

Impact of exposure to a simulated predator (*Mergus merganser*) on the activity of juvenile Atlantic salmon (*Salmo salar*) in a natural environment

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Abstract: Some laboratory studies suggest that the presence of predators influences the short-term behaviour of juvenile Atlantic salmon. However, few studies have been conducted in the natural environment to confirm these observations and to document how biological and environmental factors influence the behaviour of fish faced with a predator. Of the many potential predators of juvenile Atlantic salmon, *Salmo salar*, the common merganser, *Mergus merganser*, is a major one. This study was designed to investigate the immediate and short-term impact of exposure to a simulated avian predator on the activity of juvenile Atlantic salmon in their natural habitat. The influence of riverbed sediment grain size, a major determinant of habitat choice in salmon, and body size of juvenile salmon on the nature and intensity of their response to the predator was also investigated. Observations were made before and after exposure to a model of *M. merganser* in three situations: (1) fry (young salmon during their first summer of life) on fine sediment, (2) fry on coarse sediment, and (3) parr (young salmon during their second or third summer of life) on coarse sediment. Observations were also made on fry exposed to a harmless floating stimulus to evaluate if the decoys were perceived as threat. Following exposure, the feeding rate of juvenile salmon decreased by 25–39% and the moving rate increased by 123–386%. Sediment grain size influenced the nature of the immediate response of juvenile salmon, while body size influenced the intensity of the moving response. Parr moved significantly more than fry after exposure to the simulated predator.

Résumé : Des études de laboratoire semblent indiquer que la présence de prédateurs influence le comportement à court terme des saumons de l'Atlantique juvéniles. Cependant, peu d'études ont été faites en milieu naturel pour vérifier ces observations et évaluer l'impact des facteurs biologiques et environnementaux sur le comportement des poissons en présence de prédateurs. Le grand bec-scie, *Mergus merganser*, compte parmi les plus importants prédateurs potentiels des juvéniles du saumon de l'Atlantique, *Salmo salar*. Cette étude a pour but d'évaluer les impacts immédiats et à court terme de l'exposition à un modèle de prédateur aérien sur l'activité des juvéniles du saumon de l'Atlantique dans leur milieu naturel. L'influence de la taille des sédiments au fond de la rivière, un facteur important dans le choix de l'habitat du saumon, et de la taille corporelle des jeunes saumons sur la nature et l'intensité de leurs réactions face au prédateur ont également été évaluées. Les observations ont été faites avant et après l'exposition au modèle de grand bec-scie dans trois situations : (1) chez les alevins (jeune saumon au cours de leur premier été) sur des sédiments fins, (2) chez les alevins sur des sédiments grossiers et (3) chez des tacons (jeunes saumons au cours de leur deuxième ou troisième été) sur des sédiments grossiers. Nous avons également observé des alevins exposés à un objet flottant inoffensif afin de vérifier si le modèle de prédateur était réellement perçu comme une menace. Suite à l'exposition au modèle de prédateur, le taux d'alimentation a diminué de 25 à 39 % et le taux de déplacement a augmenté de 123 à 386 %. La taille des sédiments influence la nature de la réaction immédiate des jeunes saumons, alors que la taille corporelle influence l'intensité de la réaction de déplacement. Les tacons se sont déplacés significativement plus que les alevins suite à l'exposition au modèle de prédateur.

Introduction

The presence of a predator can affect its prey by changing the latter's behaviour for a short period of time (e.g.,

Reinhardt and Healey 1997; Lima and Bednekoff 1999). In many cases, the presence of predators modifies the behaviour of the prey by changing, for example, the type of food ingested (Dill 1983; Magnhagen 1988), by reducing the at-

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Table 1. Physical characteristics of the Sainte-Marguerite River at each of the two study sites.

| | Water depth (cm) | Sediment grain size (cm) | Water velocity (cm·s ⁻¹) | |
|--------------------------|---------------------|-----------------------------|---|---|
| | | | 10 cm from the bottom (<i>N</i> = 20) | 5 cm from the surface (<i>N</i> = 20) |
| Site 1 (coarse sediment) | 39.4 ± 7.9 | 8.8 ± 1.7 | 27.1 ± 11.6 | 42.0 ± 14.2 |
| Site 2 (fine sediment) | 31.0 ± 7.1 | 3.8 ± 1.5 | 32.5 ± 10.3 | 54.3 ± 15.2 |

Note: Treatments 1, 2, and 4 were conducted at site 1 and treatment 3 at site 2 (see Methods section for a description of the treatments). Values are given as the mean ± standard error.

tack distance of the prey towards food particles (e.g., Dill and Fraser 1984; Gotceitas and Godin 1993), reducing the overall activity of the prey (eg. Lima and Dill 1990; Martel 1996), or forcing the prey to move to a protected habitat that might be less profitable in terms of energy (e.g., Grand and Dill 1997; Roussel and Bardonnnet 1999).

