

Feeding and aggressive behaviours in juvenile coho salmon (*Oncorhynchus kisutch*) under chemically-mediated risk of predation

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Summary. Juvenile coho salmon (*Oncorhynchus kisutch*) spend the first year of their lives in their natal streams, where they may often hold feeding territories. They also face significant risk of predation by birds and fish, and should alter their behaviour to reduce risk of mortality when these predators are present. Although there is laboratory evidence that coho react to predator visual stimuli, chemoreception of avian predator presence has not previously been reported. We tested the influence of chemical stimuli of common merganser (*Mergus merganser*), preying on juvenile coho, on two aspects of coho territorial behaviour, foraging and aggression, in flow-through aquaria. After a mixture of merganser- and coho-conditioned water was introduced into the system, juvenile coho significantly reduced their attack distance on drifting prey. The fish also significantly decreased their aggressive behaviour directed towards mirrors (total number of acts, intensity of acts and time spent) when the same odour was present. They did not change their behaviour in either experiment after control introductions of water treated with fish alone. These results are interpreted within the framework of a trade-off between juvenile growth and mortality.

Introduction

Juvenile coho salmon (*Oncorhynchus kisutch*) characteristically spend their first year after emergence in streams, where they often hold feeding territories, foraging mainly on drift and sometimes on benthos (Chapman 1962; Hartman 1965; Dill et al. 1981; Puckett and Dill 1985). These streams are often shallow and subject to rapid changes in turbidity. Although vision has typically been used as the channel of presentation of predator stimuli in experiments involving salmonids (e.g. Dill and Fraser 1984; Metcalfe et al. 1987; Rosenau and McPhail 1987; Magnhagen 1988; Swain and Riddell 1990; Gotceitas and Godin 1991), it is unlikely to be their only mode of sensory perception of predation risk. Vision may con-

vey accurate information about predator spatial location and behaviour but it can be restricted to short distances, depending on the turbidity. Chemoreception, on the other hand, may provide information about the presence of predators at longer distances, although its use in detecting spatial location will be limited by the direction of water movement in streams. This sense can in some instances supply information about some predators' recent diet (e.g. Keefe 1992). Chemoreception plays an important role in salmonid life history (e.g. Cooper and Hirsch 1982) and has been shown to be well developed in juvenile coho (e.g. Hara 1972; Quinn and Busack 1985; Rehnberg et al. 1985). Under laboratory conditions, coho parr avoided rinses of a piscine predator (Rehnberg and Schreck 1987).

When presented with models of predators, juvenile salmonids alter their foraging patterns in a way that minimizes their risk of detection. Both juvenile coho and Atlantic salmon (*Salmo salar*) decrease their attack distances on drifting prey items when shown a model of a trout (Dill and Fraser 1984; Metcalfe et al. 1987) or a kingfisher (Gotceitas and Godin 1991). Common merganser ducks (*Mergus merganser*) routinely patrol streams inhabited by coho and represent a significant risk of predation for these fish (Munro and Clemens 1937; Mace 1983; Wood 1987). Juvenile coho should therefore be sensitive to merganser presence, and they should be able to detect these birds through chemoreception. Based on previous studies, we hypothesized that juvenile coho will travel less far to intercept prey when merganser odour is present than when it is absent. Throughout this paper, we use "odour" ("olfaction") and "chemical cues" ("chemoreception") interchangeably.

Most investigations on the influence of predation risk on behavioural decisions have tested hypotheses about patch use, vigilance and escape activities (for a recent review see Lima and Dill 1990). Intraspecific aggression is one of the most attention-grabbing activities an animal can engage in, and it is likely that predation risk has also exerted selection pressure on the agonistic behav-

itorial repertoire of many species. Like most juvenile salmonids (e.g. Chapman 1962; Kratt and Smith 1979; North 1979; Abbott and Dill 1985; Davis and Olla 1987; Grant and Noakes 1988), coho parr show high levels of intraspecific aggression. Parr are also naturally cryptic (Donnelly and Dill 1984), and are more likely to elicit attacks from common mergansers when moving than when stationary (G. Martel and L.M. Dill, submitted). We therefore also predicted that these fish would decrease the frequency, duration and intensity of their aggressive behaviours when confronted by cues of merganser presence and predatory activity, namely chemical stimuli from a merganser preying upon the fish's conspecifics.

