INFLUENCE OF PREDATION RISK ON THE TERRITORIAL BEHAVIOUR OF JUVENILE COHO SALMON, *ONCORHYNCHUS KISUTCH.*

by

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Abstract

Most juvenile coho salmon (*Oncorhynchus kisutch*) spend the first year of their lives in streams before smolting and going to sea, where they spend two to three years before coming back to freshwater to spawn. There are some indications that larger fish at smolting time may subsequently suffer less mortality at sea. In as much as their survival in saltwater influences their future reproductive success, juvenile coho should therefore be selected to optimize their growth in freshwater, i.e. to maximize their growth without unduly compromising their survival. In this thesis I first show that feeding territoriality is a foraging tactic through which these fish increase their growth rate over that of non-territorial conspecifics.

A high growth rate usually entails a high foraging rate, and young salmon seeking or defending food may expose themselves to predators. They therefore face a tradeoff between food intake and mortality risk. Territoriality, as a foraging tactic, should thus be affected by predation risk. The main purpose of this thesis was to examine how variation in risk of predation influences the territorial behaviour of juvenile coho. I chose common mergansers (*Mergus merganser*) as predators because they are likely to have exerted strong selection pressure on these fish over evolutionary time.

Marked territorial coho were observed under semi-natural conditions (in enclosures built in a spawning channel) and exposed to temporal and spatial variation of merganser presence, which they could smell but not see. The fish reacted to the predators' presence by reducing their movements and decreasing the average duration of, and the percentage of their time budget devoted to, agonistic interactions. A reduction in movement while under an increased risk of predation is adaptive only if it reduces the probability of detection by predators, and therefore if prey motion is an important cue used by mergansers to detect prey. This was tested under

laboratory conditions: the birds attacked moving fish significantly more often than stationary ones, regardless of the fish' size.

It could not be ascertained whether the territorial fish were less aggressive in the field study because they simply had fewer opportunities to be, or because they responded directly to the predators' presence. I therefore tested the direct effect of merganser odour on the fish's aggressive behaviour in the laboratory, by measuring the frequency and intensity of coho aggressive behaviours directed towards mirror images. When merganser odour was present, all measures of aggressive behaviour were significantly reduced.

Overall, this thesis shows that territorial behaviour affects both sides of the tradeoff between growth and mortality faced by juvenile coho. While territorial fish grow faster, they also act in ways that increase risk of detection by predators, and perhaps compete for time which could be used to increase vigilance for predators.

Dedication

Pour Marianne. De la façon la plus profonde, il s'agit de son oeuvre...

Quotations

...Je voudrais pas crever

Avant d'avoir connu

Les chiens noirs du Mexique

Qui dorment sans rêver

Les singes à cul nu

Dévoreurs de tropiques

Les araignées d'argent

Au nid truffé de bulles

Je voudrais pas crever

Sans savoir si le soleil est froid

Si les quatre saisons

Ne sont vraiment que quatre...

Boris Vian

O caminho da Tradição não é o caminho dos poucos escolhidos, mas o caminho de todos os homens. E o Poder que você pensa que tem não vale nada, porque não é um Poder que se divida com os outros homens.

Paulo Coelho

Acknowledgments

One of the main aspects which will always stand out for me about my time at SFU is ...well just that, my *time*. So it is only fitting that these acknowledgements have a chronological bent. Time is money, and that alchemy was performed for my benefit through scholarships from SFU (the Open and Graduate Fellowships) and NSERC, various t.a.ships, the Clements Fund, plus research funding coming from the R.H. Wright Fund and Larry Dill's NSERC grant (these four magic numbers which opened, among others, the vaults of the Science Store).

Throughout my stay I have had the good fortune of basking, both figuratively and literally, in an impressive shadow. Although Larry had to appoint himself stout defender of the English language against my repeated assaults, he was always supportive, fiscally and intellectually. He also had the most annoying habit of anticipating most of my needs, even if these included the occasional jolt. If respect is a currency, Larry must be a rich man indeed. Alex Fraser is GOD (Grand, Omnipresent and Dependable) in everything except poker: he provided me with tools, logistical and administrative expertise, rides at every hour of the night, shelter and storage room, helped me to move, construct and demolish (the world of experimental biology can be a violent one at times), and knew where everything was or was going to be. The Dillerians, including their masthead, revolve around him.

My first years at SFU were much influenced by Suzan Dionne (who taught me to fight fate) and Linda Schenkeveld (who introduced me to the difficult and frustrating art of merganser rearing). The Animal Care Facility sheltered the birds while providing a unique working environment, which would have been much different were it not for the constant presence of Dick Jol and Loekie van der Wal. Merci to all the ACF work students who put on brave smiles when asked to curb the mergs during the occasional week-end. When I think about Ron Ydenberg, the word

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Chapter 1:
General Introduction

Probably the most encompassing generalization one can make about the behaviour of animals is that they all strive to feed and (eventually) to reproduce. The second most encompassing assertion is that they will be affected by some risk of predation at one time or another in their life. In as much as it affects fitness, predation risk is an important selective force, and the literature on how animal decisions are affected by predation risk is constantly growing (for a recent review, see Lima and Dill, 1990). Because of their frequency of occurrence, reproductive and especially foraging activities are most likely to be affected by predation risk. In the case of juveniles, immediate reproductive considerations are not so important. Rather, juveniles should be selected to maximize their probability of reaching reproductive age or size. In species where growth determines long term survival, juveniles might be expected to maximize their net energy intake through some foraging strategy (e.g., Schoener, 1971), so long as it does not unduly affect their short term survival.

The coho salmon (*Oncorhynchus kisutch*) is one such species where rapid growth may translate into higher survival. The juveniles usually stay from one to two summers in their natal streams before smolting and going to sea (Sandercock, 1991). There are some indications that larger fish at smolting time may subsequently suffer less mortality at sea (Mathews and Buckley, 1976; Olson, 1978; Bilton *et al.*, 1982). Juvenile coho salmon should thus be selected to attain the largest possible size, for a given cost in mortality, at the end of their residence in freshwater. Feeding territoriality appears to be a foraging tactic adopted by many juvenile salmonids in streams (e.g., Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*—Kalleberg, 1958; brook charr, *Salvelinus fontinalis*—McNicol and Noakes, 1981; coho salmon, and steelhead trout, *O. mykiss*—Hartman, 1965), and some territorial salmonids are larger, and therefore probably grow faster, than their non-territorial counterparts (e.g., Bachman, 1984; Puckett and Dill, 1985; Grant,

1990). Territoriality can thus be said to be a foraging tactic through which juvenile salmonids increase their growth rate compared to that of non-territorial fish. Territorial coho defend areas in shallow parts of streams (glides) against their territorial neighbours and against other non-territorial individuals. The latter are usually "floaters", who occupy the same area and remain in the spaces between territories (Puckett and Dill, 1985), or more rarely, non-territorial fish, who normally frequent other, deeper habitats such as pools, where they do not defend any specific area.

But a high growth rate usually entails a high foraging rate, and animals such as young salmon seeking or defending food may expose themselves to predators. They may therefore be forced to solve a tradeoff between food intake (growth) and mortality risk. A simple rule of thumb for non-reproductive animals is to minimize the ratio of mortality rate over growth or gross foraging rate (Gilliam, 1982; Werner and Gilliam, 1984; Gilliam and Fraser, 1987). The minimization of the mortality : growth ratio can be achieved either by behaving in ways which decrease the risk of mortality to which one is subjected or by increasing one's growth. The main advantage of territoriality in juvenile coho seems to be higher growth achieved through preferential access to food, usually drifting particles (Mundie, 1971; Mason, 1975; Sandercock, 1991). But it is unclear how territoriality relates to risk of mortality. Juvenile salmonids have been shown to react to the presence of predators (Dill and Fraser, 1984; Metcalfe *et al.*, 1987; Gotceitas and Godin, 1991) and like most foraging tactics, territoriality should be affected by predation risk. However, very little is known about how predation risk affects territorial behaviour, although it is generally recognized that it should be an important influence (Carpenter, 1987). Much of the emphasis of the work on territoriality so far has been on the determinants of territory size (e.g., Covich, 1976; Pyke, 1979; Norman and Jones, 1984; McNair, 1987; Schoener, 1987; Ydenberg and Krebs, 1987; Tricas, 1989), and territorial juvenile salmonids are no exception in that regard (e.g., Allen,

1969; Dill, 1978; Dill *et al.*, 1981; Noakes and McNicol, 1982; Grant and Noakes, 1987; Grant *et al.*, 1989; Gustafson-Greenwood and Moring, 1990).

In juvenile salmonids, the only study relating territoriality to predation risk of which I am aware is that of Symons (1974): Atlantic salmon parr who had been given 15 days to acclimate to a stream channel suffered less mortality from brook trout than did parr which had been installed in the system only 24 hours prior to introduction of the predators. Since parr from the 15-day treatment had established territories, Symons interpreted this result as evidence that territoriality decreased the fish' vulnerability to predation. However, as Donnelly and Whoriskey (1991) have pointed out, this result could also be explained through differences in colour acclimation or crypsis.

Any factor affecting territoriality in juvenile salmonids is bound to affect their growth in freshwater. In a commercially important species such as coho salmon, whose stream survival determines to a large extent the magnitude of the returns (e.g., Bilton *et al.*, 1982), data on the effects of predators on juvenile territoriality could be critical for management decisions. Consequently, this research was designed to investigate the effects of predation risk posed by common mergansers (*Mergus merganser*) on the territorial behaviour of juvenile coho.

I chose the common merganser as the source of predation risk because I needed a naturally occurring predator which is likely to have exerted strong selection pressure on the fish throughout evolutionary time. Common mergansers (hereafter referred to as mergansers) are just such predators: they feed almost exclusively on fish and have been reported to prey on Atlantic salmon (White, 1936, 1937, 1957; Lindroth, 1955; Mills, 1962; Erskine, 1972; Carter and Evans, 1988; Carss, 1989; Suter, 1991) and on Pacific salmon (Munro and Clemens, 1937; Fritsch and Buss, 1958; Mace, 1983; Wood, 1987). They are the merganser species most often associated with streams (Bellrose, 1976; Palmer, 1976). They usually lay their eggs from late March to mid-June

(White, 1957; Eriksson and Niittylä, 1985), and the males leave the nesting areas shortly after mating, to form moulting aggregations (Bellrose, 1976). The chicks are precocial, hatch from late May to July (White, 1957; Erskine, 1971; Erskine, 1972; Eriksson and Niittylä, 1985), and stay on their natal stream with the females for most or all of their growth period, up to early to mid-November (Erskine, 1971). In one case, Wood (1987) estimated that merganser broods consumed 25 to 65% of the salmon smolt production of a small stream on Vancouver Island.

Coho populations may differ markedly in terms of intraspecific aggression (e.g., Rosenau, 1984; Rosenau and McPhail, 1987). The first step was therefore to ensure that the population to be tested had many territorial individuals. Tagged fish were assigned to enclosures built in a stream channel and their locations within these enclosures were recorded at regular intervals over the course of a summer. It was found that some individuals did defend the same area for periods of many days, a result not previously reported in the literature, although frequently assumed. Some of these mainly descriptive data are presented in Appendix A.

My research hinges on Chapter 2, which shows the main results of an experiment conducted under semi-natural conditions, to study the effects of predator presence and intrusion rate on the territorial behaviour of juvenile coho. Predation risk was provided by two male mergansers who were introduced upstream of the territorial fish. It was assumed that chemoreception was an important sensory channel of predator detection for juvenile coho; this was later confirmed in the laboratory. In this chapter I also show that territorial juveniles have a growth advantage over floaters. Although there was no apparent effect of variation in merganser intrusion rate, the territorial fish clearly did react to the predators' presence: when mergansers were present territory owners reduced their movements and decreased the duration of their agonistic interactions.

One probable function of a reduction in movement while under a perceived risk of predation is to reduce the probability of detection by predators. This assumes that motion is an important cue used by mergansers to detect prey. This assumption was tested under laboratory conditions. Chapter 3 describes an experiment in which hatchery-reared coho were presented to mergansers over a substrate precluding crypsis. The birds attacked moving fish significantly more often than stationary ones, regardless of the fish's size.

As mentioned above, the fish tested in the field also reduced the duration of their agonistic interactions, and the percent of their time budget allocated to aggression. However, it could not be ascertained whether they were less aggressive simply because they had fewer opportunities to do so (i.e., the frequency of intrusions onto the territories may have decreased, but could not be monitored) or because they responded directly to the predators' presence, although some preliminary data on the behaviour of floaters under risk of predation (Appendix B) indicate that these fish may actually have increased their rate of intrusion onto the territories. Chapter 4 presents the results of a laboratory experiment designed to test the direct effect of merganser odour on coho aggressive behaviour. After having ascertained that wild fish taken from the field site did react to merganser odour in the laboratory (they significantly decreased the distance they travelled to intercept brine shrimp), I measured the frequency and intensity of their aggressive behaviours directed towards mirror images. When merganser odour was present, all measures of aggressive behaviour were significantly reduced. The results of these laboratory experiments enable me to state that the presence of mergansers in the field experiment directly affected the behaviour of territorial juvenile coho.

Because territorial fish are larger than other fish, they may be easier for mergansers to detect . If this is the case, territoriality may actually carry a cost in terms of higher risk of predation. Appendix C contains the results of an experiment in which I presented to mergansers groups of

fish whose modal sizes corresponded to those of territory owners and floaters. Three male mergansers ate fish of both sizes equally, but the fish eaten by the only female tested were significantly smaller than the fish who survived. Thus, if females frequent streams more often than males in the summer months, the higher growth achieved through territoriality might reduce predation risk in the long term.

The combined results are further discussed in Chapter 5 in terms of their relevance to the growth-mortality tradeoff. This final chapter also contains some suggestions about further tests of this tradeoff, and briefly discusses the relation between mortality risk and risk of detection by mergansers.

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Chapter 2:

Territoriality and growth rate in juvenile coho salmon (<u>Oncorhynchus kisutch</u>): influence of predation risk.

Abstract

Juveniles of species in which size determines survival should be selected to optimize their growth rate. Although the monopolization of feeding territories is a common foraging tactic among stream-dwelling salmonids, the direct benefits of territoriality in terms of growth rate have yet to be demonstrated in these fish. I followed individually marked juvenile coho salmon, Oncorhynchus kisutch, for three months in enclosed populations in the field. Territorial fish grew faster than other fish (floaters) confined to the same area. Territorial juveniles face a growth-mortality tradeoff when predators are present, since the movement associated with aggressive behaviour may increase their risk of predation. When piscivorous birds (common mergansers, Mergus merganser) were present upstream, territorial coho rarely left their territories, but they did decrease the average duration of their aggressive interactions and movements, and the total amount of time they devoted to territorial activities and to moving. Some fish also allowed intruders to approach to a closer distance before intercepting them. However, there were no effects attributable to different frequencies of predator presence.

Introduction

In species where size determines survival, juveniles should maximize their net energy intake through their foraging strategy (e.g., Schoener 1971). Since reproductive considerations are not of immediate importance, such juveniles face a tradeoff between eating (growing) and avoiding getting eaten. A foraging tactic conferring greater benefits than alternative tactics in terms of growth or survival should thus spread in a population. Many stream-dwelling juvenile salmonids hold feeding territories (e.g., Atlantic salmon, Salmo salar, and brown trout, Salmo trutta— Kalleberg 1958; brook char, Salvelinus alpinus—McNicol and Noakes 1981; coho salmon, Oncorhynchus kisutch—Chapman 1962), and territoriality can thus be considered to be a foraging tactic in these fish (I use the term "tactic" as opposed to "strategy" because there is no indication as yet that some fish are genetically predisposed to be territorial ; cf. Gross 1984). However, although large individuals have in some instances been shown to be dominant over other individuals in the field (Bachman 1984; Puckett and Dill 1985; Grant 1990), there has been no empirical demonstration that territorial individuals in wild populations grow faster than non-territorial conspecifics.

Juvenile coho salmon spend their first year in streams, where they forage on both drifting and benthic prey (Chapman 1962; Hartman 1965), before migrating to sea . Individuals can be placed into one of three behavioural categories (Puckett and Dill 1985): some fish actively defend feeding territories over shallow water areas (glides) against conspecifics ("territorial"), whereas others either remain in the spaces between territories ("floaters") or occupy habitats such as pools where they do not defend any area ("non-territorial"). In this paper I provide field evidence that territorial juvenile coho salmon grow faster than floaters.

