta* (Z between 0.20 and 0.54 and P between 0.85 and 0.62). Regardless of whether wild salmon were present, 0+ stocked salmon showed no difference (Wilcoxon's test, $Z = -1.06$, $P = 0.29$). In contrast, the ecological profiles of wild salmon revealed major differences in habitat descriptions (Wilcoxon's test, $Z = -2.98$, $P < 0.01$), with strong choice and avoidance behaviour being evident. At the meso-habitat scale, wild salmon preferred glides and avoided pools and riffles. At the micro-habitat scale, they preferred deeper habitats without aquatic vegetation and a substrate composed of small particles. They also preferred habitats containing fish shelters. In summary, our analyses of the ecological profiles revealed habitat partitioning and selection based more on the origin than on the size of the salmon and showed that wild salmon avoided habitats used by stocked salmon.

Discussion

In our study, ecological profiles indicated only minor habitat differences in salmon of different origins (stocked or wild) under allopatric conditions, whereas major differences appeared under sympatric conditions. In numerous studies concerning salmon/habitat relationships, micro-habitat parameters such as velocity, water depth, substrate and geomorphological unit type have generally been used to evaluate the suitability of habitats for young salmon. The impact of biotic parameters has received relatively little attention. However, the spatial niche occupied depends both on intra- and inter-specific competition, and on habitat availability. In this study, other salmonids (native *Salmo trutta* and non-native *Oncorhynchus mykiss*) were present in low numbers, and salmon habitats were not different with or without the presence of *Salmo trutta*, suggesting that inter-specific competition was certainly limited from salmonid

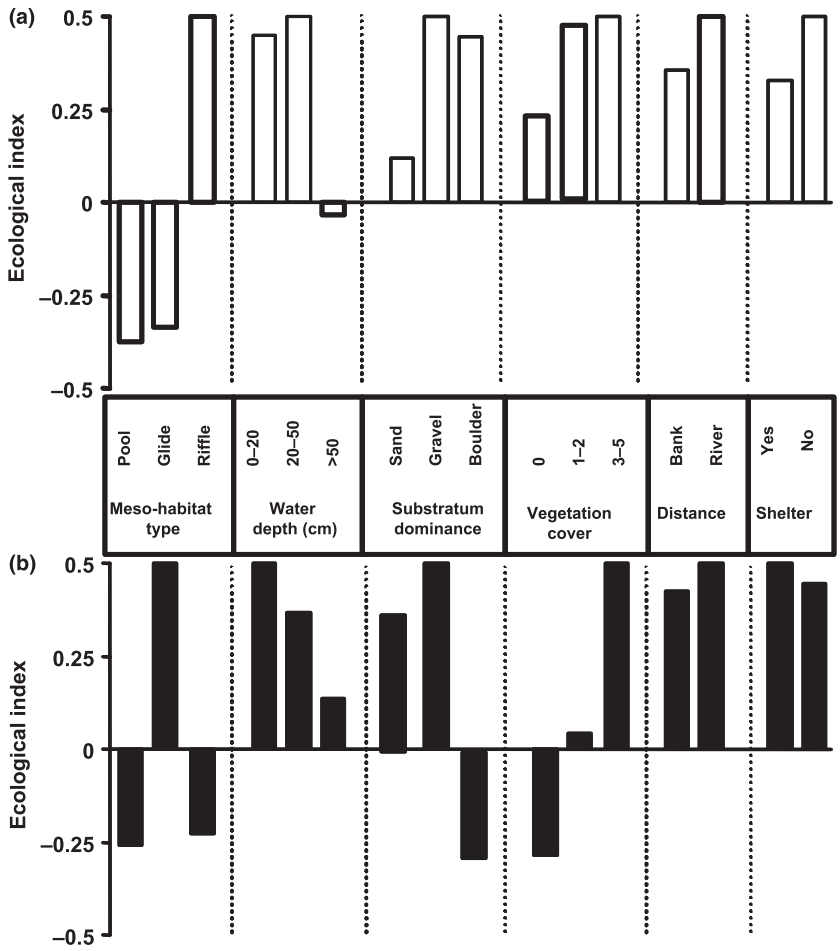

Fig. 4. Meso- and micro-habitat profile (*Y* axis) of (a) the total 0+ stocked salmon (in white) and (b) the total 0+ wild salmon (in black) under sympatric conditions calculated for each environmental variable (*X* axis – see text for details).