Some laboratory studies have evaluated the impact of avian predators on the activities of certain species of salmonids, but the results obtained are not consistent. Some studies suggest that the presence of an avian predator increases the feeding and moving rates of the fish (e.g., coho salmon, *Oncorhynchus kisutch*; Reinhardt and Healey 1997), while other studies show that potential prey decrease their feeding rate (e.g., rainbow trout, *Oncorhynchus mykiss*; Angradi 1992) and decrease their moving rate (e.g., coho salmon; Martel and Dill 1995) after exposure to a predator.

Juveniles of salmonids such as the Atlantic salmon, *Salmo salar*, are potential prey for many avian predators, especially the common merganser, *Mergus merganser*, a piscivorous bird present on many rivers in North America (e.g., Wood 1985, 1987a, 1987b), Scotland (e.g., Feltham 1995), and Sweden (e.g., Sjoberg 1988) during summer. These birds were estimated to be responsible for 24–65% of coho salmon mortality on a river on Vancouver Island (Wood 1987b) and for 3–16% of Atlantic salmon mortality in a Scottish river (Feltham 1995).

During the early stages of life, juvenile Atlantic salmon are territorial and are closely associated with the substratum by holding station against the current in the vicinity of rocks. Juvenile salmon are particularly vulnerable to avian predators. This vulnerability may be enhanced by the visibility of juvenile salmon, which may increase when they are seen against fine sediment (Donnelly and Dill 1984) and when body size increases (Magnhagen 1988), as movements potentially become more evident to the avian predator. Consequently, the risk of being detected may increase and the antipredator response may be modified as a function of sediment grain size (hereinafter sediment size) and body size.

This study examines, in the field, the impact of exposure to a simulated avian predator on the activities of juvenile Atlantic salmon, considering the influence of sediment size and body size. To clarify this issue, four hypotheses were tested. First, it was predicted that predator exposure would decrease the feeding rate and increase the moving rate of juvenile salmon as an avoidance and an escape response, respectively. Secondly, we predicted that exposure to a harmless floating stimulus would induce no change in the feeding and moving rates of juvenile salmon. Thirdly, we predicted that the decrease in feeding rate and the increase in moving rate

would be more pronounced on a small sediment size and, fourthly, for large juvenile salmon.

Methods

Sampling method

All the experiments were conducted on the Principal branch of the Sainte-Marguerite River (48°21'N, 70°8'W) in Quebec, Canada, during August 1998, between 09:00 and 16:00. Focal-animal sampling of free-swimming salmon was conducted by one person while snorkelling. A minimum distance of 1.5 m between diver and fish was respected, corresponding to the minimum distance that a brook charr (*Salvelinus fontinalis*) and a brown trout (*Salmo trutta*) can be approached before the fish's behaviour is affected by the diver (Cunjak and Power 1986). If this distance was not respected or if the fish was lost from sight before the end of the experiment, the fish was not considered in the analyses. Each dive was initiated from the downstream end of the study area. The diver moved slowly in an upstream direction following a predetermined zigzag pattern. Each fish observed was at least 3 m from the previous focal fish. These precautions were taken to make sure that no fish would be disturbed before the beginning of the observation period. No fish was observed more than once. During the juvenile stages of life, salmon are very territorial and stay behind the same rock, exploring approximately 1 m² of the river's bed. It was therefore possible to discriminate fish that had been previously used in the experiment.

Physical environment

Two observation sites were used. They had similar water depths and water velocities at the surface as well as at the bottom of the water column but had different sediment sizes (Table 1). Similar environments were chosen, as environmental factors such as depth of the water column can affect salmon response to a predator (Lonzarich and Quinn 1995; Mather 1998). The location of the head of each fish was marked with a coloured stone following each observation period. Depth and water velocity were then measured at this position. Depth was measured using a 1 m (±1 cm) ruler positioned perpendicularly to the riverbed. A portable electromagnetic flowmeter was used to measure surface and bottom water velocity. To estimate sediment size at both sites, the visual Woolman technique was used (see Church et al. 1987) for 20 quadrats of 1 m² per site. In each quadrat, three rocks were haphazardly picked and the length, width, and thickness of each rock were measured.