Predation risk may affect foraging by influencing patch or habitat choice, diet choice or foraging activity per se (for a recent review see Lima and Dill 1990). Juvenile salmonids modify their activities when in the presence of predators: they decrease their attack distance to prey items (Dill and Fraser 1984; Gotceitas and Godin 1991, Gotceitas and Godin in press), reduce their overall activity (Metcalfe et al. 1987; Huntingford et al. 1988) or move to other habitats (Magnhagen 1988; Bugert and Bjornn 1991). If one assumes that the defense of a territory entails a cost in either reduced vigilance for predators or increased risk of detection by predators, it follows that territory owners should reduce the intensity of their territorial activities if a predator is detected. Since leaving a territory may require future eviction of intruders (e.g., Ydenberg and Krebs 1987), even unsuccessful predator attacks, which may force fish to abandon their territories temporarily, may entail potential costs.

Common mergansers (Mergus merganser) frequently prey on coho in streams (e.g., Munro and Clemens 1937; Wood 1987). Since prey activity has been shown to influence the likelihood of attack by many vertebrate predators (e.g., Rimmer and Power 1978; Crowl 1989; Morey 1990), prey should move less when visually hunting predators are present. There is evidence that this is indeed the case (Lima and Dill 1990). I therefore predicted that territorial coho would reduce the proportion of their time budget allocated to activities involving movement, including agonistic interactions, when in the presence of common mergansers.

The presence of mergansers represents a temporal variation in predation risk for juvenile coho. But predation risk also varies through space: birds often preferentially frequent some reaches of streams. Fish holding territories in areas more prone to merganser visits than others will face a higher mortality risk than those in other stream areas (assuming equal density), and their territorial behaviour, in as much as it mediates their risk of being detected, should be affected. I therefore predicted that coho would be less aggressive in areas subjected to frequent merganser visits than in areas devoid of mergansers. If foraging affects the animals' vulnerability to predators, or if

predators restrict the use of profitable foraging areas, another possible effect of predation risk could be to lower growth rate (e.g., Werner et al. 1983), and I also predicted that coho would grow less in those areas frequented more often by mergansers.

Materials and Methods

Field site and fish

The experiment was conducted in Moody's Channel, Brackendale, British Columbia, an artificial spawning channel sustaining a wild population of coho salmon. The channel was subject to minimal human disturbance, had a fairly stable water level during the summer (receiving most of its water through underground channels from the adjacent Cheakamus River), and harboured intermittently a variety of salmon predators: great blue herons (Ardea herodias), belted kingfishers (Ceryle alcyon), American dippers (Cinclus mexicanus), common mergansers, and Pacific water shrews (Sorex bendirie) were all sighted during the summer or fall. Juvenile coho usually emerge from the gravel of the channel from mid-May to early June (pers. observations), but are not large enough to withstand tagging before early August. On August 6, 1989, some juvenile coho were seined at the site and were transferred to a temporary pen in the stream. Ninety of these fish were tagged with a unique colour combination of two sequin beads, measured (total length) and weighed before being released into one of three enclosures (see below) from August 7 to August 9. All fish in a given enclosure were released on the same day. On Oct. 9 and 10, 1989, at the conclusion of the experiment, all three enclosures were seined, and the marked fish thus caught measured and weighed.

Experimental design

Three 5 x 3 x 0.15 m enclosures (average water depth 9.5 cm), were each stocked with 30 marked young-of-the-year coho salmon. The sides facing the observers were made of clear plexiglass to allow for continuous viewing of the fish (Fig. 2.1B). The up- and downstream ends of each enclosure consisted of hardware cloth (0.5 cm mesh), allowing free passage of drifting food through the enclosures. The enclosures were spaced at intervals of approximately seven m. Before introduction of the fish, the enclosure substrates were graded so that all three pens had a similar gravel size and distribution. Fifty numbered flat rocks (approximately 100 cm^2 each) were distributed in a 10 x 5 grid pattern within each enclosure, and maps (1:500) were prepared for each pen. Each enclosure was regularly inspected and dead fish replaced with fish of the same size, to keep fish density constant throughout the duration of the experiment.

The enclosure situated the furthest upstream was used as a control, while the other two were used to examine the effect of frequency of predator intrusion (Fig. 2.1A). One of two tame male common mergansers was lowered into the water in screened cages (1 x 1 x 0.5 m), 1.5 m upstream of each enclosure, by means of pulleys operated from the bank of the channel (Fig. 2.1B). Preliminary snorkeling observations showed that it was impossible for a human observer to detect the cages from inside the enclosures once they were in the stream. To avoid any potential effect of mammalian skin secretion on the fish (salmonids have been shown to be sensitive to some amino acids peculiar to mammalian skin—Idler et al. 1956; Rehnberg et al. 1985) the birds were handled with plastic gloves. The mergansers could easily swim in the cages and readily probed the substrate through the mesh; they did not appear disturbed by their confinement or the procedure. The cages were lowered in front of all three enclosures twice a day (they were introduced between 06:00 and 07:00 and at least five hours later) and left for 20 min, but the mergansers were present only in the cages upstream of the two treatment enclosures. The middle
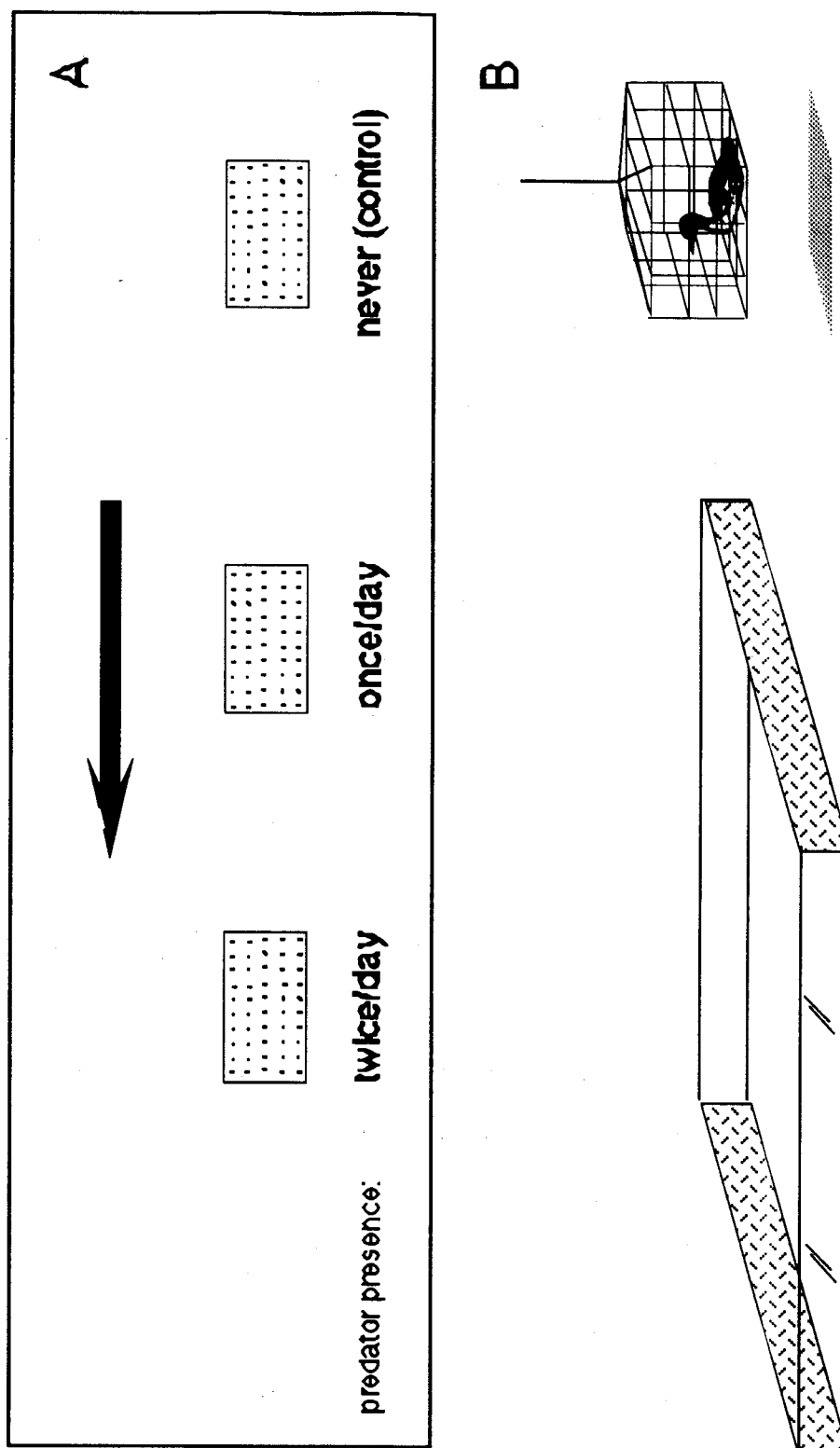
Figure 2.1. Experimental set-up. A. Spatial arrangement of the three enclosures. Arrow indicates direction of water flow. Dots inside the enclosures represent the rocks forming the grid. B. Merganser being lowered in a mesh cage upstream of the enclosures.

enclosure was exposed to a merganser once a day (around noon), and the downstream enclosure twice a day (once at the same time as the upstream one). With this spatial design, there could be no unwanted effect on one enclosure of a treatment occurring in other enclosures upstream. The two birds were assigned randomly to a treatment each day.

Time budgets of focal territorial fish were recorded on a lap-top computer (Epson PX-8) using an event-recording program modified from Unwin and Martin (1987). Each experimental day, territorial fish in one or two enclosures (depending on the availability of a second observer) were selected at random. One fish was monitored per enclosure per day. The fish were observed through binoculars from the bank of the channel for six 20 min periods distributed before, during, and up to 3 hours after the mergansers' afternoon appearance. The observation periods after the mergansers' removal were centered around periods of 30 min relative to the predators' presence (Table 2.1). Behaviours recorded are described in Table 2.2. Whenever a fish remained stationary for 15-20 sec, its position was noted on a map of the enclosure. The locations of aggressive interactions were also recorded on these maps. Time budgets of 30 fish (10 in each enclosure) were recorded in this manner. The number of fish in each enclosure was regularly monitored throughout the season, and their status (territorial or floater) and location were recorded. At the end of the experiment all fish were collected, measured and weighed again. Only fish who could be reliably classified as territorial or floaters for four or more consecutive weeks were included in the analyses. The data on fish length and weight, and aggressive distances, were normalized using Box-Cox-Bartlett transformations (Sokal and Rohlf 1981).

Table 2.1. Example of the schedule of observations on territorial juvenile coho. Each observation period lasted 20 min. All post-predator observations are referred to according to the number of minutes elapsed from the time of predator removal to their midpoint. In this example, the bird was introduced at 12:25 and removed at 12:45 h.

Nominal time relative to predator's presence	Example of time period
before (20 min before predator introduced)	11:55 - 12:15
during ("D", when predator present)	12:25 - 12:45
30 min after predator removed	13:05 - 13:25
60 min after predator removed	13:45 - 14:05
120 min after predator removed	14:45 - 15:05
180 min after predator removed	15:45 - 16:05

Table 2.2. Description of the behaviours observed in territorial juvenile coho.

| Behaviour	Description
feeding	fish darts quickly towards the surface or to the bottom, often with a snatching movement (food items could rarely be seen)
swimming	fish moves at constant speed, usually about 1 cm off the bottom; excludes aggressive interactions
aggressive interactions	fish directs one or more of the following behaviours towards another fish — approach, chase, frontal, lateral and nip (refer to Chapter 4 for more detailed description)
station holding	fish remains at the same position, usually close to the substrate

Results

Territory owners vs. floaters

Total length and weight of territorial fish did not differ significantly among the three enclosures ($F_{2,34}$ = 0.644 & 1.085 for total length in August and October, and 1.202 & 1.563 for weight in August and October; $P > 0.05$ in all cases) and all territorial fish were pooled for subsequent analyses. Floater size also did not differ among the three enclosures ($F_{2,14}$ = 1.313 & 1.036 for total length in August and October, and 0.301 & 3.19 for weight in August and October). Although territorial fish were not significantly longer than floaters at the beginning of the experiment (3.1 %, Fig. 2.2A), they were slightly heavier (13.2%, Fig. 2.2C). By the end of the experiment, territorial coho were both longer and heavier than their floater counterparts (9.5% and 31.8%, Figs. 2.2B, D), indicating that their growth rate had been greater (Fig. 2.3).