Materials and methods

Apparatus. Trials were conducted indoors at the Simon Fraser University, Burnaby, B.C. Animal Care Facility in flow-through tanks ($92 \times 47 \times 39$ cm, water depth kept at 20 cm) modified from those described by Soluk and Collins (1988) (Fig. 1). Four identical tanks were enclosed in a $3.6 \times 1.8 \times 2.4$ -m metal frame surrounded by black curtains. On top of the frame was a 60-l header tank which provided water to the experimental tanks. Each tank was surrounded on three sides by black construction paper ('sp' in Fig. 1) and had a grid on a white background positioned below its transparent floor. Three hinged mirrors (14×6.5 cm) were affixed to the floor of each tank 2 cm from the side farthest from the blind. During trials, a camera was inserted through a hole 1.2 m directly above the middle of the tank. Dark plastic tubes of the same diameter as the camera lens were placed in the holes when trials were not in progress. Water flowed into each tank from the header tank through a dark Tygon tube (feeding tube, Fig. 1) and out a drain at the opposite end of the tank. Mean turn-over time of the 64-l volume was 30 min. Food items could be inserted through a Y-connection grafted to the feeding tube approximately 50 cm above the tank and concealed behind a blind. Live brine shrimp (*Artemia salina*) thus injected were neutrally buoyant and usually drifted

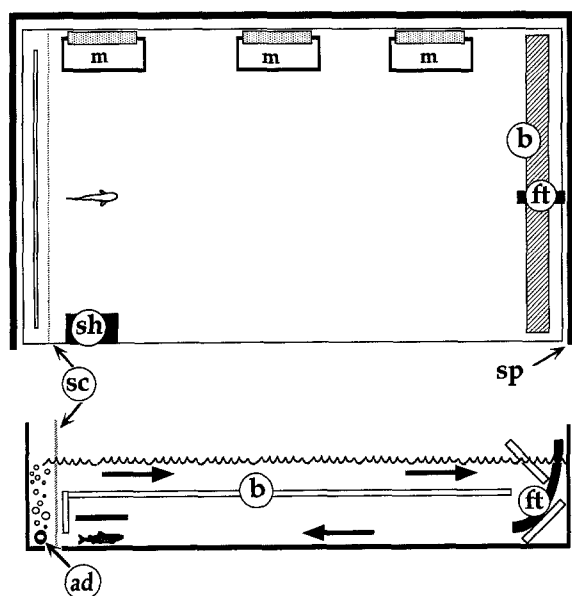


Fig. 1. Views from above and the side of a flow-through tank used in these experiments. *m*: mirrors (shown down), *b*: clear plexiglass baffle, *sh*: shelter, *ft*: feeding tube, *sp*: side panel, *sc*: screen, *ad*: air diffuser. Arrows indicate direction of current. Fish not to scale

in a linear trajectory. Water velocity could be varied by adjusting the air pressure delivered to the diffuser, and was maintained at approximately $10 \text{ cm} \cdot \text{s}^{-1}$. The illumination cycle was 16 h light:8 h dark.

Fish. Wild young-of-the-year coho were seined in May 1991 from Moody's spawning channel, a tributary of the Cheakamus River, B.C., and housed in an indoor tank at SFU. Prior to a trial, each fish was measured, weighed and then transferred to one of the flow-through tanks, where it was held singly. The fish's acclimation to their new surroundings took on average 2–4 days, and was considered complete when they fed readily on brine shrimp injected through the feeding tube at random intervals throughout the day. During the trial period, each fish was fed 15% of its wet weight in white worms (genus *Enchytrae*) at the end of each day. The same fish were used for both prey attack distance and aggression experiments. We used 19 fish (mean \pm SE = 45.8 ± 3.9 mm Total Length) in the attack distance experiment and 16 fish (46.3 ± 2.9 mm TL) in the aggression experiment (three did not behave aggressively enough in the apparatus).

Odour treatments. Odour treatments were of three types: fish (conspecific), predator and no odour. Fish odour was prepared by letting three juvenile coho (approximately 80 mm TL) of hatchery stock rest in 1 l of filtered water (the same water used in the tanks) for 30 min. At the end of this period, the fish were gently removed, and the water was chilled to the same temperature as that of the fish tanks, if necessary (throughout the trial period, water temperature varied between 10.5 and 13.5°C). Predator odour was similarly prepared, except that at the end of the 30-min period a tame common merganser was allowed to seize, manipulate and (sometimes) ingest some of the fish. After 1 min, the bird's head was rinsed three times with the same water. Thus, "predator" odour actually represents a mixture of fish and bird odours. Fish and birds were handled with nets and rubber gloves rinsed in freshwater. The "no odour" treatment consisted of filtered water, chilled if necessary. Each experimental fish tested was subjected to one treatment per day over 3 consecutive days. The order of the treatments was drawn randomly for each experimental fish.