Table 2. Exclusive categories of behaviour of juvenile Atlantic salmon (*Salmo salar*) recorded for each observation period.

| Activity | Description |
|------------|---|
| Moving | A swimming motion longer than half the body length of the fish, which results in displacement from a position; this category includes escape behaviours |
| Stationary | Holding position in the current or on the bottom, usually close to the substratum; it includes movements shorter than half of the body length of the fish |
| Feeding | Interception of a particle from the surface or the water column regardless of the distance travelled |
| Hiding | A move followed by a stop under an object on the substratum |

Experimental design

To simulate the presence of the predator, *M. merganser*, commercial duck decoys were used. They included one 52 cm long bird representing the mother and five 28 cm long birds representing juveniles, together forming the typical group size of a *M. merganser* family on this river (N. Aubin-Horth, 1998, personal communication). The decoys were plastic, usually used for hunting, and painted in the colours of real *M. merganser*. Flexible leather legs were added to each bird to make the decoys more realistic when seen from under water. The ducks were loosely attached together by cord to form a group covering a surface area of 155 × 54 cm. The decoy was then handled by an assistant for a controlled release approximately 10 m upstream of the focal fish and well outside the fish's visual range.

Four treatments were designed to test our hypotheses. The first treatment involved fry (0+ fish measuring from 5 to 6 cm in length) on coarse sediment exposed to duck decoys (see Table 1). The second treatment also involved fry on coarse sediment, but they were exposed to a leafless branch having the same surface area as the decoys. This treatment was designed to validate the assumption that decoys were perceived as a threat and to evaluate if juvenile salmon respond to any harmless floating stimulus. In the third treatment, fry on fine sediment exposed to duck decoys were used to evaluate the influence of sediment size on the intensity of response of juvenile salmon to avian predators. Finally, in the fourth treatment, parr (1+ fish measuring from 7 to 11 cm in length) on coarse sediment exposed to duck decoys were used to evaluate the influence of body size on the intensity of their response.

Treatments were conducted one after the other in a randomized order. For each treatment, 19 or 20 salmon were observed individually for a period of 20 min each. They were initially observed for 1 min to make sure that their behaviour was not obviously affected by the diver. All salmon were then observed for a 10-min period without any disturbance. After the 10th minute, the decoy was released and allowed to drift directly over the focal fish, resulting in approximately 5 s of exposure. The observation period was continued for another 10 min after exposure, for a total of 20 min of observation per focal fish. The diver was motionless during the whole observation period. Four exclusive categories of behaviour were noted: moving, stationary, feeding, and hiding (Table 2). Verbal codes identifying each activity were mouthed by the diver directly into the snorkel and an assistant on the river's bank tape-recorded on a continuous basis the amount of time the fish spent at each activity during the observation period.

For each treatment, three temporal scales were considered to describe the salmon response. First, an immediate re-

sponse (scale of 1 s) was examined, which corresponds to the type of reaction (hiding, moving, or stationary) occurring within the first 5 s after exposure to the predator. Second, a short-term response (scale of 1 min) was examined, comparing feeding and moving rates 1 min before and 1 min after exposure to the predator. Finally, a long-term response (scale of 10 min) was examined, comparing the feeding and moving rates observed during the 10-min period before and the 10-min period after exposure to the predator.

Statistics

Differences in immediate response (scale of 1 s) for each of the four treatments were tested using Fisher's exact test. A repeated-measure analysis of variance (ANOVA) was used on proportion of time per minute spent feeding and moving to compare the results of treatments through time. Two sources of variation were taken into account: the between-subjects effect (treatment factor) and the within-subjects effect (time factor). The corrected Akaike information criterion was used to investigate the type of dependency between variances coming from the different times and treatments. For both feeding and moving rates, a compound symmetry structure, specific for each treatment, best fit the data. Specific contrast comparisons were chosen and used to identify significant differences. We first tested if there was a difference in activity rates before and after exposure to the predator for each treatment, and second, if these differences were the same between treatments. Two time intervals were investigated: short-term effects comparing activity 1 min before and 1 min after exposure to the predator and long-term effects comparing activity in the 10-min period before and the 10-min period after exposure to the predator. Data analyses were generated using SAS/STAT software (version 8.2 of the SAS system for Windows, © 1999 SAS Institute Inc., Cary, N.C., U.S.A.). Data were square-root transformed to meet the assumptions of homoscedasticity and normality. Normality was checked using the Kolmogorov–Smirnov test and by looking at the skewness and kurtosis parameters. Homoscedasticity was verified using Cochran's test and by examining the distribution of the residuals.