Effect of predator presence

There were no significant differences between the two treatment enclosures for any time budget variable, so pooled values of each variable were calculated. Territorial fish reacted to merganser presence: while a bird was upstream, they engaged in proportionally less movement. When all activities involving movement are grouped (feeding, swimming and aggressive interactions), the percent of the time budget devoted to movement drops significantly after the predator is introduced (Fig. 2.4). The fish also significantly reduced the proportion of their time budget allocated to aggression (Fig. 2.5) and decreased the average duration of their aggressive and swimming bouts (Fig. 2.6). They did not vary the total number of behaviours they performed (NS, Wilcoxon signed-rank, N= 20), although the number of bouts of swimming and station holding increased marginally ($P < 0.1$, Wilcoxon signed-rank, Fig. 2.7) during the predators' presence. The fish in
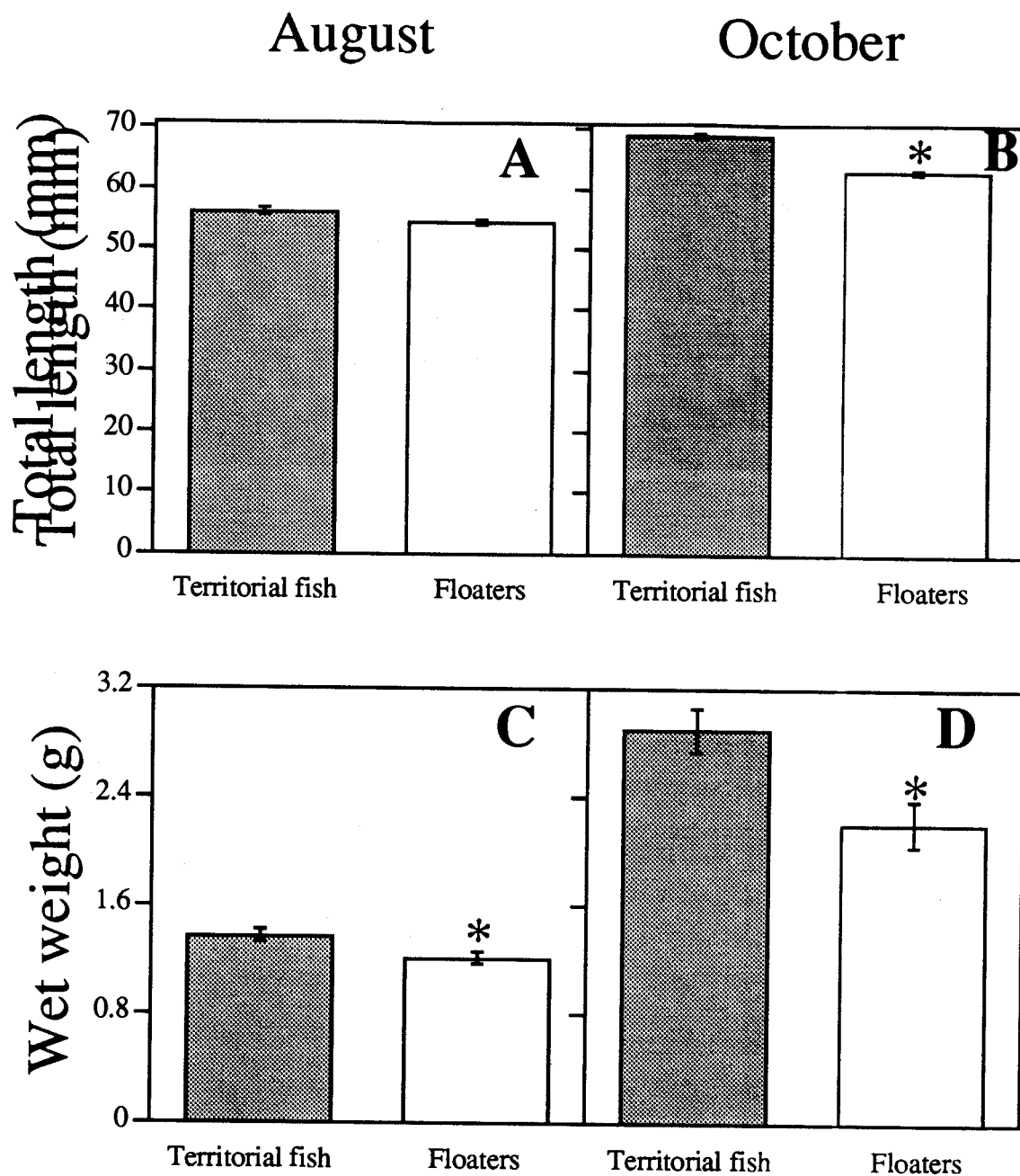
Figure 2.2. Mean total length and wet weight (± s.e.) of territorial juvenile coho and floaters at the start and end of the experiment. N = 37 for territorial fish and 17 for floaters. *: P < 0.05, t-test on transformed values (Box-Cox-Bartlett).
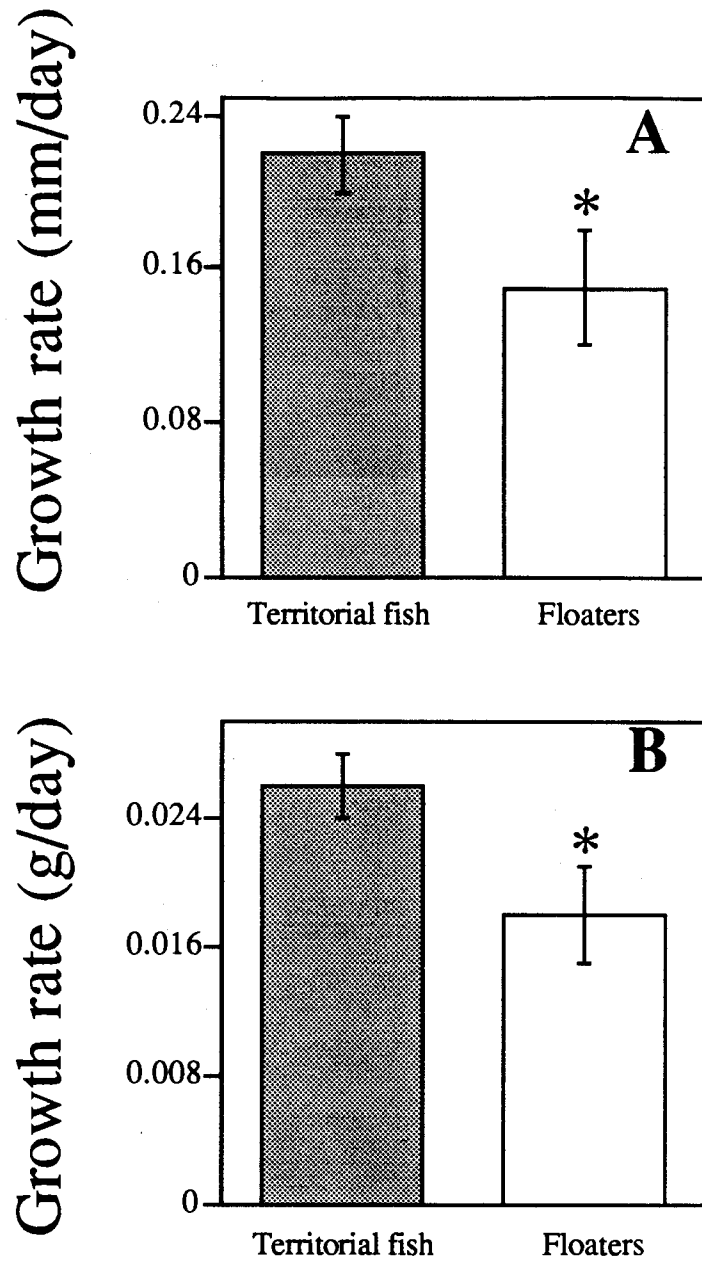
Figure 2.3. Mean growth rates (± s.e.) of territorial coho and floaters throughout the experiment. *: P < 0.05, t-test on transformed values (Box-Cox-Bartlett).
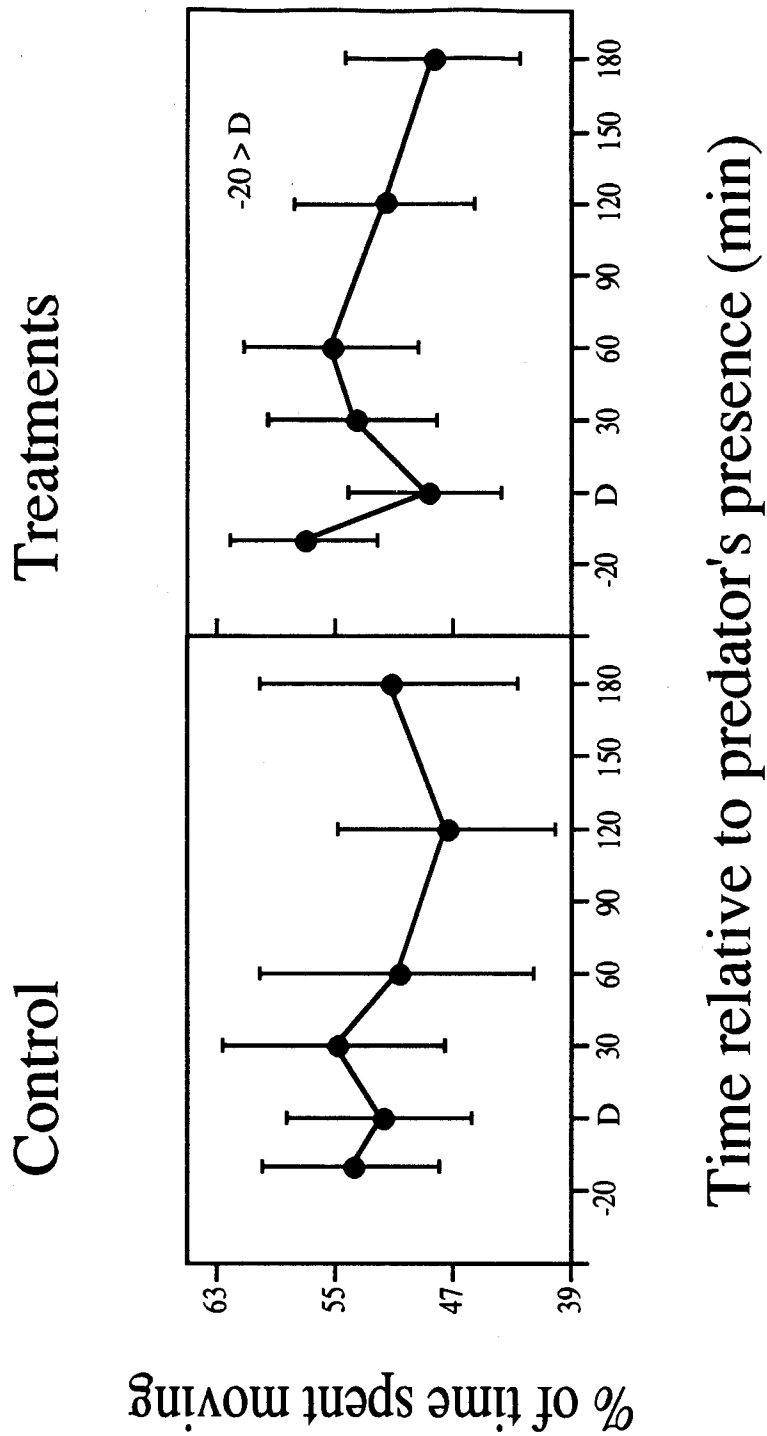
Figure 2.4. Mean percent of total time budget (± s.e.) spent in activities involving movement (refer to text) by territorial juvenile coho as a function of the time elapsed relative to a merganser's presence. Label represents the result of a paired comparison between the values of the variables before the merganser was present (t = -20) and while it was present (inequalitiy is significant at P < 0.05, Wilcoxon signed-rank test).
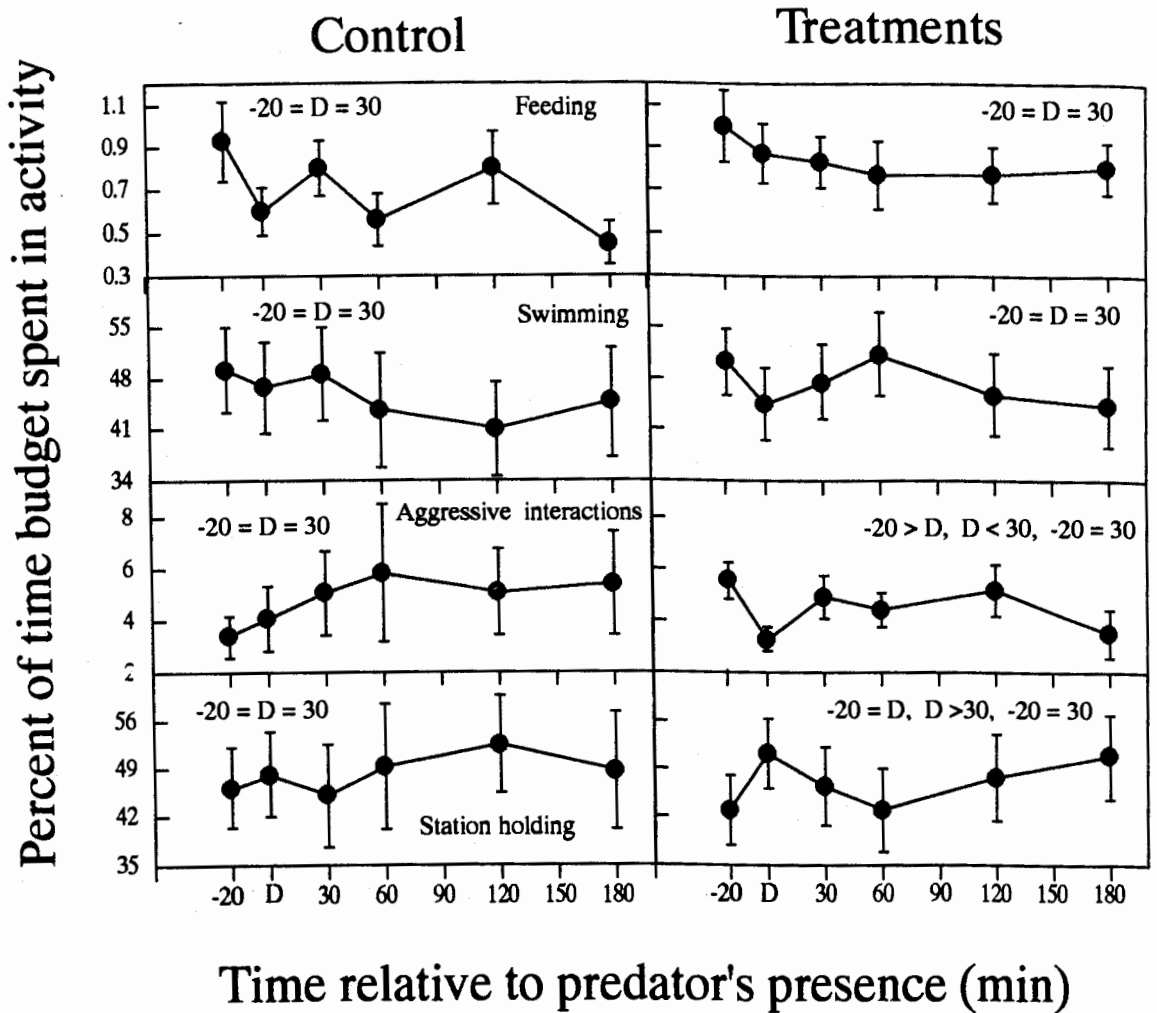
Figure 2.5. Mean percent of total time budget (± s.e.) spent in each behaviour category by territorial juvenile coho as a function of the time elapsed relative to a merganser's presence upstream (D = time during which predator present). Labels represent results of paired comparisons between the values of the variables before the merganser was present, while it was present, and 30 min after it had been removed (inequalities are significant at $P < 0.05$, Wilcoxon signed-rank test).
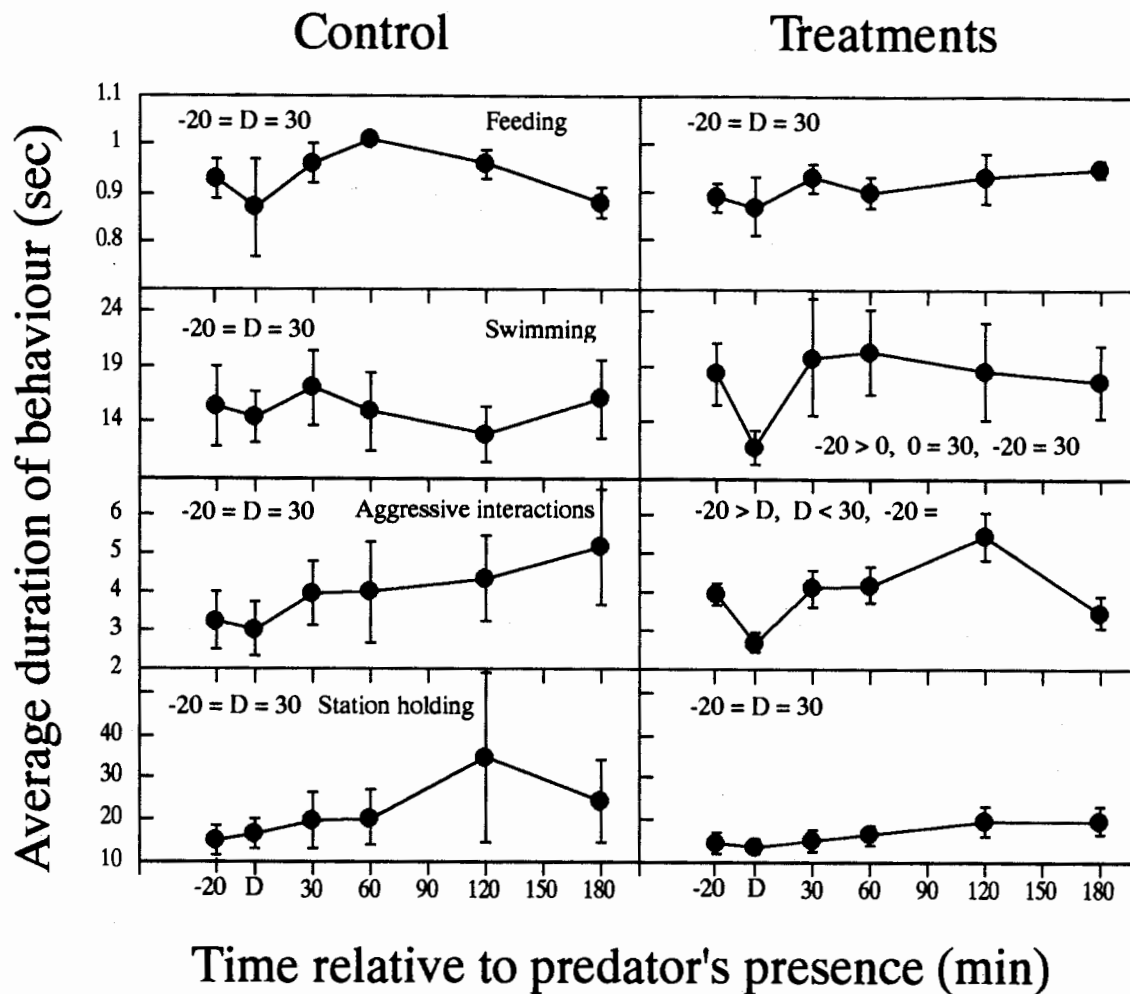
Figure 2.6. Mean duration of behaviours (± s.e.) recorded for territorial juvenile coho as a function of the time elapsed relative to a merganser's presence. Labels as in Fig. 2.5.
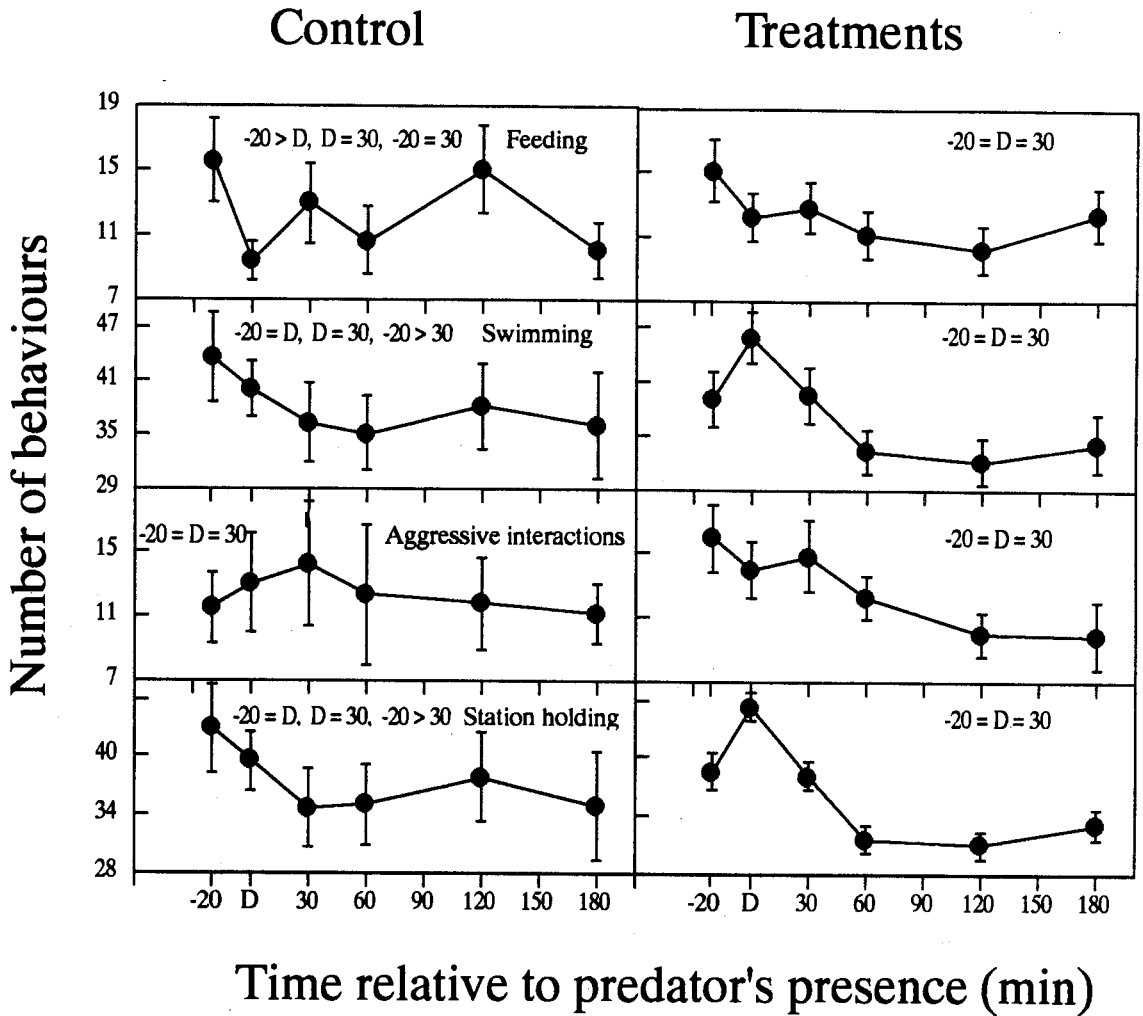
Figure 2.7. Mean number of behavioural acts (± s.e.) recorded for territorial juvenile coho as a function of the time elapsed relative to a merganser's presence. Labels as in Fig. 2.5.

the control enclosure did not show any significant variation in their behaviour for the same periods (Figs. 2.5 - 2.7), except for number of feeding behaviours, which dropped when the empty cage was present (Fig. 2.7).