populations. Heggenes (1990) characterised the habitat preference of young salmon in terms of depth, as shallow to intermediate (20–70 cm), and in terms of water velocity, as relatively fast flowing (10–60 $cm \cdot s^{-1}$). However, young salmon are generally found towards the lower end of these values (Bardonnet & Baglinière 2000). Generally, under allopatric conditions, in the summer, young-of-the-year (0+) are mainly present in riffles and glides with a coarse substrate and markedly avoid pools (see for example Bardonnet & Baglinière 2000). Although we did find that salmon were more abundant in certain habitat types, this species does appear to be generally tolerant of a wide range of habitats and sometimes occupies less typical habitats, such as deeper pools. For example, Bremset & Berg (1997) and Blanchet et al. (2006) have both reported extensive use of pools by Atlantic salmon, but these pools appear to have included areas with high water flow rates and low to medium fish densities, respectively. When confronted by competition, young salmon demonstrate flexibility in their choice of habitat (Heggenes et al. 1995). Our results show that when two salmon populations (wild and stocked origin in our study) live under sympatric conditions: the stocked fish used riffles, whereas the wild salmon mainly used glides. Consequently, the habitat used by wild salmon in Aulne tributaries probably reflects the limited space available in these relatively small streams, potentially aggravated by intra-species competition for space, because in small streams, salmonid populations are generally present at high densities.

Body size has a considerable impact on inter-species interactions among fish. For example, size is known to be a decisive factor in competitive interactions between brown trout and other stream salmonids (Fausch 1998, Faush & White 1986). Size is also an important element in intra-species interactions, because spatial segregation is determined largely by the body size of the fish (Vehanen et al. 1999). Different size classes of Atlantic salmon are often segregated spatially in rivers. Generally, small salmon are found in shallow riffle areas, whereas larger fish occupy deeper habitats (Bardonnet & Baglinière 2000). In our study, size is not a significant factor in allopatric conditions and for each salmon origin in sympatric conditions. Then, salmon origin rather than size contributed to spatial distribution and habitat use

under sympatric conditions. However, the stocked salmon were larger than the wild salmon. Stocked salmon have adapted to an aquaculture niche, and this has made them maladapted to the wild niche (Gross 1998). However, the establishment of a stocked population in a river suggests that some of the habitats in this river must be suitable for the wild population, because they have similar habitat requirements, which are indeed similar to those of non-native salmonids (see for example, Fausch 1998; Harwood et al. 2002; Armstrong et al. 2003). After a growth period spent in a high-density niche environment of aquaculture, stocked juveniles are larger than wild salmon and aggressively out-compete wild juveniles in competition experiments (Einum & Fleming 1997). Thus, the presence of stocked salmon modifies the characteristics of the habitats occupied by wild salmon despite their prior residence. This indicates that the newcomers (the stocked salmon) are able to displace the wild salmon that were already in the habitats, which suggests that there must be strong interaction between these two groups of salmon. Consequently, ecological impacts can occur through food and space competition. The difference in body size depending on salmon origin was certainly the most important factor explaining the meso- and micro-habitat segregation. Moreover, farm background may affect the behaviour of the fish, because probably even in the case of similar sized fish, stocked fish are more aggressive than wild fish because of high rearing densities, differences in food delivery and the absence of predators. The stocked salmon clearly behaviourally displaced the wild fish into meso- and micro-habitats, where feeding rates were probably lower. The origin-dependent distribution observed is a consequence of this size-dependent segregation.

The findings of this study provide evidence of the impact of stocking with farmed salmon (in our case, fish originated from wild spawning salmon caught in the river and reared in specific salmon hatchery before stocked in the same river) on habitat use by wild salmon, and especially on the selection of more suitable meso- and micro-habitats. Thus, wild salmon are found in sheltered habitats or in replacement habitats in the presence of stocked salmon, which probably reduces their food intake, and consequently their growth, and ultimately their chances of survival as demonstrated with escaped salmon from hatchery (McGinnity et al. 2003). The actual cost of this change in habitat remains to be determined. Given that intensive stocking with farmed Atlantic salmon was carried out to enhance recreational angling and conservation programs (see for example Parrish et al. 1998; Scott et al. 2005; Descroix et al. 2009), this study warns us that this can have negative impacts on extant wild Atlantic salmon populations, especially in small rivers, if the stocked salmon are larger than the wild salmon present. Stocking should not therefore be carried out in tributaries used by wild fish. This is certainly applicable generally throughout the European salmon distribution range, and so these consequences should be taken into account in global and local management plans.

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