Results

Response of salmon to predator exposure

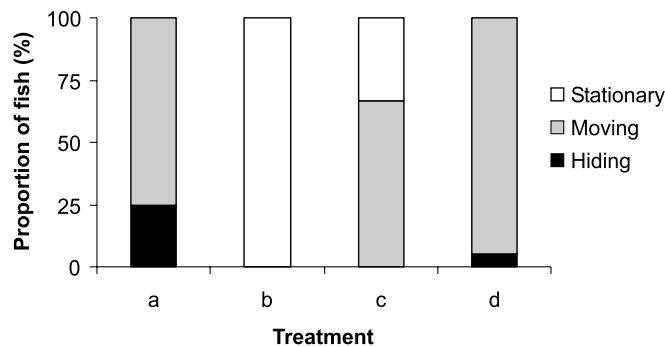
The immediate response of fry over coarse sediment after exposure to the predator was significantly different from that observed when they were exposed to the branch (Fisher's exact test, $\chi^2_2 = 36.129$, $P < 0.001$; Fig. 1). Seventy-five percent of fry exposed to the decoys moved and 25% hid in the sediment, whereas 100% of fry exposed to the branch remained stationary when the object was passing over them.

Table 3. Results of repeated-measure ANOVA on proportion of time per minute spent feeding and moving by juvenile Atlantic salmon.

| Source | df | Feeding | | Moving | |
|--------------------------------------|------|---------|--------------|--------|--------------|
| | | F | P | F | P |
| Treatment | 3 | 7.64 | <0.001 | 5.63 | 0.002 |
| 1. Predator | 1 | 16.76 | <0.001 | 0.88 | 0.352 |
| 2. Sediment grain size | 1 | 0.89 | 0.349 | 0.47 | 0.497 |
| 3. Body size | 1 | 11.88 | <0.001 | 7.47 | 0.008 |
| Fish (treatment) | 74 | | | | |
| Time | 19 | 6.33 | <0.001 | 4.37 | <0.001 |
| 4. Short-term effect | 1 | 0.64 | 0.423 | 38.82 | <0.001 |
| 5. Long-term effect | 1 | 52.10 | <0.001 | 4.43 | 0.036 |
| Treatment × time | 57 | 1.58 | 0.004 | 2.25 | <0.001 |
| 6. Short term in treatment 1 | 1 | 5.85 | 0.016 | 8.41 | 0.004 |
| 7. Short term in treatment 2 | 1 | 5.80 | 0.016 | 2.89 | 0.089 |
| 8. Short term in treatment 3 | 1 | 0.80 | 0.371 | 16.17 | <0.001 |
| 9. Short term in treatment 4 | 1 | 5.53 | 0.019 | 43.47 | <0.001 |
| 10. Long term in treatment 1 | 1 | 22.20 | <0.001 | 0.55 | 0.46 |
| 11. Long term in treatment 2 | 1 | 1.18 | 0.278 | 3.20 | 0.074 |
| 12. Long term in treatment 3 | 1 | 24.64 | <0.001 | 0.85 | 0.358 |
| 13. Long term in treatment 4 | 1 | 15.16 | 0.001 | 16.06 | <0.001 |
| 14. Short term × predator | 1 | 11.65 | <0.001 | 10.83 | 0.001 |
| 15. Short term × sediment grain size | 1 | 5.79 | 0.016 | 1.22 | 0.270 |
| 16. Short term × body size | 1 | 0.00 | 0.984 | 7.42 | 0.007 |
| 17. Long term × predator | 1 | 6.41 | 0.012 | 3.06 | 0.080 |
| 18. Long term × sediment grain size | 1 | 0.06 | 0.803 | 0.04 | 0.839 |
| 19. Long term × body size | 1 | 0.28 | 0.596 | 5.60 | 0.018 |
| Error | 1406 | | | | |

Note: “Short term” denotes 1 min before versus 1 min after exposure to the predator; “long term” denotes the 10-min period before versus the 10-min period after exposure to the predator. Treatment 1 is fry on coarse sediment exposed to duck decoys; treatment 2 is fry on coarse sediment exposed to the branch; treatment 3 is fry on fine sediment exposed to duck decoys; and treatment 4 is parr on coarse sediment exposed to duck decoys. Two sources of variation were considered: the between-subjects effect (treatment factor) and the within-subjects effect (time factor). Significant *P* values are shown in boldface type. Data were square-root transformed. Terms numbered from 1 to 19 represent the selected contrasts.