Prey attack distance. Trials were conducted in June and July 1991, between 1400 and 1630 hours. A video camera was installed above a tank 20 min prior to the start of the trial. Preliminary trials had shown this to be a sufficient time to minimize any disturbance caused to the fish. Before each trial, the readiness of a fish to feed was assessed by sending a single brine shrimp through the feeding tube. If the fish had not responded after two brine shrimp had been presented, the camera was moved to another tank. At the beginning of each trial, 100 ml of water (no odour, fish or predator) were injected through the feeding tube. The fish were then filmed until they had intercepted 15 brine shrimp (mean mass = 1.88 mg for groups of 10 shrimp, SE = 0.16 mg, $n = 10$), and the distances they moved to attack these shrimp were later measured from the videotapes. These attack distances were then averaged for each fish. Most fish assumed a stationary position within two body lengths of the screen (Fig. 1), and brine shrimp were injected only when fish were within 1.5 body lengths of their customary position. All trials were stopped after 15 min (the mean trial duration was 12 min). Attack distance has been previously defined as the distance travelled by the fish from its stationary position to the prey-interception point, in the horizontal plane (Dill and Fraser 1984). In this apparatus, there was frequently a vertical component to attack distance when brine shrimp and fish were not in the same horizontal plane. This component was noted by an observer through a slit in the blind, and incorporated in the calculation of attack distance. Brine shrimp would sometimes get caught temporarily in microvortices along the bottom, and prey trajectory could thus not be accurately inferred from water velocity alone (prey were too small to be seen on videotape). We therefore could not calculate reaction distances (i.e. distances from which fish actually began their attack).

Aggression. Aggressive behaviours (Table 1) were stimulated with mirrors, since juvenile coho readily engage in agonistic activities towards mirror-images (Rosenau and McPhail 1987; Swain and Riddell 1990). In the aggression trials, a camera was installed above the tank as previously described. Each fish was fed one brine shrimp at the beginning of each trial. After 1 min, all three hinged mirrors (Fig. 1) were raised with monofilament lines so the fish could see its reflection. Timing started when the first aggressive behaviour was directed towards any of the mirrors (usually within 1 min). After 15 min, 100 ml of either fish- or predator-conditioned water were injected through the feeding tube. Trials ended after 30 min. The frequency and duration of aggressive interactions at each mirror, and the time spent within one and two body lengths of the mirrors, were later transcribed from the videotapes, and compared between the 15-min periods before and after introduction of the odour. We also ranked the behaviours seen in terms of aggressive intensity. We followed the scheme used by Mason (1966) for this species, except that we included an additional behaviour, "swim against mirror"; we ranked this as being between a nip and a charge in terms of intensity.

Results

Prey attack distance

Prey attack distances varied significantly between treatments (Friedman's test $\chi_r^2 = 20.63$, $P < 0.0001$). Exposure to predator-conditioned water caused a significant decrease in attack distance, whereas there was no significant

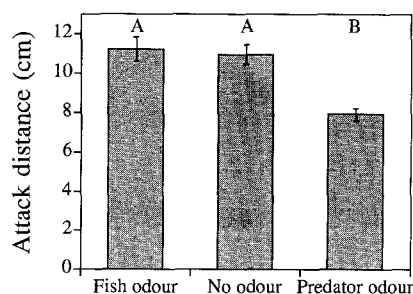


Fig. 2. The influence of odours on mean attack distance (\pm SE) of juvenile coho salmon. Means with different letters are significantly different ($P < 0.01$, Tukey's procedure modified for ranked data, Zar 1984), $n = 19$

difference in behaviour in fish-conditioned and filtered ("no odour") water (Fig. 2). In some instances, the reaction to the predator-conditioned water was striking: in the first few minutes following the injection of the water some fish remained totally stationary and did not take food items even if these hit them. However, fish not already under the shelter did not move there in response to the introduction of the odour.

Aggression

Exposure to predator-conditioned water, but not to fish-conditioned water, significantly depressed the total