While mergansers were present, territorial coho also allowed intruders to approach more closely before attacking them (Table 2.3). Since these distances varied significantly between enclosures, results are presented separately for each.

Predator intrusion rate

There was no effect of frequency of predator intrusion on the three time budget variables measured (no significant difference between the two treatment enclosures), and fish growth rate did not differ from enclosure to enclosure, either for territorial fish ($F_{2,34}$ = 1.639 & 1.745 for growth in total length and weight, respectively) or for floaters ($F_{2,14}$ = 1.748 & 2.883). Although fish from the other enclosures attacked conspecifics at significantly longer distances than did fish in the enclosure with the highest predator intrusion rate (Table 2.3), the lack of a significant difference between the midstream enclosure and the control rules out any simple negative correlation between predator intrusion frequency and mean aggressive distance.

Recovery

All fish were back to pre-predator levels for all behavioural variables within 30 min of the predator departure (-20 = 30, Figs. 2.4 - 2.7). Although the average duration of aggressive interactions seemed to increase beyond the pre-predator level for 120 min after the departure of the predator (Fig. 2.6), the effect was not significant for either control or treatments. Two hours after the predator had gone, however, the fish from the treatment enclosures had significantly decreased the

Table 2.3. Mean distances (cm ± s.e.) territorial fish travelled to attack intruders before and while a merganser was present upstream. Midstream enclosure subjected to one merganser presence a day; downstream enclosure to two. Means with the same letter within a column are not significantly different (two tail t-test). P: significance of paired t-tests (one tail) on transformed data (Box-Cox-Bartlett).

Enclosure	Before predator in	While predator in	P
Control (N = 9)	57.7 (6.0) A	56.9 (5.7) A	0.24
Midstream (N = 10)	60.6 (9.9) A	46.4 (5.0) A	0.06
Downstream (N =9)	38.9.(3.3) B	29.6 (1.7) B	0.01

number of their aggressive interactions below their pre-predator level (Fig. 2.7, $P < 0.01$, Wilcoxon signed-rank). This might be attributable to lower light intensity in the treatment enclosures at that time of day (the control enclosure received direct sunlight for about 35 min longer than the treatment enclosures).

Discussion

Upon hatching, juvenile coho typically remain in their natal stream for one year, and their freshwater feeding activities are concentrated in their first summer (Mundie 1971; Sandercock 1991). For coho, a larger size at smolting may translate into higher survival at sea (Mathews and Buckley 1976; Bilton 1978; Olson 1978; Bilton et al. 1982; but see Holtby et al. 1990), and thus into a higher probability of returning to spawn. They should therefore be selected to maximize their growth rate in freshwater, so long as this does not unduly reduce their survival. This study demonstrates that fish which adopted the foraging tactic of territoriality grew faster than fish who were floaters. Although dominant salmonids have been shown to grow faster than subordinates under laboratory conditions (e.g., Fenderson et al. 1968; Li and Brocksen 1977; Fausch 1984), this is the first time a growth benefit of territoriality has been demonstrated under field conditions in a single population. The mean growth rate of juvenile coho in Moody's Channel is comparable to that reported for juvenile coho elsewhere (Sandercock 1991).

The present investigation did not measure directly the frequency of aggressive acts performed by floaters, but their categorisation as floaters was due in part to the fact that they exhibited a lower rate of intra-specific aggression than did territorial fish. Territorial coho were somewhat larger than floaters when the study began in August. At least two other field studies on juvenile stream salmonids have found dominant fish to be larger than subordinates: Puckett and Dill (1985) for

coho, and Grant (1990) for brook char. In Moody's Channel, juvenile coho usually emerge from the gravel from mid-May to early June, and the fish first measured in August had already been involved in aggressive interactions for a few months. The differences in size at that time therefore cannot be unequivocally assigned to differences in either genotype (e.g. Ferguson and Danzman 1985) or environment (hatching time, rearing environment, food abundance, etc.).

Effect of predator presence

When they detect predators, territorial coho are faced with a tradeoff between growth rate and mortality risk. Leaving a feeding territory unattended may result in either its loss, or in future energetic costs necessitated by the eviction of intruders, both of which result in a reduction of growth rate. On the other hand, maintaining defence of the territory at pre-predator levels may increase vulnerability to predators since movement increases risk of detection by mergansers (Chapter 3) and tasks such as territory defense or foraging probably constrain the fish's ability to monitor the danger (e.g., Milinski 1984). Threespine sticklebacks (Gasterosteus aculeatus) exhibit lower levels of intraspecific aggression in the presence of a predator (Huntingford 1976), and Helfman (1989) reported that threespot damselfish (Stegastes planifrons) curtail their territorial defense during presentation of a model predator.

This study provides evidence that territorial coho are sensitive to such a tradeoff: when a bird was present, they altered their behaviour in ways which reduced their risk of being detected (they moved less), but rarely left their territories. Although they significantly decreased the duration of some of their moves (swimming and aggression), they maintained some level of aggression.

Although the number of swimming bouts increased marginally, their average duration decreased, which may compensate for this. Juvenile coho are cryptic over their natural substrate (Donnelly and Dill 1984), and crypsis is usually enhanced by immobility. Cryptic fish detecting predators

and yet still needing to move may split their swimming bouts into shorter segments than when predators are absent, resulting in a higher frequency of swimming bouts. The fact that stationary bout frequency also increased marginally during predator presence lends support to this argument. For this to be adaptive requires that mergansers looking for cryptic prey can detect only those prey who have been moving for longer than a certain duration. In another study (Chapter 3) mergansers attacked significantly more often coho who were moving when the birds were looking in the fish's direction than coho who were stationary. Another possibility is that stationary fish may monitor their environment more efficiently than when preforming other tasks, or that other activities bear a cost in lost vigilance for predators (e.g., Godin and Smith 1988). Less vigilant individuals may be at greater risk of attack by predators (e.g., FitzGibbon 1989). Thus, fish may need more frequent updates about their world after a predator has been detected.

Of all the activities in which territorial coho engaged, aggression was the most affected by predator presence. Territorial fish reduced the proportion of their time budget allocated to aggression when the birds were present, and decreased the average duration of aggressive acts. Since the average distance travelled to intercept or challenge intruders also decreased (significantly so in enclosure 2), while the frequency of agonistic interactions remained stable, the functional territory size of juvenile coho may be said to shrink when predators are present. The frequency of intrusions on the territories and the behaviour of the intruders could not be monitored during the experiment, although their behaviour is probably influenced by predation risk as well. The ratio territorial : floater was slightly (but not significantly so) higher in the enclosures submitted to merganser presence (1 : 0.7 for control vs 1 : 0.5 for both treatment enclosures). Territorial fish in treatment enclosures may thus have faced a lower intrusion frequency. It is doubtful, however, that the effect of predation risk on territorial fish is due entirely to its indirect influence on intruders. The frequency of aggressive acts by territorial fish did not drop significantly during the birds' presence, and the aggressive behaviour of juvenile coho has been shown to be directly affected by a similar predation risk under laboratory conditions (Chapter 4).

Coho in the predator treatments did not decrease their feeding frequency nor did they decrease the average duration of their feeding bouts. However, since these were so short (< 1 s), the accuracy of measurement was limited by the observers' reaction time. The fish could well have reacted to predator presence by reducing their attack distance on prey, as laboratory studies on salmonids have shown (Dill and Fraser 1984; Metcalfe et al. 1987; Gotceitas and Godin 1991; Chapter 4), but this could not be assessed in the present study.

Frequency of predator intrusion

The experiment did not detect any effect of frequency of predator presence on fish growth or on fish aggression level; the frequency of agonistic behaviours, their mean duration and the percentage of the time budget they accounted for did not vary significantly between the two enclosures submitted to merganser presence. Fish from the downstream enclosure allowed intruders to approach to shorter distances than did fish in either of the two other enclosures before attacking them, whether or not a predator was present. This may have resulted from variation among enclosures in food densities (coho territory size varies inversely with benthic food density ; Dill et al. 1981), but this could not be ascertained.

The lack of an effect of predator intrusion frequency could be due to the low power of the tests, resulting from the relatively small sample size (power varied from 0.19 to 0.53 for the variables tested; Cohen 1988). Alternatively, a difference of one merganser incursion per day may not represent a significant change in perceived predation risk between habitats. A merganser brood was present in the channel and four wild chicks were once sighted near the enclosures. Perhaps repeated daily merganser incursions acted to minimize differences in perceived predation risk between the enclosures, and made it difficult to detect the relatively small experimental manipulation of intruder frequency.

Territorial fish returned to their pre-predator activity level within 30 min of the predator's departure. This is a shorter recovery time than that reported for juvenile Atlantic salmon under laboratory conditions (Metcalfe et al. 1987; Huntingford et al. 1988). Moreover, the presence of mergansers upstream caused a relatively small reduction in the time budget of the fish: movement decreased to 84 % of its pre-predator level, aggression to 58 %, and feeding to 87 %. In contrast, Metcalfe et al. (1987) reported that juvenile Atlantic salmon attacked prey at 33 % of their pre-predator rate in the 20 min immediately following a 30 sec presentation of a model predator. The predators used in the Atlantic salmon studies were trout models presented close to the fish, whereas it is unlikely that the fish in the present experiment ever saw the mergansers. Thus, a possible explanation for the different results is that vision mediates a stronger and longer-lasting effect of predation risk than does chemoreception. This hypothesis deserves further study.

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Chapter 3:

Influence of movement by coho salmon (<u>Oncorhynchus kisutch</u>) parr on their detection by common mergansers (<u>Mergus merganser</u>)

Abstract

A common reaction of juvenile salmonids who detect predators is to decrease their activity. To test whether there is a survival advantage to reduced movement under such circumstances, juvenile coho salmon were put in the presence of common mergansers under laboratory conditions which precluded crypsis. Mergansers were more likely to attack fish who moved than fish who remained stationary, and the relation between bird detection lag time and fish movement is best described as inversely exponential. Bird detection lag time was not correlated with fish size. The risk of detection of prey by visual predators should be determined by both predator and prey behaviour, but our results suggest that in this case prey behaviour is the most important factor. We discuss the relevance of these results to juvenile coho feeding strategies in the field .

Introduction

Coho salmon (Oncorhynchus kisutch) typically spend the first and sometimes the second year of their lives in streams (Chapman 1962), where they hold feeding territories (Dill et al. 1981; Puckett & Dill 1985). They then migrate to sea, where they spend two to three years before coming back to freshwater to spawn. Because larger smolts may enjoy a higher survival at sea (Mathews & Buckley 1976; Bilton 1978; Olson 1978; Bilton et al. 1982; but see Holtby et al. 1990), juvenile coho should maximize their growth rate in freshwater. But rapid growth requires high food intake. Consequent investment in feeding activity should expose individuals to predation as a result of increased activity levels (Dill 1983). One of the most important predators of juvenile coho is the common merganser (Mergus merganser); in some instances these birds have been estimated to be responsible for 24 to 65% of the fish mortality in a given stream (Wood 1987).

Juvenile coho significantly reduce their activity in the presence of common mergansers, both in the field and the laboratory (Chapter 4). Other juvenile salmonids respond similarly to predation risk: they may curtail the distance they will travel to attack prey items (Dill & Fraser 1984; Gotceitas & Godin 1991) and reduce their movement (Metcalfe et al. 1987; Huntingford et al. 1988). Prey activity influences the likelihood of attack by many vertebrate predators (e.g., warty newt - Cook 1971; rainbow trout — Ware 1973; Irvine & Northcote 1983; barn and screech owls — Kaufman 1974; Atlantic salmon — Rimmer & Power 1978; common goby — Magnhagen & Wiederholm 1982; white crappie — Wright & O'Brien 1982; turbot — Holmes & Gibson 1986; dace, roach and minnows — Scott 1987; pinfish — Luczkovich 1988; largemouth bass — Crowl 1989; three- and 15-spined sticklebacks — Ibrahim & Huntingford 1989; Kislalioglu & Gibson 1976; garter snakes — Morey 1990).

Potential prey decrease their activities when they detect predators (see Lima & Dill 1990 for a recent review) suggesting that prey reduce their risk of detection by visual predators by moving less. This is especially likely to be true for cryptic prey. Coho parr are cryptic over natural substrate (Donnelly & Dill 1984) and it is therefore probable that they gain a survival advantage from immobility in the presence of visual predators.

Diving birds are capable of great ocular accommodation (Sivak 1988), and mergansers typically dip their heads underwater while searching for prey (Lindroth & Bergström 1959). The probability of a merganser detecting a fish will be a function both of the bird's sensory (we assume primarily visual) capabilities and its rate and duration of scanning bouts while foraging; detection will also depends on the amount of time the fish spends moving. This can be expressed as either movement rate (moves per unit of time) or the percentage of the fish's time budget spent moving. These two measures are expected to be correlated and an increase in either should translate into a higher probability of a foraging bird looking at a fish when that fish is moving . The average movement bout duration may also influence the probability of detection.

Based on the previously observed changes in behaviour of salmon in the presence of predators, we predicted that, in an environment where crypsis is ineffective, salmon who were moving when a merganser was looking would be more likely to be attacked than salmon who were stationary, and that the risk of detection of salmon by mergansers would be strongly related to the amount of fish movement.

Materials and Methods

Trials were conducted outdoors at the Animal Care Facility at S.F.U. in August 1990, and March and May 1991 in the pool section (1.2 x 2.4 x 1.2 m) of a U-shaped flow-through stream channel (Fig. 3.1). Water was pumped through the system at a rate of approximately 2.3 l/s (for more details, see Donnelly 1985). This channel usually housed three adult common mergansers, who were fed commercial dog food *ad* *libitum* and live salmon parr occasionally. These birds had been captured as approximately ten day old chicks and had therefore had the experience of capturing live prey in the wild (White 1957). Coho salmon juveniles were obtained from the Chilliwack Hatchery, Chilliwack, British Columbia. They were housed in indoor tanks at S.F.U. (16:8 photoperiod) and transferred to outdoors tanks at least a week prior to experiments.