Fig. 1. Immediate reaction of juvenile Atlantic salmon (*Salmo salar*) after exposure to common merganser (*Mergus merganser*) decoys. Treatments are as follows: *a*, fry on coarse sediment exposed to the predator; *b*, fry on coarse sediment exposed to the branch; *c*, fry on fine sediment exposed to the predator; *d*, parr on coarse sediment exposed to the predator.



Fry on fine sediment also showed a significantly different immediate response from fry on coarse sediment, with 66.7% moving and 33.3% remaining still after exposure to the decoys (Fisher’s exact test, $\chi^2_2 = 12.017$, $P < 0.01$). Parr showed no differences in response from fry on the same sediment size (Fisher’s exact test, $\chi^2_1 = 2.92$, $P > 0.05$). Ninety-five percent moved and 5% hid after exposure to the decoys.

We observed a significant interaction between treatments and time, indicating that feeding and moving rates varied

through time and between treatments (Table 3; ANOVA, $F = 1.58$, $P = 0.004$, and $F = 2.25$, $P < 0.001$). We also observed significant differences in feeding and moving rates between treatments and between time intervals, but those factors are not interpreted individually, as the interaction between them is significant. For the same reason, contrasts 1–5 (see Table 3) are not interpreted. Moreover, these contrasts do not respond to our original hypotheses, as they represent the effect of different treatments when all time intervals are pooled (contrasts 1 and 2) and the effect of time when all treatments are pooled (contrasts 3–5). They are presented to represent the structure of the analysis. The contrasts from the interaction between treatments and time (contrasts 6–19) respond directly to our hypotheses.

Feeding response

In the first treatment, fry on coarse sediment decreased their feeding rate after exposure to the predator on a short and a long temporal scale (Table 3; contrasts 6 and 10: $F = 5.85$, $P = 0.016$, and $F = 22.20$, $P < 0.001$, respectively). In the second treatment, fry exposed to the branch increased their feeding rate significantly on a short temporal scale after exposure to the predator, but no change was observed on a longer temporal scale (Table 3; contrasts 7 and 11: $F = 5.80$, $P = 0.016$, and $F = 1.18$, $P = 0.278$, respectively). In the third treatment, fry on fine sediment did not change their feeding rate on a short temporal scale after exposure to the predator, but a significant decrease was observed on a longer

temporal scale (Table 3; contrasts 8 and 12: $F = 0.80$, $P = 0.371$, and $F = 24.64$, $P < 0.001$, respectively). Finally, parr on coarse sediment decreased their feeding rate after exposure to the predator on a short and a long temporal scale (Table 3; contrasts 9 and 13: $F = 5.53$, $P = 0.019$, and $F = 15.16$, $P = 0.001$, respectively).

Contrasts between fry exposed to the predator and fry exposed to the branch (treatments 1 and 2), both on coarse sediment, revealed that the response in terms of feeding rate differs between the two groups on a short as well as on a long temporal scale (Table 3; contrasts 14 and 17: $F = 11.65$, $P < 0.001$, and $F = 6.41$, $P = 0.012$, respectively).

Moving response

An increase in moving rate was observed through contrasts, on a short temporal scale only, for fry on coarse sediment exposed to the predator (Table 3; contrasts 6 and 10: $F = 8.41$, $P = 0.004$, and $F = 0.55$, $P = 0.460$, for a short and a long temporal scale, respectively). In the second treatment, fry exposed to the branch did not change their moving rate (Table 3; contrasts 7 and 11: $F = 2.89$, $P = 0.089$, and $F = 3.20$, $P = 0.074$, for a short and a long temporal scale, respectively). Fry from treatment 3, observed over fine sediment, increased their moving rate after exposure to the predator on a short temporal scale, but this change was not observed on a longer temporal scale (Table 3; contrasts 8 and 12: $F = 16.17$, $P < 0.001$, and $F = 0.85$, $P = 0.358$, respectively). Finally, in the fourth treatment, parr on coarse sediment increased their moving rate after exposure to the predator on a short and a long temporal scale (Table 3; contrasts 9 and 13: $F = 43.47$, $P < 0.001$, and $F = 16.06$, $P < 0.001$, respectively).

The ANOVA revealed a significant difference when the intensity of response of fry exposed to the predator was compared with that of fry exposed to the branch on a short temporal scale, but this difference disappeared after a longer period of time (Table 3; contrasts 14 and 17: $F = 10.83$, $P = 0.001$, and $F = 3.06$, $P = 0.080$, respectively).