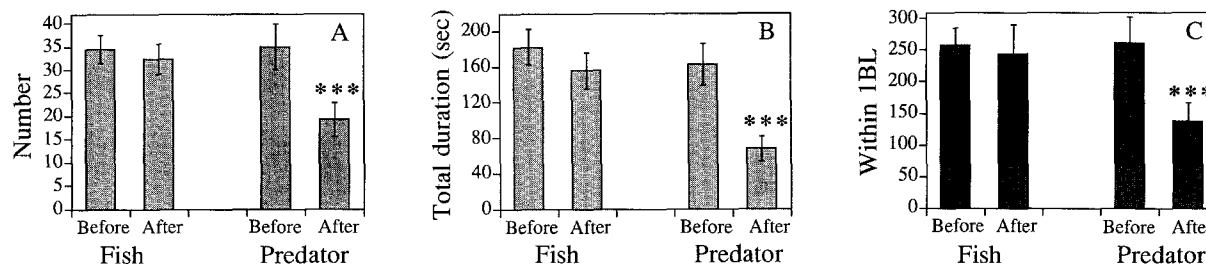


Fig. 3A-C. The influence of fish- or predator-odour treatment on mean aggression parameters (\pm SE) of juvenile coho salmon. All measures pertain to all mirrors combined. *Fish*: fish-conditioned water, *Predator*: predator-conditioned water. A Number = total number of aggressive behaviours; B total duration = total duration (sec) of all aggressive behaviours combined; C within 1BL = total time (s) spent within one body length of mirrors. *** = $P < 0.001$ (Wilcoxon's signed-rank test, two-tailed: A: $z = -3.52$, B: $z = -3.52$, C: $z = -3.36$). $n = 16$

Table 1. Mean percent of their agonistic time budget juvenile coho devoted to various aggressive activities before and after injection of merganser odour

Behaviour	Percentage of time spent in aggressive activities			
	Before predator odour ($n = 16$)	After predator odour ($n = 13$)	<i>U</i>	<i>P</i>
Nip ⁵	1.46	0.00	52	<0.01
Swim against mirror ^{3, 4, 5}	53.98	39.55	65	<0.05
Charge ^{2, 5}	1.64	2.59	—	—
Lateral display ^{4, 5}	11.80	5.99	89	0.26
Facing mirror ^a	5.06	2.34	69	<0.05
Approach ^{1, 2, 5}	26.09	49.49	—	—

Behaviours are ranked in decreasing order of intensity. *P* = significance of one-tailed Mann-Whitney *U*. Changes in the direction opposite to that predicted were not tested

^a "Facing mirror" is defined as the fish being perpendicular to and within one body length of the mirror, either stationary or slowly moving back and forth, usually with mouth open. For definitions of the other behaviours, refer to ¹ Dill 1978, ² Kratt and Smith 1979, ³ Rosenau 1984, ⁴ Swain and Riddell 1990, ⁵ Taylor and Larkin 1986

number of aggressive behaviours (by 44.9%, Fig. 3a), the total time engaged in these actions (by 58.2%, Fig. 3b) and the total time spent within one body length of the mirrors (by 47.4%, Fig. 3c). Fish also changed the relative composition of their aggressive interactions: they significantly reduced the proportion of their time budget allotted to nipping and swimming against mirror, the most intense activities. They also increased the proportion of time devoted to approaching, the least intense form of aggression (Table 1). The fish also significantly reduced the average duration of their agonistic behaviours when exposed to predator-conditioned water (4.7 ± 0.3 s vs. 2.7 ± 0.4 s, Wilcoxon signed-ranked z corrected for ties = -2.98 , $P=0.003$). Three fish did not show any aggressive behaviour after the merganser odour was injected, and thus are not included in the "after" part of this analysis.

Discussion

Juvenile coho salmon significantly reduced their prey attack distance when exposed to predator-conditioned water. Previous studies have shown that juvenile coho (Dill and Fraser 1984) and Atlantic salmon (Gotceitas and Godin 1991) presented with visual models of predators similarly reduce their prey attack distances. Juvenile pink salmon (*O. gorbuscha*) facing live predators also reduced their food intake (Magnhagen 1988). This is the first time, however, that chemoreception has been shown to mediate this type of response in salmonids. It is unlikely that the fish used in the current experiment were reacting to injured conspecific odour alone. Adult and juvenile coho sometimes show a fright reaction (Brett and MacKinnon 1954) thought to be mediated by two amino acids present in mammalian skin, L-serine (Idler et al. 1956) and L-alanine (Rehnberg et al. 1985), but our experimental procedures precluded such contamination of the water (see Materials and methods). To our knowledge, the presence of these two amino acids has not been reported in birds, but if they are present in merganser skin it could explain our results. The fish were probably not responding to alarm pheromones ("Schreckstoff"; von Frisch 1938); such pheromones are contained in epidermal cells and released when the skin is broken, but there is no report in the literature suggesting the presence of such cells in any salmonid (Pfeiffer 1977; Smith 1992). The fish may, however, have reacted specifically to the combination of chemical stimuli released by predator and injured prey. Some invertebrates have been reported to show stronger avoidance behaviours (Alexander and Covich 1991) or reduced feeding (Appleton and Palmer 1988) when exposed to water from predators feeding on prey conspecifics than to water containing only predator cues. We did not test for the effect of merganser chemical stimuli alone, and it is thus possible that coho may react strongly only to the scent released by a merganser attacking salmon. Such a mixture would give more reliable information about impending predation risk than the odour of either merganser or injured conspecific alone. For example, juvenile brook trout (*Salvelinus fontinalis*) avoided water

conditioned by Atlantic salmon fed on fish but not water conditioned by salmon fed on mealworms (Keefe 1992).