An hour before the beginning of trials, the birds were transferred to another holding pen. At the beginning of each trial, a salmon parr ($\bar{x}$= 9.5 cm TL, s.d. = 1.7, N = 33) was released into an open-top transparent plexiglass enclosure (0.5 x 0.5 x 0.7 m) in the pool section of the channel (Fig. 3.1) and left to acclimate for 5 min. The enclosure was set on a white background and had white panels along two of its sides to make the fish more visible. The fish's behaviour was filmed through a 75 x 95 cm underwater window, using a video camera. After five min, one of three common mergansers (two females and a male) was selected randomly and released at the downstream end of the stream channel (Fig. 3.1A). Its actions were filmed using a second camera installed above the channel. The cameras were synchronized so that fish movement could subsequently be correlated to bird behaviour. Observers concealed behind a blind could watch the bird's behaviour via a mirror set at an angle above the pool area and the fish's behaviour via a TV monitor. Birds were tested only once a day (except on one occasion when the two females were tested twice in the same day), with at least a one hour separation between trials. Since testing

could be carried out only when weather conditions were not inclement, time between trial days varied. To minimize the likelihood of birds diving without looking, in the expectation that a fish was present, 'blank' trials, in which no fish was present in the enclosure, were randomly interspersed in the trial sequence. The birds were also regularly fed fish in the area around the enclosure, so they could not be certain that only the enclosure needed to be searched.

Variables measured for birds were number of head dips (head submerged beyond eye level), timing and duration of each dip and lag time. Our operational index of the probability of salmon detection by mergansers is lag time, or time elapsed from the first look (head dip) in the direction of the prey to the onset of attack. This makes the simplifying assumption that whenever a merganser detects a fish, it will attack regardless of its internal state (satiation level) or the cost of attack. While this is probably not true in field situations, the assumption is reasonable under laboratory conditions where the satiation level of the birds can be controlled and where there is no variance in the physical surroundings of the prey.

Lag time was defined as the time elapsed from the first head dip in the direction of the underwater enclosure to the onset of the first dive into the enclosure. The variables measured for fish were the number of moves per min (a fish was considered to have moved if it moved at least 0.25 body length in any direction), duration of moves and stationary bouts, and percent of time spent moving. These measures were grouped as "before bird" (from 1 min after introduction of the fish to introduction of the bird) or "after bird ". It was possible, using the synchronized cameras, to determine for each bird dip whether the fish was moving or motionless at that moment.
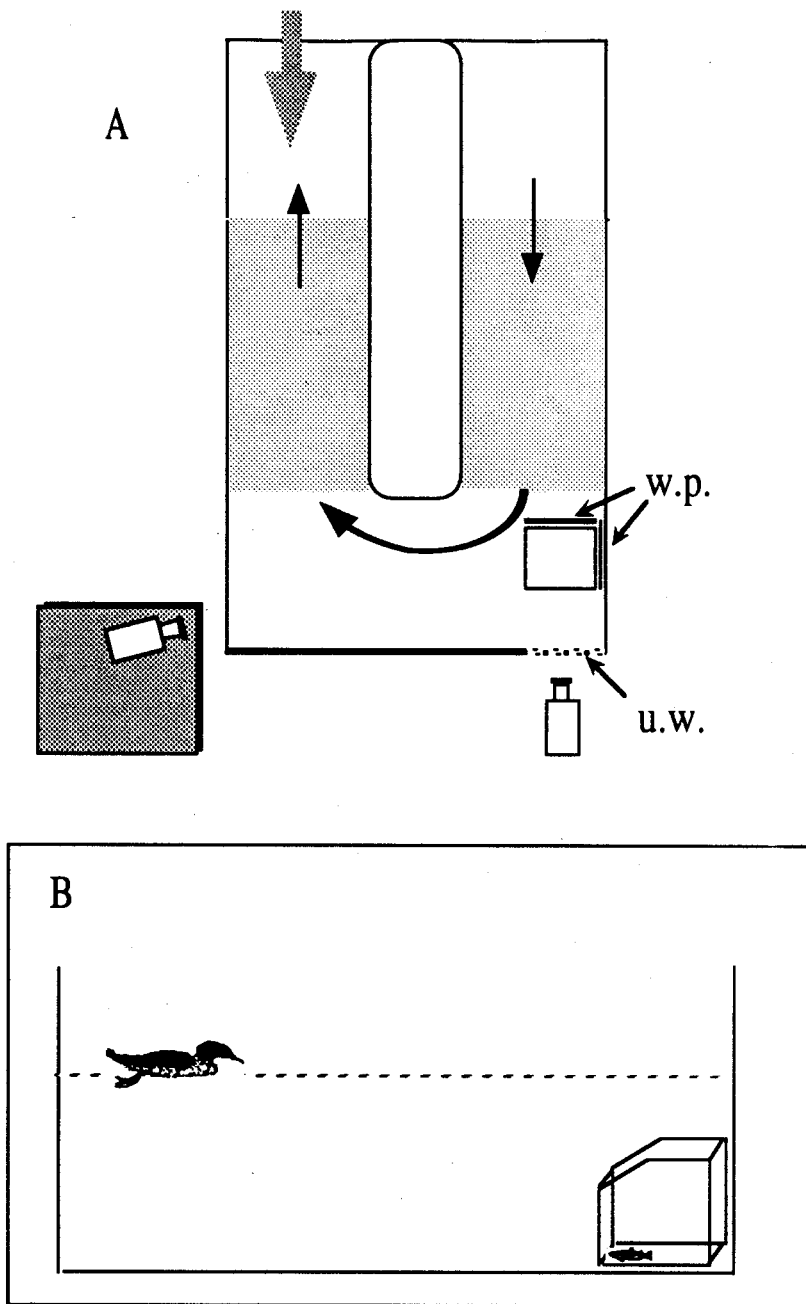
Figure 3.1 A. Stream channel viewed from above, showing relative positions of the two cameras. Grey arrow indicates birds' entrance point, black arrows the direction of water flow. Stippled areas are shallow sections (< 0.2 m depth), white areas are pool sections. w.p. : white panels, u.w.: underwater window . **B.** View of pool area from the side. Animals not to scale.

Results

Fish who moved when a merganser was watching were significantly more likely to elicit dives than fish who stayed motionless (Table 3.1). Fish moving when birds dipped their heads were attacked 15.2% of the time, whereas stationary fish were attacked only 1.4% of the time.

Influence of birds on fish movement

There was no difference in fish movement rate (moves per min) when fish were grouped by individual bird (Kruskal-Wallis H corrected for ties = 0.03, df = 2, P = 0.98, N = 33), so the results were pooled for all birds. However, the presence of birds did influence fish movement: fish decreased their rate of movement in the first two min after the introduction of a bird into the system (Fig. 3.2). Average duration of fish movement was also shorter when birds were present (12.9 s vs 28.8 s, Z = -2.73, P < 0.01, Wilcoxon's signed rank test, N = 32). There was no significant difference in the percent of time the fish spent moving before and after introduction of a bird (t = 0.786, df = 32, P = 0.44, paired t-test on arcsine transformed data).

Influence of fish movement on head dipping by birds

Birds varied significantly with regard to duration of head dips (Kruskal-Wallis H corrected for ties = 99.408, df = 2, P < 0.001, N = 824), and results are consequently presented separately for each bird. The average duration of birds head dips was not significantly different when fish were moving or stationary (Table 3.2). Birds also varied significantly in terms of dip rate (Kruskal-Wallis H corrected for ties = 9.506, P < 0.01, N = 327). However, bird dip rate (dips per 30 s

Table 3.1. Contingency table analysis of bird behaviour (dive or not) in relation to whether the fish was moving when the bird dipped its head in that direction.

Fish behaviour	Bird dives	Bird does not dive	Total
moving	22	123	145
stationary	11	757	768

$\chi^2_1 = 7.623$, $P < 0.01$, G test.
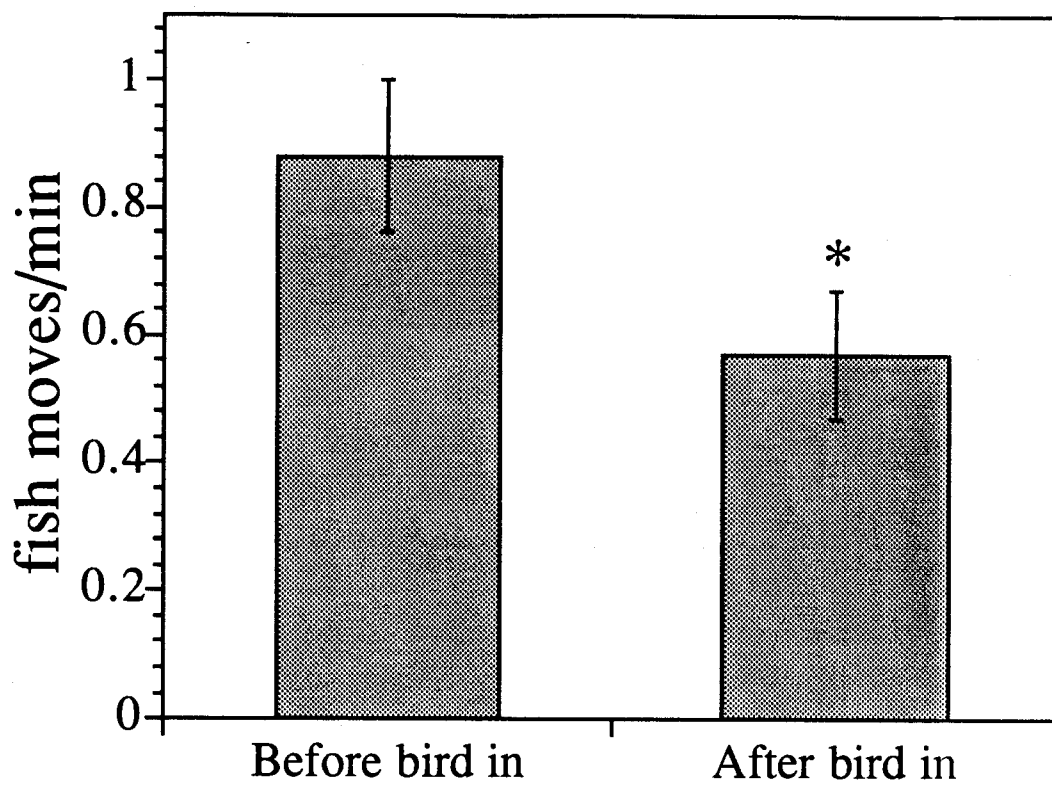
Figure 3.2. Average fish movement rates (± s.e.) in the two minutes before and two minutes after introduction of a merganser to the stream channel. Z corrected for ties = -1.852, P = 0.03, one -tail test, Wilcoxon signed-rank test. N=33.

Table 3.2. Average duration (sec) of head dips for the three mergansers tested.

Bird	N (trials)	Dips while fish moving		Dips while fish stationary		U'	P
		Duration	N	Duration	N		
female 1	14	0.62 (0.02)	36	0.70 (0.02)	226	4736.5	0.11
female 2	13	0.56 (0.02)	101	0.53 (0.01)	446	24486.5	0.16
male	6	1.05 (0.05)	2	0.59 (0.08)	13	24	0.10

U' = Mann-Whitney U. Standard errors are in parentheses. NOTE : durations of dips immediately preceding a dive are not included.

interval) and fish movement rate (moves per 30 s interval) were not significantly correlated for any of the three birds ($r_s = 0.1$, N = 201; $r_s = -0.06$, N = 116; $r_s = 0.71$, N = 8).

Influence of fish size and movement on bird detection lag time

Fish size did not influence fish movement rate ($r_s = 0.128$, P = 0.47, N = 33), so the effect of size and movement in detection lag time may be examined independently. Birds were significantly different in duration of their lag times ($F_{2, 30} = 8.98$, P<0.001, ANOVA on transformed data to respect the test's assumptions (Box-Cox-Bartlett $\lambda = 0.22168$)). The male's lag times were shorter than those of either female (P < 0.03, Tukey HSD tests) and were dropped from subsequent analyses, except where noted. Bird lag time and fish size were not correlated, either for the female mergansers (Fig. 3.3) or the male ($r_s = 0.029$, P = 0.94, N = 6). Bird lag time and fish size were also not significantly correlated when the fish were divided as having been moving before the bird dived ($r_s = -0.44$, P = 0.66, N = 19) or as having been stationary ($r_s = 0.57$. P = .13, N = 8).

The correlations between the various fish movement characteristics, lag time duration and number of dips are shown in Table 3.3. Bird lag time is positively correlated with total number of head dips and duration of fish stationary bouts, and negatively correlated with fish moves/min; the latter relationship is best described as an inverse exponential (Fig. 3.4).
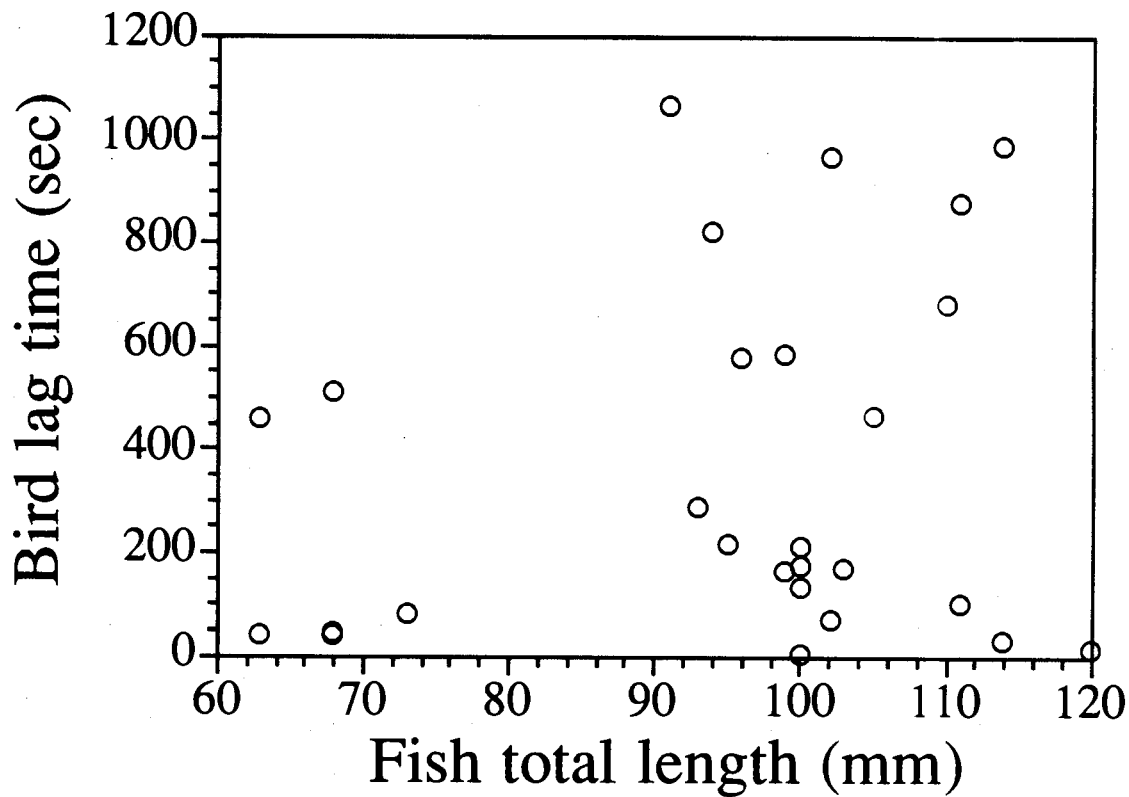
Figure 3.3 . Merganser lag time (sec) as a function of fish total length (mm). Analysis done on BCB-transformed data ($\lambda = 0.22168$ for lag time and 3.29625 for fish total length). r = 0.054, P = 0.79, N = 27.

Table 3.3. Spearman rank correlations between fish movement characteristics and bird detection indices.