Effect of sediment size

A difference in feeding response was observed between fry on coarse sediment and fry on fine sediment exposed to the predator, but this difference disappears when analysed on a longer temporal scale (Table 3; contrasts 15 and 18: $F = 5.79$, $P = 0.016$, and $F = 0.06$, $P = 0.803$, respectively). However, no difference in moving response was observed between these two groups (Table 3; contrasts 15 and 18: $F = 1.22$, $P = 0.230$, and $F = 0.04$, $P = 0.839$, for a short and a long temporal scale, respectively).

Effect of body size

No significant difference in the decrease in feeding rate was observed between parr and fry on coarse sediment exposed to the predator (Table 3; contrasts 16 and 19: $F = 0.00$, $P = 0.984$, and $F = 0.28$, $P = 0.596$, for the short- and the long-term comparison, respectively). However, the increase in moving rate after exposure to the predator differs between parr and fry on coarse sediment (Table 3; contrasts 16 and 19: $F = 7.42$, $P = 0.007$, and $F = 5.60$, $P = 0.018$, for the short- and the long-term comparison, respectively). Parr

Table 4. Quantification of the decrease in feeding rates and the increase in moving rates of juvenile Atlantic salmon after exposure to the predator.

| Treatment | Feeding rate (%) | Moving rate (%) |
|------------------------|------------------|-----------------|
| Fry (coarse sediment) | 39.1 ± 2.2 | 123 ± 27 |
| Fry (fine sediment) | 30.9 ± 3.1 | 269 ± 38 |
| Parr (coarse sediment) | 25.0 ± 5.7 | 385 ± 50 |

Note: Values are given as the mean ± standard error.

have a more marked reaction in terms of moving than fry do after exposure to the predator.

Duration and intensity of response

The generalized decrease in feeding rate and increase in moving rate of juvenile salmon after exposure to the decoys was quantified and is shown in Table 4. During the period following exposure, the feeding rate of juvenile salmon decreased by 25–39% and the moving rate increased by 123–386% (2.2–4.8 times more than the initial rate) on a long and a short temporal scale, respectively. Considering that the feeding rate stays lower during the entire 10-min period following predator exposure (Figs. 2a, 2c, and 2d), data from the 10-min temporal scale were used to quantify the change in feeding rate. However, we observed that the moving response is a short-lasting reaction (1–2 min; Figs. 3a, 3c, and 3d), which could be hidden by a longer temporal scale comparison. As a result, we quantified the change in moving rate using data from the short temporal scale, 1 min before and 1 min after exposure to the predator.