Prey attack distance decreased by about one body length in the presence of predator-conditioned water. This is comparable to the reduction in attack distance observed by Dill and Fraser (1984) when coho parr were presented with a model of a trout (a salmon predator) every 20 min. This 'lost' distance can be viewed in terms of lost opportunity cost and risk of mortality. Juvenile coho hold feeding territories which are frequently intruded upon by either territorial neighbours or non-territorial fish (Puckett and Dill 1985). It is probable that the failure to attack food items beyond a certain distance translates into a loss of energy (and consequently growth) due to interception of food by competitors.

On the other hand, a decrease in movement when an avian predator is nearby reduces the risk of detection, which should translate into reduced risk of mortality (G. Martel and L.M. Dill, submitted). For juveniles of species such as coho salmon, rapid growth is probably at a premium: after their first year in freshwater, coho typically migrate to sea, and larger smolts may enjoy a higher rate of survival there (Mathews and Buckley 1976; Bilton 1978; Olson 1978; Bilton et al. 1982; but see Holtby et al. 1990). Juvenile coho should therefore maximize their growth rate in freshwater, and should be particularly sensitive to this trade-off between growth and mortality (Gilliam 1982; Werner and Gilliam 1984). If juvenile coho are sensitive to such a trade-off, they should attack prey at shorter distances (i.e. accept less risk) when competitors are absent (when the mirrors are kept down) than when competitors are present (mirrors up), given the same perceived risk of predation. There is indeed evidence that this is the case (Dill and Fraser 1984).

When merganser-conditioned water was injected into their environment, juvenile coho also significantly reduced the frequency of their aggressive activities, the amount of time engaged in such activities, the amount of time they spent near mirrors, and the average intensity of their aggressive behaviours. Although the experimental fish always faced "competitors" performing the same behaviours simultaneously, we feel justified relating our results to field situations, as there is evidence that results obtained from mirror tests are a good predictor of aggressive interactions between juvenile coho in natural settings (Swain and Riddell 1991, and references therein).

In juvenile salmonids, proximity to conspecifics is not necessarily dictated only by agonistic motivation. Indeed, when predators are nearby, fish sometimes form "fright huddles" (Mason and Chapman 1965), and territorial juvenile coho have been observed to do this when mergansers are detected upstream (G. Martel, unpubl. obs.). However, in the laboratory, any time spent in close proximity of the mirror is likely to have reflected aggressive motivation alone: time spent within one body length of the mirrors decreased when merganser-conditioned water was injected into the system.

Aggressive, territorial coho grow faster than non-territorial individuals (Martel 1992), probably as a result

of increased access to food. Thus, the ultimate benefit of aggression in this and other salmonid species (Li and Brocksen 1977; Fausch 1984; Metcalfe 1986) is improved individual growth. However, aggression has costs as well, since the movement associated with agonistic interactions appears to increase the probability that the fish will be detected by predators (G. Martel and L.M. Dill, submitted). Our results provide evidence that juvenile coho salmon adjust their behaviour when a change in predation risk alters the balance of this trade-off: fish committed less time to aggression when they sensed merganser odour, and the agonistic behaviours they did display were of lower intensity.

Additional tests of a trade-off between mortality risk and growth in juvenile coho are possible. Perceived mortality risk could presumably be affected by varying the concentration of merganser odour, but a detailed study of the chemoreception thresholds of coho would have to be conducted first (e.g. Rehnberg et al. 1985). Competitor density (and thus, the cost of failure to behave aggressively enough) could be altered by varying the number and placement of mirrors.

In another study, territorial juvenile coho decreased their aggression levels in the field when mergansers they could not see were upstream (Martel 1992). Because intrusion rate on the territories could not be monitored independently, it was not possible to determine whether merganser odour had a direct effect on the territory owners, or if its effect was indirect through a reduction of the intrusion rate of conspecifics (i.e. fewer attacks could have reflected fewer intrusions). Although predation risk may affect other fish, and hence intrusion rate, our results now enable us to conclude that, in the case of juvenile coho salmon, it also affects directly the agonistic behaviour of territorial fish.

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