	Average mvt bout	Average stnry bout	Moves/min	% moving	# dips
Average stnry bout	0.11 NS				
Moves/min	-0.18 NS	-0.88 **			
% moving	0.48 *	-0.74 **	0.67 **		
# dips	0.30 NS	0.53 *	-0.54 *	-0.24 NS	
Lag time	0.30 NS	0.50 *	-0.49 *	-0.22 NS	0.93 ***

Average mvt bout: duration of average fish moving bouts while bird is present (sec), Average stnry bout: duration of average fish stationary bouts while bird is present (sec), Moves/min: fish movement rate, % moving: percent of fish time budget spent moving, # dips: total number of bird head dips, Lag time: bird lag time (defined in text). * : $P < 0.05$, ** : $P < 0.01$, ***: $P < 0.0001$. $N = 27$.
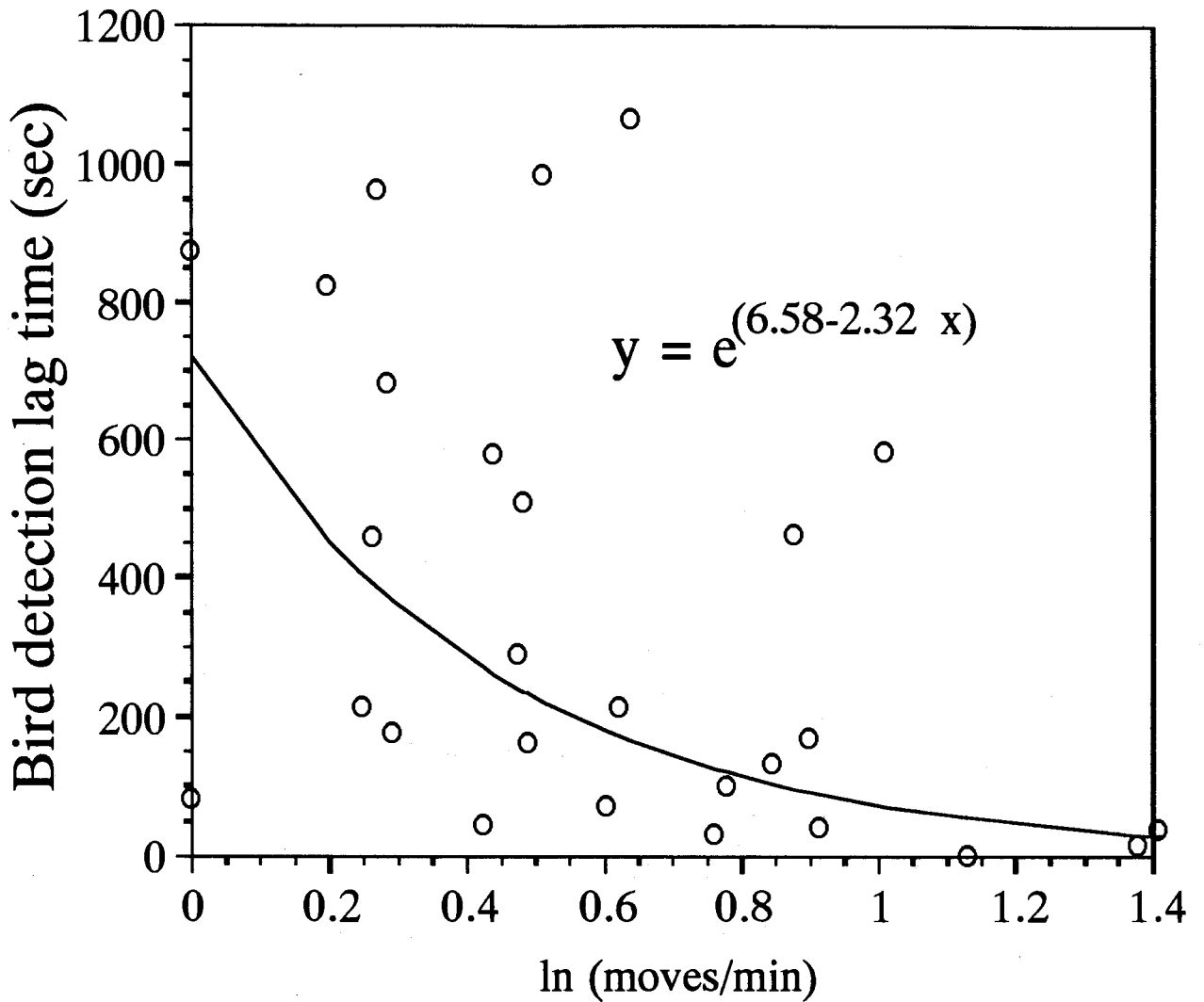
Figure 3.4. Bird detection lag time as a function of fish moves/min (ln transformed). Proportion of variance accounted for by exponential function: 0.33, P < 0.002. A straight line fit through these data points is also significant (P < 0.02) but does not explain as much of the variance (R^2 = 0.19).

Discussion

Movement may be the cue mergansers used to recognize prey: they attacked moving prey disproportionately more often than stationary ones. Similar results have been found for at least two other avian orders (Kaufman 1974; Goss-Custard 1977) and for other vertebrate classes (see literature cited in Introduction).

Juvenile salmonids have been shown to reduce their activity in the presence of predators: Atlantic salmon parr (Salmo salar) curtailed their activities (Metcalfe et al. 1987; Huntingford et al. 1988) and coho and Atlantic salmon parr significantly reduced their attack distance on food items (Dill & Fraser 1984; Gotceitas & Godin 1991) when in the presence of piscine or avian predator models. Overall, the activity budget of the fish in this experiment were the same whether birds were present or not. However, when a bird entered the stream channel, fish significantly reduced their average movement duration. Typically, fish froze when the bird first appeared and this is reflected in their change in movement rate in the first two minutes of the birds' presence (Fig. 3.2). The increased activity rate after this time may reflect escape motivation in circumstances of contrasting background and absence of shelter. Although fish with different experience may have behaved differently, it is unlikely that the hatchery fish used in the experiment had previously experienced merganser's attacks, although Howard (1983) does suggest that avian predation occurs at some B.C. salmon hatcheries.

Fish movement did not influence the amount of time birds spent looking underwater. This was not due to the birds all looking for the maximum allowable time, since mergansers routinely stay underwater for more than three sec per dive (Dewar 1924; Wood & Hand 1985; Martel unpubl. obs.), and physiological limitations on the part of the birds can be ruled out. Because the

birds often made the transition from the last dip to a dive without raising their heads above the water level, it was difficult to assess the exact duration of the last head dips, and they were not included in the data set. But even when they were estimated and compared to the rest of the dips, the head dips immediately preceding a dive were only of significantly longer duration for female 2 $(1.1 \pm 0.15$ sec vs 0.69 ± 0.01, $U'_{262,14} = 2653$, $P < 0.01$) and there was no difference related to fish movement. There was also no correlation between fish movement rate and bird dip rate. This supports our assumption that mergansers do not detect the fish, and consequently change their scanning behaviour, prior to attacking them; rather, scanning rate is constant and risk of detection is influenced only by fish movement rate.

Lag time was significantly correlated with total number of dips (Table 3.3), and using the latter as our index of detection would have led to similar results. We feel that lag time is a more realistic index of probability of salmon detection by mergansers because it takes into account the influence on merganser foraging behaviour of factors such as vigilance for their own predators. The trials were conducted outside, and the birds frequently scanned the sky. The overflight of birds such as hawks, or distant noises, sometimes briefly startled the mergansers, and this may have led to an increase in their lag time.

The fact that fish size was not correlated with detection time suggests that mergansers may not rely on visual acuity alone for the detection of their prey. The foraging success of the mink (Mustela vison), a piscivorous predator operating in an environment similar to that of mergansers, is more readily explained in terms of detection of directional movement (Dunstone & Clements 1979) than in terms of visual acuity (Sinclair et al. 1974). Mergansers have been observed both in the field and under laboratory conditions to probe with their bills under rocks and into fissures (White 1957; Lindroth and Bergström 1959; Martel unpubl. obs.), and fish thus flushed are quickly snatched, a tactic that emphasizes motion perception. It is more important for birds

foraging under these conditions to assess where a potential prey is going rather than its nature. Mergansers were often observed to lunge at quickly moving objects (Martel unpubl. obs.).

The lack of correlation between fish size and detection time suggests that even the smallest fish we used subtended a supra-threshold visual angle in the experimental environment. A bird looking from the surface at the farthest end of the pool would be approximately 2.7 m from a fish at the bottom of the enclosure. The angular size of the smallest fish (TL = 6.2 cm), when normal to the birds' line of sight, would thus be 39 min, well within the spatial resolution capability reported for birds (Kirschfeld 1976), even when the effect of fish viewing angle on angular size is taken into account.

The use of a white background eliminating crypsis enabled us to isolate the effect of prey movement on predator detection time and to describe the shape of this function (Fig.3.4). Even small increases in parr movements per min can translate into great increases in probability of detection by mergansers, or reduced detection lag time. Activity levels while an avian predator is detected nearby are therefore expected to drop, which they did in the first two min after bird introduction in this study, as well as in a field study (Chapter 2). Conversely, the average duration of fish stationary bouts should affect the likelihood of fish being detected. In extreme cases, fish who did not move were detected later (the birds had longer lag time) than those who moved. But the exact relationship between stationary bout duration and lag time is unclear: the correlation is reduced to 0.23 (cf. 0.50 in Table 3.3) when the effect of fish moves/min is partialled out.

This experiment clearly establishes that risk of detection by avian predators is directly related to coho parr movement. Movement can thus be used as an index of risk of predation, although the exact shape of the relation between detection and mortality is not known. Territorial coho parr have been shown to spend a smaller proportion of their time engaged in swimming activities than

either "floaters" or non-territorial fish (Puckett and Dill, 1985). Territorial fish also enjoy an advantage in net energy intake over fish adopting the two other tactics (Puckett and Dill, 1985), and territory size is inversely related to benthic food density (Dill et al., 1981). Thus, although non-territorial fish may use anti-predator tactics such as schooling, territoriality in coho may not only result in energetic advantages but may also reduce predation risk. Since the energy intake advantage will translate into higher growth rates, territoriality could minimize the ratio of mortality risk to growth rate (Werner & Gilliam 1984; Gilliam & Fraser 1987) and be strongly selected for in areas where avian predation is important.

The amount of coho parr movement is correlated with their detection by birds; this suggests that coho mortality rate is affected by their behaviour and can thus be viewed as being at least partially under their control (Lima and Dill, 1990). The precise shape of the function relating risk of detection versus prey movement should be of considerable use in models of prey selection where encounter probabilities have to be estimated (cf. Stephens & Krebs 1986).

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Chapter 4:

Chemoreception, risk of predation, feeding and agonistic behaviours in juvenile coho salmon (*Oncorhynchus kisutch*).

Summary

Juvenile coho salmon (Oncorhynchus kisutch) spend the first year of their lives in their natal streams, where they may 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 predator presence has not previously been reported. We tested the influence of common merganser (Mergus merganser) odour 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 agonistic behaviour directed towards mirrors (total number 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. The relevance of these results to field studies of juvenile salmonid behaviour is discussed.

Introduction

Juvenile coho salmon (Oncorhynchus kisutch) characteristically spend their first year after emergence in streams, where they may 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, or even their primary mode of sensory perception. 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 trout (Dill and Fraser 1984; Metcalfe et al. 1987) or kingfisher (Ceryle alcyon, Gotceitas and Godin 1991). Common mergansers (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 odour is likely to be a reliable indicator of such presence. Based on previous studies, we hypothesized that juvenile coho would travel less far to intercept prey when merganser odour is present than when it is absent.

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 in shaping the agonistic behavioural 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 (Chapter 3). We therefore predicted that these fish would decrease the frequency, duration and intensity of agonistic behaviours they were engaged in when confronted with merganser odour.

Materials and Methods

Trials were conducted indoors at the S. F. U. Animal Care Facility in flow-through tanks (92 x 47 x 39 cm, water depth kept at 20 cm) modified from those described by Soluk and Collins 1988 (Fig. 4.1). Four identical tanks were enclosed in a 3.6 x 1.8 x 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 tanks. Each tank was surrounded on three sides by black construction paper ('sp' in Fig. 4.1) and had a grid on a white background positioned below its transparent floor. During trials a camera was inserted through a hole 1.2 m 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. 4.1)

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. Brine shrimp (Artemia salina) thus injected were neutrally buoyant and usually drifted in a linear trajectory. Water velocity could be varied by varying the air pressure delivered to the diffuser, and was kept at approximately 10 cm. s^{-1}. The photoperiod was constant at 16:8 (light:dark hrs).

Fish

Wild young-of-the-year coho were seined in May, 1991 from Moody's spawning channel, a tributary to 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. The fish's acclimation to their new surroundings took on average two to four days, and was considered complete when they readily fed on brine shrimp injected through the feeding tube at random intervals through 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 attack distance and aggression experiments. We used nineteen fish (45.8 ± 3.9 mm TL) in the attack distance experiment and 16 fish (46.3 mm ± 2.9 mm TL) in the aggression experiment.

Odour

Odour treatments were of three types: fish, predator and no odour. Fish odour was prepared by letting three juvenile coho 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 from 10.5 to 13.5 °C). Predator odour was prepared the same way,
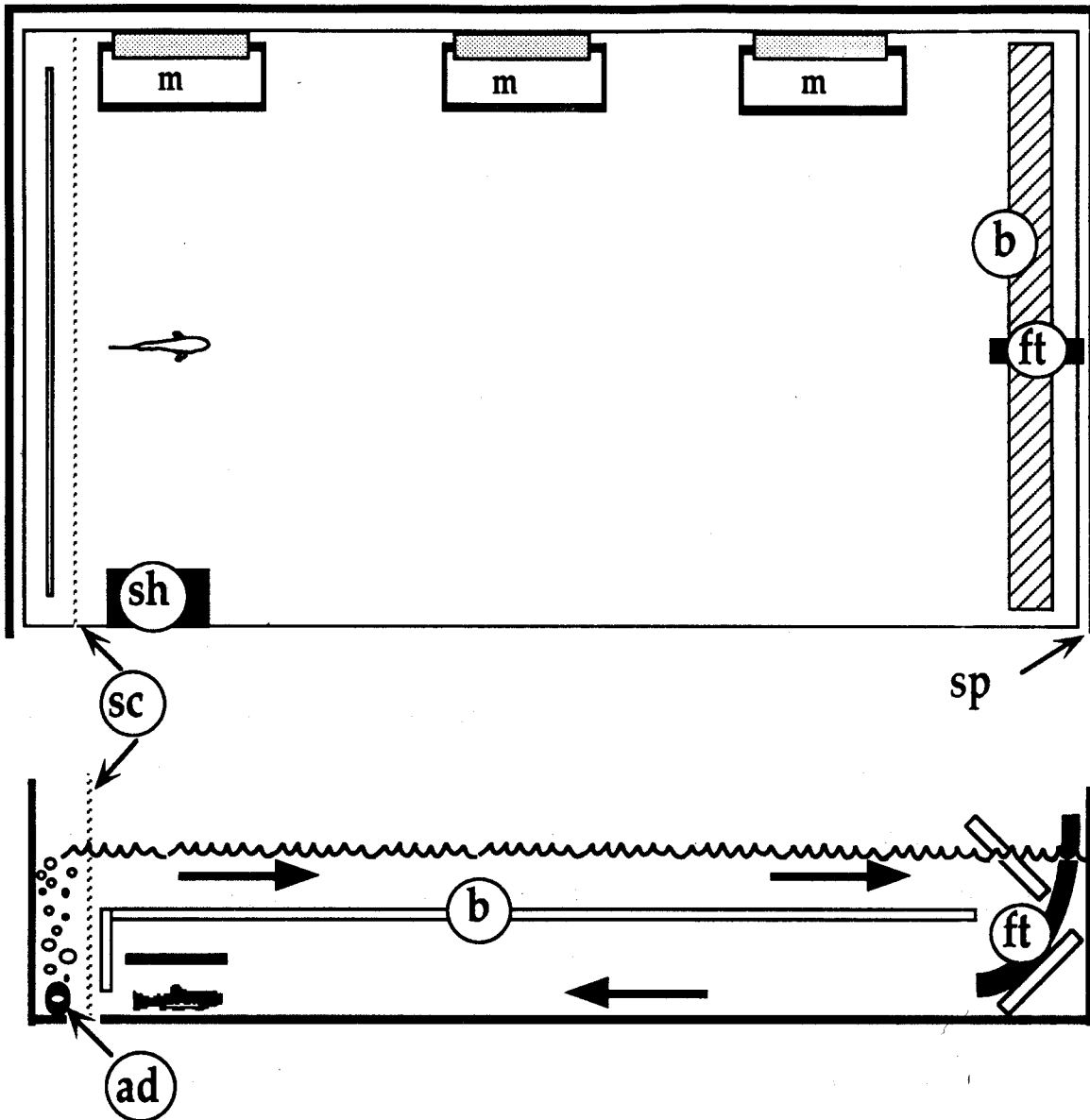
Figure 4.1. Views from above and the side of a flow-through tank used in these experiments.
m: mirrors, **b**: clear plexiglass baffle, **sh**: shelter, **ft** : feeding tube, **sp** : side panel, **sc**: screen,
ad: air diffuser. Arrows indicate direction of current.

except that at the end of the time period a tame common merganser was allowed to seize, manipulate and (sometimes) ingest some of the fish. After one min, the bird's head was rinsed three times with the same water. Thus, the "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. The order of the treatments was drawn randomly for each experimental fish. Each fish tested was subjected to one treatment per day.

Prey attack distance

Trials were conducted in June and July, 1991, between 1400 and 1630 h. 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 the 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 = 18.8×10^{-4} g for groups of 10, s.e. = 1.6×10^{-4}g, N = 10), and the distance they moved to attack these shrimp was later measured from the videotapes. Most fish assumed a stationary position within two body lengths of the screen (Fig. 4.1), and brine shrimp were injected only when fish were within 1.5 body length 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 interception point, in the horizontal plane (Dill and Fraser 1984). In this apparatus, there frequently was 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

calculations. 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 picked up on videotape). We therefore could not calculate reaction distances (i.e., distances from which fish actually began their attack).