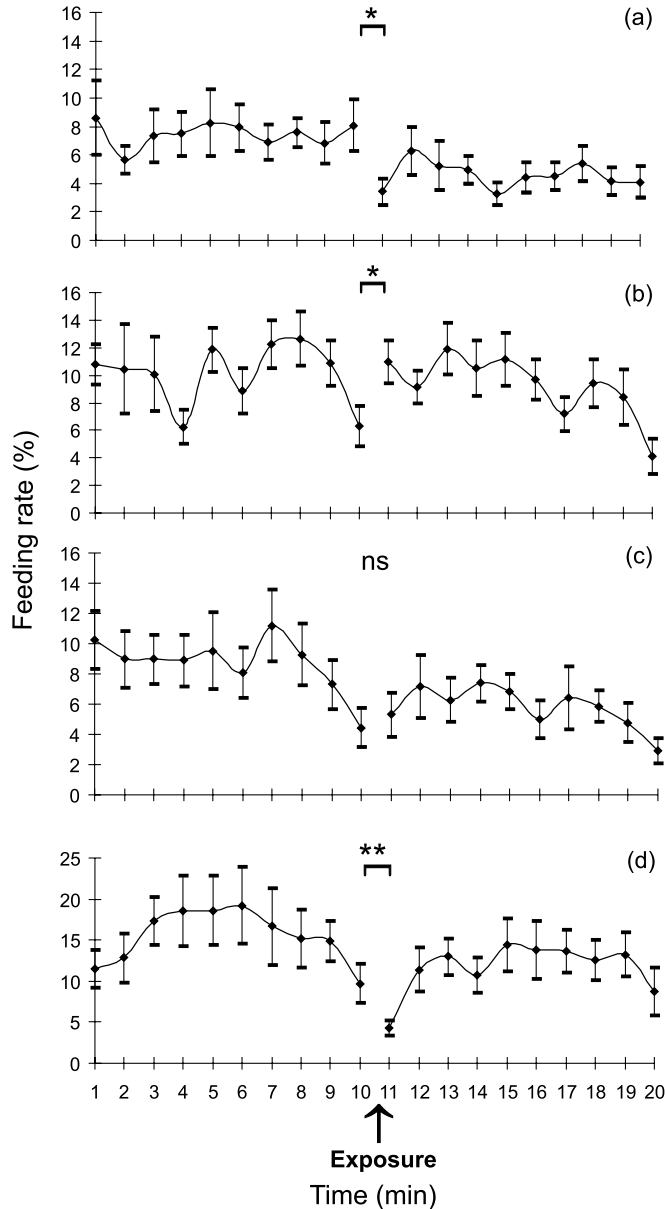
Discussion

We evaluated the importance of specific biological and environmental factors on the behaviour of juvenile salmon faced with the threat of predation in a natural environment. This research has demonstrated that juvenile salmon detect a potential predator and react so as to decrease their risk of predation. This response changes with body size and appears to be influenced by sediment size, an environmental variable that is important in habitat choice made by juvenile Atlantic salmon (Tremblay et al. 1993).

Response of salmon to predator exposure

In general, fry and parr decreased their feeding rate by 25–39% of their initial rates for the entire duration of the post-observation period and they increased their moving rate by 2.2–4.8 times their initial rate during the 1 min following exposure to the predator, results that support our predictions. The differences in behaviour of the fry exposed to the predator and the fry exposed to the branch indicate that they discriminated between a potential predator and a harmless floating stimulus. The differences also suggest that juvenile salmon can adjust their activity rate as a function of the level of risk they encounter. Similar results were obtained by Dill and Fraser (1984) with juvenile coho salmon exposed to a rainbow trout, *Salmo gairdneri*, by Gotceitas et al. (1995) with Atlantic cod, *Gadus morhua*, exposed to passive or actively foraging predators, and by Roussel and Bardonnnet (1999) with brown trout exposed to different sizes of bullheads, *Cottus gobio*, their predator.

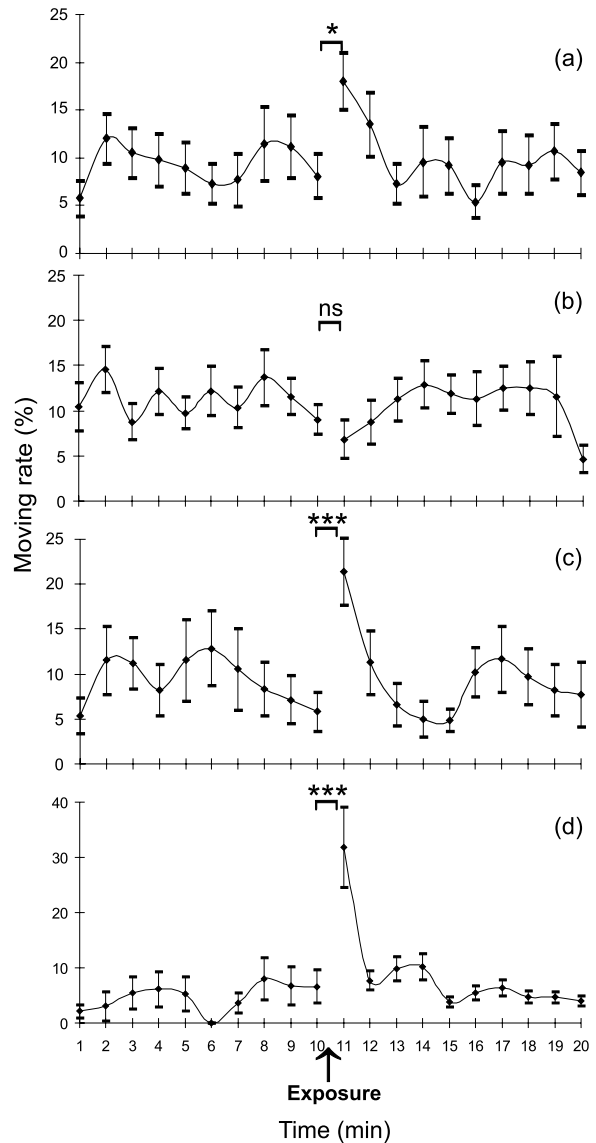
Fig. 2. Proportions of time per minute spent feeding (mean \pm SE) by fry on coarse sediment exposed to the predator (a), fry on coarse sediment exposed to the branch (b), fry on fine sediment exposed to the predator (c), and parr on coarse sediment exposed to the predator (d). The exposure occurs between the 10th and 11th minutes. Note that the scale on the y axis is different in d. ns, not significant; *, $P < 0.05$; **, $P < 0.01$.