Agonistic behaviour

Aggressive behaviours (Table 4.1) were stimulated with mirror images (Gallup 1968), since juvenile coho readily engage in agonistic activities towards mirror-images (Rosenau and McPhail 1987; Swain and Riddell 1990). We later ranked these behaviours in terms of aggressive intensity. We related the intensity of an action to its probability of contact with the opponent and its force (acceleration of the fish). For example, both nipping and 'swim against mirror' involved contact, but we ranked nipping higher than 'swim against mirror' because the former entailed a quick acceleration. Similarly, charging was ranked higher than 'lateral' because charging often led to nipping. Our ranking follows that of aggressive scores given by Mason (1966) for juvenile coho.

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 one min, all three mirrors were raised along their hinges (Fig. 4.1) with monofilament lines. Timing started when the first aggressive behaviour was directed towards any of the mirrors (usually within one min). After 15 min, 100 ml of either fish- or predator-conditioned water was 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.

Table 4.1. Agonistic behaviours recorded for juvenile coho salmon in this study.

Behaviour	Description
Nip	quick biting motion ('peck') by the fish (Taylor and Larkin 1986) at the mirror; contact always occur.
Swim Against Mirror	fish swims along mirror with its snout against it (Rosenau 1984; Taylor and Larkin 1986; Swain and Riddell 1990).
Charge	rapid, direct and accelerated movement of the fish (Kratt and Smith 1979; Taylor and Larkin 1986) to within one body length of the mirror.
Lateral display	fish either stationary or slowly swimming, but always parallel to mirror, within one body length, and with dorsal and anal fins usually erect (Taylor and Larkin 1986; Swain and Riddell 1990).
Facing mirror	fish, either stationary or slowly moving back and forth, perpendicular to mirror, usually with mouth open; within one body length of mirror.
Approach	direct movement of the fish to within two body lengths of the mirror; distinguished from charge by lower velocity (Dill 1978; Kratt and Smith 1979; Taylor and Larkin 1986).

Results

Prey attack distance

Exposure to predator-conditioned water caused a significant decrease in attack distance, whereas there was no significant difference in behaviour in fish-conditioned and filtered water (Fig. 4.2). In some instances, the reaction to the predator-conditioned water was striking: in the first few min following the injection of the water some fish remained totally stationary and did not take food items even if these hit them. No fish moved under the shelter provided unless they were already there.

Aggression

Exposure to predator-conditioned water significantly depressed the total number of aggressive behaviours (by 44.9%, Fig. 4.3a), total time spent on these actions (by 58.2 %, Fig. 4.3b) and total time spent within one body length of the mirrors (by 47.4 %, Fig. 4.3c). Fish also changed the relative composition of their agonistic interactions: they significantly reduced the proportion of their time budget alloted to nipping, the most intense activity, while increasing the proportion devoted to approaching, the least intense form of aggression (Table 4.2). Three fish did not show any aggressive behaviour after the merganser odour had been injected and are not included in the 'after' part of this last analysis. The fish also significantly reduced the average duration of their agonistic behaviours when exposed to predator-conditioned water (4.7 $\pm$ 0.3 s vs 2.7 $\pm$ 0.4 s, Wilcoxon signed-ranked Z corrected for ties = -2.98, P = 0.003).
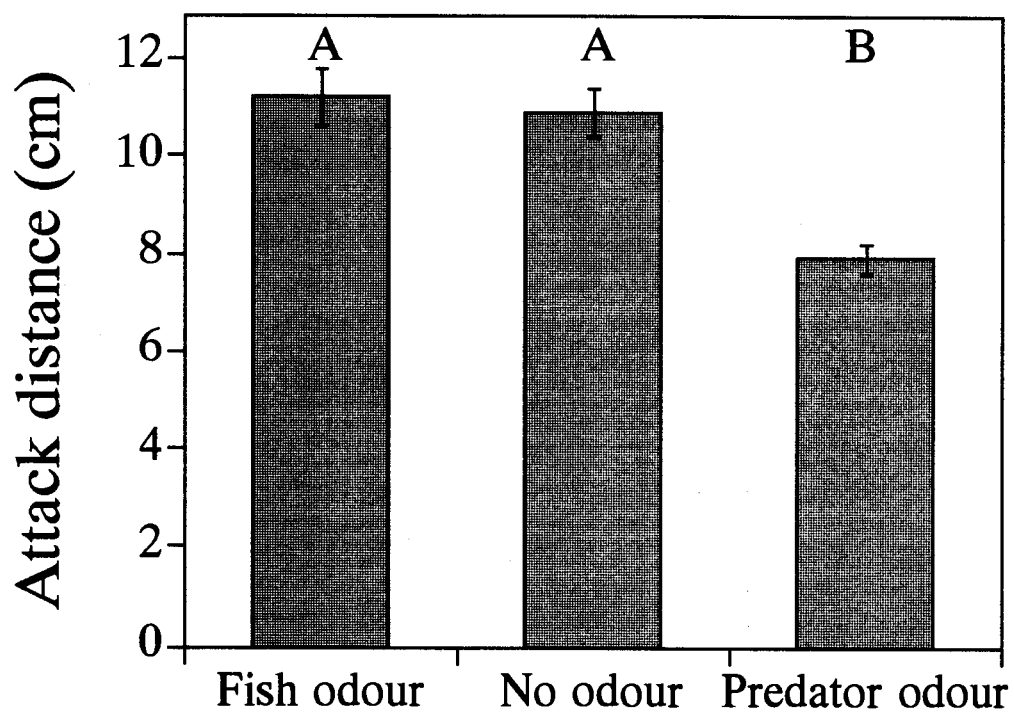
Figure 4.2. The influence of odours on mean attack distance (± s.e.) of juvenile coho salmon. Means with different letters are significantly different (P < 0.01, paired t-tests). N = 19.
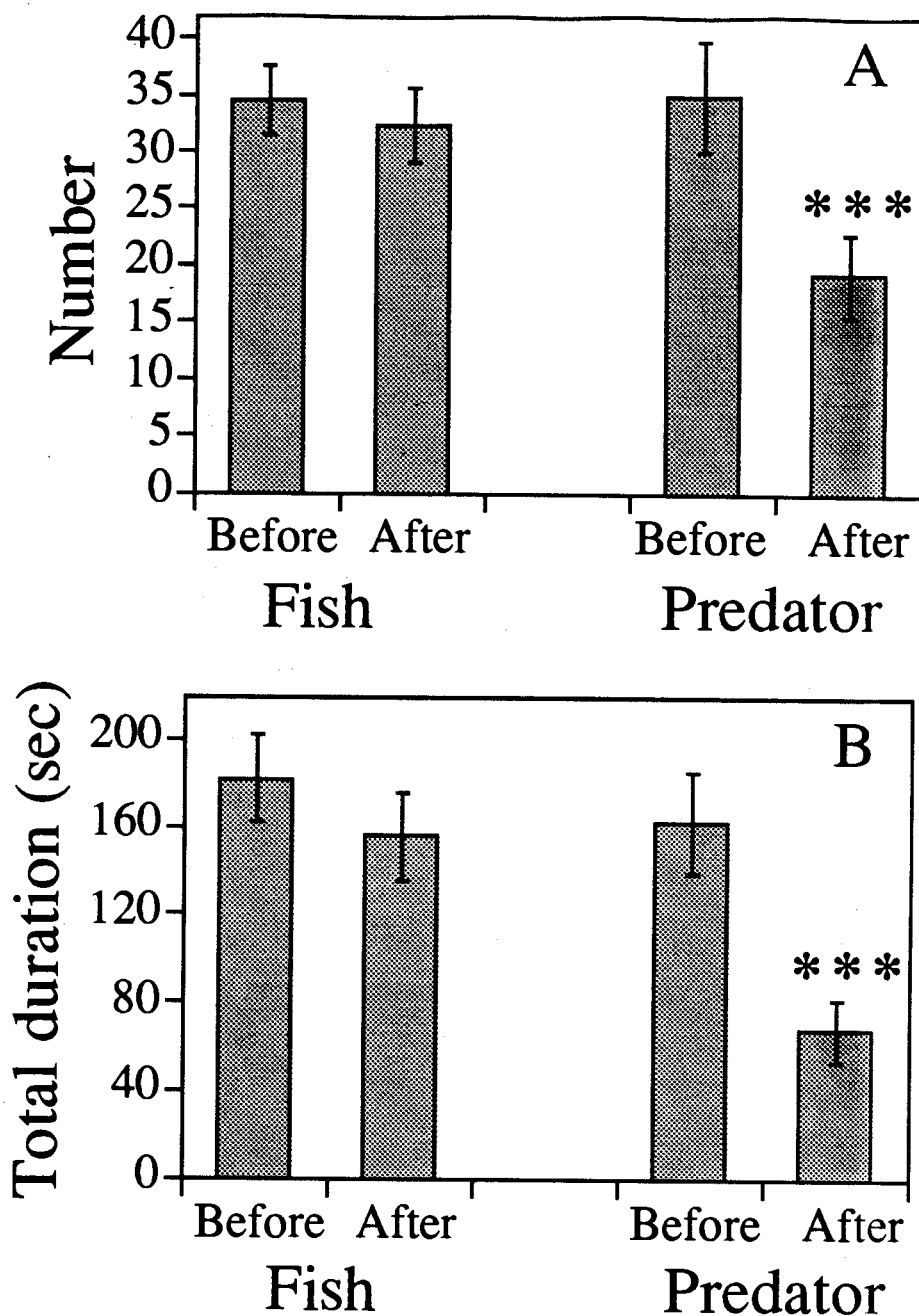
Figure 4.3. The influence of fish or predator odour treatments on mean aggression parameters (± s.e.) of juvenile coho salmon. All measures pertain to all mirrors combined. Fish : fish-conditioned water, Predator: predator-conditioned water. A) Number = total number of aggressive behaviours, B) Total duration = total duration (sec) of all aggressive behaviours combined, N = 16.
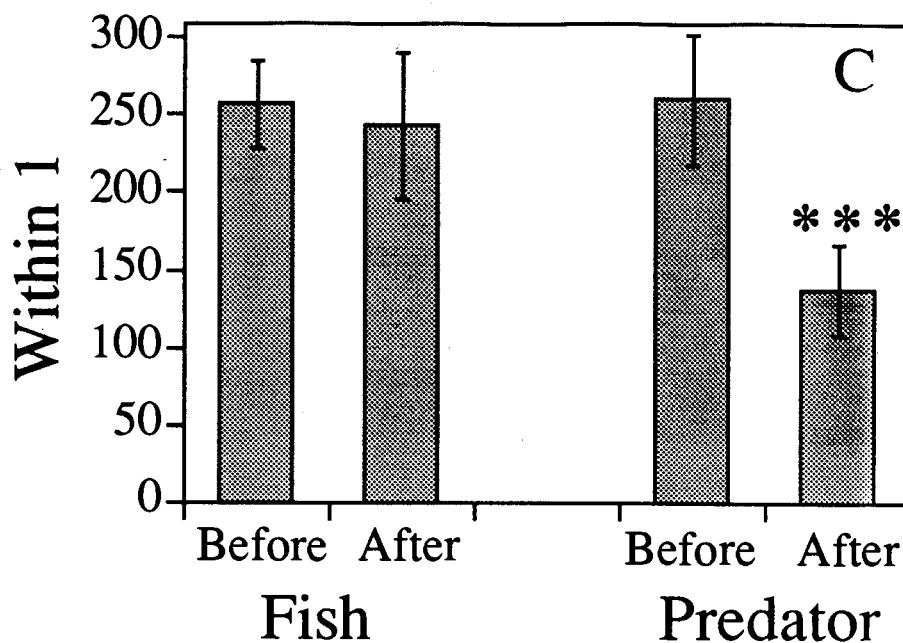
Figure 4.3. The influence of fish or predator odour treatments on mean aggression parameters (± s.e.) of juvenile coho salmon. All measures pertain to all mirrors combined. Fish : fish-conditioned water, Predator: predator-conditioned water. C) Within 1 = Total time (sec) spent within one body length of mirrors. ***: P < 0.001 (Wilcoxon's signed rank test). N= 16.

Table 4.2. Percentage of their time budget juvenile coho spent in various aggressive activities before and after injection of merganser odour. S.e. are in brackets. Behaviours are ranked in decreasing order of intensity. P = significance of Mann-Whitney U', N = 16 before and N = 13 after.

Behaviour	Percentage of time spent in aggressive activities		
	Before predator odour	After predator odour	P
Nip	1.46 (0.89)	0.00 (0.00)	< 0.01
Swim Against Mirror	53.98 (4.89)	39.55 (6.62)	0.09
Charge	1.64 (0.50)	2.59 (1.45)	0.46
Lateral display	11.80 (3.69)	5.99 (1.58)	0.51
Facing mirror	5.06 (3.11)	2.34 (2.34)	0.05
Approach	26.09 (3.22)	49.49 (5.94)	< 0.01

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 juvenile Atlantic salmon (Gotceitas and Godin 1991) presented with visual models of predators 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. It is possible but unlikely that the fish used in the experiment were not reacting to merganser odour alone. Adult and juvenile coho sometimes show a fright reaction (Brett and MacKinnon 1952) 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 methods). The fish were probably not responding to alarm pheromones ("Schreckstoff"; Frisch 1938): such pheromones are contained by epidermal cells and released when the skin is broken, but there is no report in the literature about the presence of such cells in any salmonid (Pfeiffer 1977).

Prey attack distance decreased by about one body length (29 %) 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 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 eventually 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 (Chapter 3). 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 at sea (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 in their environment, juvenile coho significantly reduced the frequency of their agonistic activities, the amount of time they spent in such activities, the amount of time they spent near mirrors and altered the average aggressive intensity of their behaviours. They also significantly reduced the average duration of their aggressive interactions, a result similar to that obtained in the field (Chapter 2). This eliminates reduced activity as an alternate explanation for the observed decrease in aggression. Although the experimental fish always faced "competitors" performing the same behaviours simultaneously, we feel justified relating our results to those obtained in 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 1990, and references within).

In juvenile salmonids, proximity to conspecifics is not necessarily dictated only by agonistic motivation. Indeed, when predators are nearby, some fish form 'fright huddles' (Mason 1966),

and territorial juvenile coho have sometimes been observed to do this when mergansers are detected upstream (Martel, unpubl. obs.). However, in the laboratory any time spent in close proximity of the mirror is likely to have reflected aggressive interactions alone: time spent within one body length of the mirrors decreased when merganser-conditioned water was injected in the system.

Aggressive, territorial coho grow faster than non-territorial individuals (Chapter 2), 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 appear to increase the probability that the fish will be detected by predators (Chapter 3). This represents an example of the classic growth-mortality trade-off faced by juveniles of many species (Gilliam 1982; Werner and Gilliam 1984). 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.

A more convincing test of a trade-off between mortality risk and growth in juvenile coho would vary one of the two parameters and determine whether the resulting changes in behaviour agree with the predictions of the trade-off model. 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.

Territorial juvenile coho were observed to decrease their aggression levels in the field when mergansers they could not see were upstream (Chapter 2). Because intrusion rate on the territories could not be monitored independently, it was not possible to assess if merganser odour had a direct effect on the territory owners or if its effect was indirect through a reduction on the intrusion rate of conspecifics (i.e., fewer attacks could have just meant fewer intrusions). Although predation risk may affect other fish and hence intrusion rate, our results 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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Chapter 5:

General discussion

What do juvenile coho 'want'? Coho salmon first go through a period of freshwater residence, then spend from one to three summers at sea before finally coming back to their natal stream to spawn. There are indications that size at smolting is positively correlated with the probability of surviving the sojourn at sea (see literature cited in Chapter 2), and thus of spawning. Hence individual coho should be selected to optimize their size at the end of their freshwater period, and consequently their growth during that time. So any behaviour which increases growth rate in freshwater might be expected to spread among coho populations as long as it is heritable. Territoriality may be such a behaviour: territorial coho are larger than other fish (Chapter 2; Puckett and Dill, 1985) and I have shown that they grow faster than floaters (Chapter 2).

But territoriality probably has costs as well. Animals expose themselves to predators through their activities, and territorial behaviour is one activity which could affect risk of mortality. One way territorial behaviour could increase the probability of an animal being killed by a predator is if this behaviour competes for attention which could be directed towards predator detection. This has already been shown for foraging behaviour, which has been demonstrated to carry a cost in terms of reduced likelihood of predator detection or increased predator vulnerability. For example, Milinski (1984) showed that sticklebacks (*Gasterosteus aculeatus*) feeding at a high rate were less likely to react to an overhead model of an avian predator, and FitzGibbon (1989) reported that cheetah (*Acinonyx jubatus*) tended to attack more often the least vigilant Thomson's gazelles (*Gazella thomsoni*).