Feeding response

In general, feeding forces the salmon to swim closer to the surface, which may increase the risk of being detected by a visual predator (Dill and Fraser 1984; Gotceitas and Godin 1991). In this case, decreasing the feeding rate might be an important antipredator behaviour for juvenile salmonids (Magnhagen 1988; Angradi 1992), representing a trade-off between optimizing net energy intake and decreasing the risk of being detected by predators (Holierhoek and Power 1995; Martel 1996). A decrease in feeding rate was also obtained in a laboratory setting by Metcalfe et al. (1987) and

Fig. 3. Proportions of time per minute spent moving (mean \pm SE) by fry on coarse sediment exposed to the predator (a), fry on coarse sediment exposed to the branch (b), fry on fine sediment exposed to the predator (c), and parr on coarse sediment exposed to the predator (d). The exposure occurs between the 10th and 11th minutes. Note that the scale on the y axis is different in d. ns, not significant; *, $P < 0.05$; ***, $P < 0.001$.



Angradi (1992), the latter observing a 36% reduction in foraging rate 2 min after exposure to the predator. However, our observations do not support the laboratory studies of Martel (1996) and Reinhardt and Healey (1997), who observed no change or an increase, respectively, in the feeding frequency of coho salmon during the period of predation. However, in the first experiment, salmon were only exposed to the scent of real mergansers and they had short feeding behaviours (<1 s) limited by the observers' reaction time. In the second experiment, hunting mergansers were used but brushy cover was provided to coho salmon so that they could take refuge and continue to feed in security.

Moving response

The increase in moving rate observed during 1 min after exposure to the predator could be an adaptive response enabling the fish to lose the predator by fleeing its territory, as a fast-moving target becomes difficult to follow for a visual predator (Donnelly and Dill 1984; Holierhoek and Power 1995). However, others argue that the risk of detection is enhanced by fish movements (Martel and Dill 1995; Martel 1996). An increase in moving rate was also observed by Reinhardt and Healey (1997) with coho salmon exposed to *M. merganser*. However, our results differ from those of Martel and Dill (1995), who used a transparent Plexiglas enclosure to hold coho salmon while they were exposed to the predator. This environment, more restricted than the natural environment, may explain the divergence in the results.

Effect of sediment size

Sediment size influences the type of response observed immediately after exposure to the predator. In habitats where hiding places are scarce, owing to the small grain size of the substratum, remaining motionless may constitute an effective immediate antipredator response. Fry could hide better by matching the colour of the background (Holierhoek and Power 1995; Martel 1996). If so, juvenile salmon may decrease the risk of being detected and (or) captured by an avian predator by choosing an environment with a specific sediment size. However, sediment size did not influence feeding or moving rates on a long temporal scale after salmon were exposed to a predator, which only partially supports our predictions. The difference between selected sediment sizes in our experiment may not have been great enough to detect a significant long-term difference in fry response. In addition, although water depth and velocity were similar at both selected sites, other factors such as light orientation towards the river might have influenced the results.

Effect of body size

The amplified moving response of parr compared with fry after exposure to the predator suggests that body size influences the escape response of juvenile salmon to predator exposure. Larger salmon may be more visible and more easily detected by avian predators than smaller ones (Magnhagen 1988) and thus may need to move more than fry do to escape and lose avian predators. Some argue that parr have a better predator-evasion capability than fry in general (Healey and Reinhardt 1995). Some authors also observed a behavioural difference between coho salmon of different body sizes exposed to predation threat. Larger fish would take less risk than smaller ones, possibly to protect their greater accumulated fitness value (Reinhardt and Healey 1999). This is also supported by various foraging models (e.g., Brown 1988; Clark 1994). Previous predation-risk experiences may also affect the behaviour of salmon (Dill and Fraser 1984) and may explain in part the marked moving reaction of parr towards potential predators.

We conclude that juvenile salmon decrease their feeding rate and increase their moving rate when threatened by a potential avian predator. This response is dependant on ambient environmental conditions, indicating that in order to take these conditions into account, field experiments should be conducted to complete and complement laboratory studies.

Sediment size influences the immediate behaviour of salmon towards predators and may be of great importance in the habitat choice of the fish under different levels of avian predation threat. Fish of different body sizes differ by having specific physical and physiological characteristics and also by having different previous experiences. As a result, wild fish would be preferable for these behavioural experiments. Considering that piscivorous birds such as *M. merganser* are territorial and that they move and feed in the same area of a river, predation pressure may be highly site-specific and the impact of predation on the activity of juvenile salmon may be intensified accordingly. It would be interesting to evaluate when feeding activity in nature is restored to its initial rate and if the feeding rate may even exceed the initial rate to compensate for the energy lost while avoiding the predator.

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