If foraging uses time which could be spent in vigilance for predators, it is probable that territorial activities carry similar costs. A conflict will arise if territorial fish need time to assess the threat posed by intruders on their territory and if their ability to detect predators is reduced during this

period. The territorial juvenile coho that I tested reacted in ways consistent with their facing a conflict between territorial activities and vigilance for predators: they reduced the duration of their aggressive interactions when mergansers were present. The fish also decreased the average duration of their movements (aggressive or otherwise). This can be interpreted either as an attempt by the fish to make themselves less detectable by the mergansers (I showed in Chapter 3 that mergansers attacked coho who moved more often than coho who were stationary), or as an attempt to get more frequent updates about their surrounding environment, i.e., increased vigilance rate. These two hypotheses are not mutually exclusive. In either case, the territorial fish, by decreasing aggression, may trade-off some territorial gains (growth) for protection from predation, or reduced mortality.

Such a tradeoff implies that a cost in the present (probability of death by predation) is weighed against a benefit in the future (growth). Thus, the solution to the tradeoff will depend, on the one hand, on what the fish perceive the risk of predation to be (how risky the environment is), and on the other hand, on what they perceive their future growth trajectory to be. The tradeoff can therefore be tested by manipulating either potential for growth or risk of predation. I will now discuss these two aspects in more detail.

Potential for growth

The present study has shown that territory owners decrease the percentage of their time budget allocated to aggressive interactions when mergansers are present. However, most fish remained on their territories and continued to engage in intraspecific aggression while they presumably sensed the mergansers, indicating that they assessed the benefits of at least some level of

aggression as outweighing the costs of mortality. These benefits are long-term (growth), and fish need to be able to assess their growth rate into the future. An individual fish's potential for future growth should be related not only to its own state (itself a function of size, physical condition, prior duration of territory ownership, etc.), but also to the state of other individuals in the population (potential for competition for food) and to the state of the environment (food abundance, long-term predation risk). The hypothesis of a tradeoff between growth and mortality can therefore be tested through manipulation of these variables.

If aggression and movement are positively correlated with risk of death, then, when predators are detected, fish with high growth potential should choose the less risky behavioural options, i.e., reduce aggression and movement. Territorial coho grew faster than floaters (Chapter 2). Thus, their potential for growth was greater than that of floaters. Floaters were chased by territory owners and their ability to compete for space was therefore low. Under the hypothesis of a tradeoff between growth and mortality, weak competitors (fish with low growth potential) should accept proportionally more risk than strong competitors if this translates into higher energy gains. While territorial fish decreased both movement and aggression when mergansers were present, the two floaters I have data for actually increased the percentage of their time budget devoted to both swimming and feeding while a merganser was present (Appendix B), which lends support (albeit weak) to this argument.

Territorial coho are also larger than floaters (Chapter 2), and size and competitive ability are probably related. A test of the influence of relative size (and hence competitive ability) on the tradeoff between growth and mortality would be to rear fish in populations (in tanks or in field enclosures) with different size distributions. Fish of a given size should accept more risk (be more aggressive towards mirror images or travel further to attack food items when a predator is present) if they are smaller than their population's average size than if they are larger.

Growth is determined by food intake, which is in turn determined, in part, by the ability to obtain food. This ability is partly determined by the level of competition, which should depend on the relative condition of the contestants and on the number of competitors. From the point of view of territory owners, an increase in competitor density increases the likelihood that food items will be intercepted before they can seize them, and in the long term reduces growth. Juvenile coho tested in the laboratory travelled greater distances to attack drifting flies when in the presence of simulated competitors (mirrors), even following presentation of a predator model (Dill and Fraser, 1984), indicating that they traded some risk of mortality for energy gains.

One of the main effects of competitor density on territorial behaviour is that time devoted to aggression should first increase as the number of competitors increases and then gradually decrease as the benefits of aggressive acts are increasingly devalued by the cost they entail in lost foraging time and energy intake (e.g., Hixon, 1980). Thus, optimal territory size is expected to first remain constant and then decline with increases in competitor density (Dill, 1978). This negative relationship between competitor density and feeding territory size has been documented in fish (e.g., Tricas, 1989 and references within). The effects of predation risk on the relation between competitor density and territorial behaviour remain largely undocumented, however. Territorial coho reduced their general aggression level when they sensed the presence of mergansers (Chapters 2 and 4). Increasing predation risk may thus reduce the time territory owners invest in territory defense at any level of intruder pressure. However, increasing the number of competitors may also decrease the perceived predation risk per fish (dilution effect), which may negate the effect of predator presence on aggressive behaviour. In order to distinguish between these two hypotheses, further work is needed on how fish density affects their probability of detection and successful attack by piscine and avian predators.

Reduction of food availability is another possibility for testing the tradeoff between growth and mortality. Fish will face a decrease in growth rate as food availability decreases; a decrease in food availability is equivalent to an increase in competition. Under the tradeoff hypothesis, and assuming once again that aggression is positively correlated with increased vulnerability to predation, aggression level at all food densities should be lower under predation risk when compared to aggression in the absence of predation risk, but the effect of predation risk should be smallest at low food densities.

Risk of predation

Juvenile coho were shown to react to merganser odour both in the field and the laboratory (Chapters 2 and 4). The results were analysed in terms of predator presence or absence. Thus, predation risk was assumed to be either high or low, with no values in between. A more complete test of the tradeoff hypothesis would be to generate intermediate values of predation risk. The danger posed by predators is a function not only of their presence, but also of the frequency of their visits and of their distance from the prey (e.g., Dill, 1974). As suggested in Chapter 4, one could vary the perceived predation risk by varying the concentration of merganser odour. However, the threshold reactions of salmon chemoreceptors would need to be thoroughly assessed and the behaviour of the fish would need to be titrated with regard to different odour concentrations before one could vary the predation risk in a way meaningful to juvenile coho. In Chapter 2, I reported the results of an experiment in which I attempted to vary the frequency of predator presence, where this presence was sensed through chemoreception and possibly through sound (I doubt the fish could have seen the birds). These results were inconclusive, and I could not determine if this was due to a lack of power of the statistical tests or to the variation in predation risk not being meaningful to the fish.

In vertebrates, at least, vision appears to be an important sense for predator recognition. Indeed, several authors working with juvenile salmonids have successfully used models of predators to mimic predation risk (e.g., Dill and Fraser, 1984; Metcalfe *et al.*, 1987; Gotceitas and Godin, 1991). Juvenile Atlantic salmon were shown to react more strongly (in terms of latency to resume foraging) to models of avian than to models of piscine predators (Gotceitas and Godin, in press), indicating that they discriminate visually between potential predators. Studies of the effect of predation risk on juvenile salmonid territorial behaviour may therefore lead to results easier to interpret if the predators are seen, rather than smelled, by the fish.

Animals can assess differences in predation risk between habitats (predators may be more abundant in certain areas; e.g., Gilliam and Fraser, 1987), between time periods (a predator may appear and then disappear; e.g., Metcalfe *et al.*, 1987), or with regard to the distance separating them from an approaching predator (e.g., Dill and Houtman, 1989). Frequency of predator presence could easily be varied in a set-up similar to the one I used for this work while ensuring that competitor density and food abundance remained constant among treatments (although I did not assess the food density in the enclosures in the present work, the feeding frequency of the fish did not differ significantly between enclosures). Predator presence could be varied by presenting the fish with models of mergansers at various intervals. If territorial activities increase vulnerability to predation (either through competition for time with vigilance-related activities or through their associated movements), there should be a negative relationship between frequency of predator presence and aggression (measured either as percent of time budget allocated to aggressive activities or as duration of aggressive interactions).

The present work shows that some of the territorial activities of juvenile coho salmon were affected by the presence of common mergansers, who were assumed to represent a risk of

mortality. This risk could not be quantified, and throughout this thesis I have equated risk of detection by mergansers with risk of mortality. The actual risk of mortality by mergansers should be a function of the probability of attack by the birds and of the probability of attack success. Wood (1984) estimated the attack success of adult mergansers foraging for juvenile coho in stocked enclosures in the field to be between 12% (for fry ≤ 2 g) and 19 % (for smolts ≤ 40 g). The probability of attack *per se* depends in part on the probability of the fish being detected by the birds. Although it is obvious that a fish detected by a merganser is at greater risk of attack than a fish undetected, the shape of the function between probability of mortality and probability of detection remains unknown. Even though preliminary laboratory work failed to develop adequate methods to establish the nature of the information for which the birds were scanning, I can assert that movement is important in determining the probability of mergansers detecting coho. When mergansers were present upstream of them, territory owners reduced the average duration of most activities involving movement (Chapter 2). That this change in behaviour is adaptive was shown in the laboratory: mergansers took significantly less time to attack fish who moved than fish who were stationary, over a substrate which precluded crypsis (Chapter 3). Since I could not determine exactly where the birds were looking when their submerged heads were directed towards the enclosure (e.g., they could have been looking sideways), the most parsimonious assumption is that they attacked without delay any fish they recognized as such, and that movement from the fish accelerated this recognition process.

Although some individual coho were shown to remain territorial for at least several weeks (Appendix A), it is not yet known whether individuals are genetically bound to adopt the same foraging tactic for the entire length of their stream residence (this would then be termed a "strategy", following the definition proposed by Gross, 1984), or can switch between foraging tactics. Each tactic presumably has different costs and benefits, and a logical extension of this work would be to model the sequential decisions of coho juveniles regarding the adoption of

territoriality or of another foraging tactic such as floating. There was in fact an earlier attempt to use the technique of dynamic programming (Mangel and Clark, 1986, 1988; Houston and McNamara, 1988) to model these decisions. Unfortunately, this turned out to be one of these increasingly rare cases where the current state of technology limits our theoretical progress.

Coho cease to be territorial once they migrate to the sea, so the model was only concerned with the decisions juveniles made from emergence to the end of stream residence (T). This residence time was then partitioned into segments (time periods, t), and for any size x at a given t the expected fitness of each tactic was calculated from t to T. The dynamic model assumes that fish should be selected to opt for the foraging tactic which maximizes their fitness at each t. The problem lies with the fact that fitness at each size will be a function of both the size and the number of individuals in the population. This is because the decision of any individual to become territorial will depend on its ability to compete against other fish. This ability is usually size-related. Growth, as shown in Chapter 2, and mortality, if different tactics expose their adherents to different risks of predation or if the predator is size-selective (e.g., Appendix C), can thus be seen as size-dependent. Also, the model assumes that as the number of territorial fish (competitors) increases, growth decreases. Thus, fitness at time t will be a function of the population size distribution at that time. This size distribution changes over time: fish grow larger and individuals die. For each time period the algorithm thus needs to calculate the expected fitness of every size given all possible size distributions. Mangel and Clark (1988) estimate that, for a population of 100 fish ranging in size from 30 to 50 mm in 1 mm steps, the total number of size distributions would require over 10^{18} megabytes of computer memory, which in their words is "...the curse of dimensionality with a vengeance" (p. 279).

Predation risk has been documented to be important in both ecological and evolutionary time. The foraging behaviour of juvenile coho salmon is likely under strong selective pressures by

mergansers, as these birds have been shown to be capable of eating large numbers of coho (Wood, 1987). Indeed, this thesis has shown the territorial behaviour of juvenile coho to be affected by a perceived predation risk posed by mergansers, in a way which is consistent with the fish being sensitive to a tradeoff between energy gains and cost of mortality. Coho have basically three options in terms of foraging tactics —territoriality, floating, and non-territoriality— and the present work has also demonstrated some of the relative benefits of these options: territorial fish grew faster than floaters (Chapter 2), partly because of lower caloric costs per feeding motion (Puckett and Dill, 1985). In order to predict the effect of predation risk on any social system one needs to measure or estimate the relative payoffs and costs of the options available to the individuals. This thesis is a small, but hopefully significant, step towards the realization of this objective in the context of stream salmonid territoriality.

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Appendix A:
Juvenile coho salmon site fidelity

Introduction

As mentioned in the General Introduction, I first had to ascertain that the juvenile coho population whose behaviour was to be observed in the presence of mergansers did exhibit territorial behaviour. Juvenile coho have been reported to be territorial by many authors (e.g., Hartman, 1965; Mason, 1966; Dill *et al.*, 1981; Puckett and Dill, 1985), usually on the basis of their showing intraspecific aggressive interactions over specific areas in streams. However, none of these authors has reported the long-term occupation of specific areas. I present here some data on the distribution of juvenile coho in semi-natural environments which indicate that fish may remain in specific areas for many days.

Methods

The experimental design was similar to that described in Chapter 2: two 5 x 3 x 0.15 m enclosures (average water depth 9.5 cm) were built in Moody's channel, and each was stocked (on July 25 and 27, 1988, respectively) with 30 marked juvenile coho captured in the channel. Fifty flat rocks (approximately 100 cm^2 each) were painted orange, numbered and distributed in a 10 x 5 grid pattern within each enclosure, and maps (1:500 scale) were prepared for each enclosure. Observations were conducted from August 2 to September 3, weather permitting. No merganser was introduced into the channel during this time. Each observation day, fish were chosen randomly in a given enclosure and followed for 5 min with binoculars from the bank of the channel. The positions of these fish were marked on a map of the enclosure, in relation to nearby numbered rocks, every 20 sec, unless the fish was lost from sight. There were

consequently up to 15-16 observations for each fish. The 5 min time period was too short to allow for the recording of many aggressive interactions. Thus, although the fish did behave aggressively to intruders and neighbours, these observations are more indicative of site fidelity than of territoriality *per se*. Most observations were carried from 10:00 to 15:00h, and from 10 to 15 fish were observed per enclosure per day.

A grid was subsequently superimposed over each map and the number of marks (= sightings) per quadrat (approximately 0.63 x 0.63 m each) was tallied. The relative usage of each quadrat was then expressed as the percentage of the total of sightings per observation period. 17 fish were observed in each enclosure more than three times over a period of at least 12 days. The other fish were either sighted at various locations within the enclosures, escaped (some marked fish were seen outside the enclosures), or perished.

Results and Discussion

Results are presented for 14 fish whose records have been analysed at the time of this writing . Having examined the distributions for the other fish, I believe these 14 to be representative of the fish in the two enclosures. Each figure depicts the percentage occupancy of given quadrats in a 5 min observation period. Even though no statistical analysis was performed on site fidelity, it is clear that the fish remain in localized areas for periods ranging from 12 to 30 days. The fish were prevented from moving to other areas of the stream, and the relevance of these data to natural environments may be questioned. However, Nielsen (1992) reported emigration rates of marked coho from natural pools varying from 40 to 73% . Although this rate of emigration may be inflated (she did not estimate mortality and reported having found only 22 to 29% of the missing

fish in other locations), this is similar to the percentage of fish who either did not show any site fidelity or disappeared from the enclosures (43 %) in this study.

Fish: BP

day 1

day 6

≥90 %

80 - 89 %

70 - 79 %

60 - 69 %

50 - 59 %

40 - 49 %

30 - 39 %

20 - 29 %

10 - 19 %

≤9 %
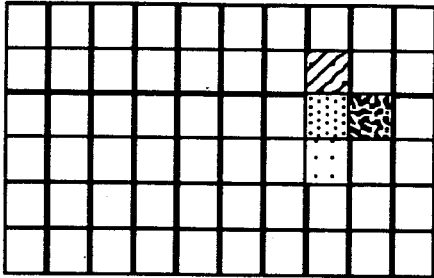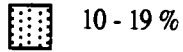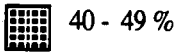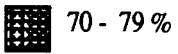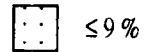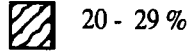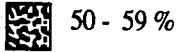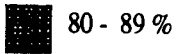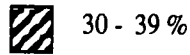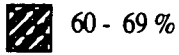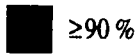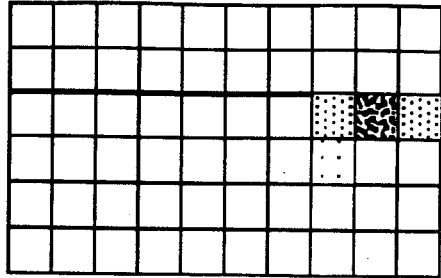
day 18

day 21
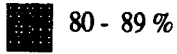
Fish: bw

day 1

day 2

≥ 90 %

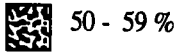80 - 89 %

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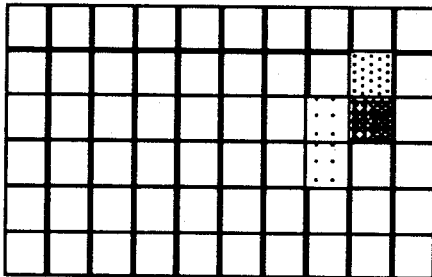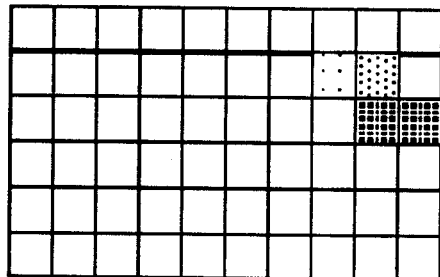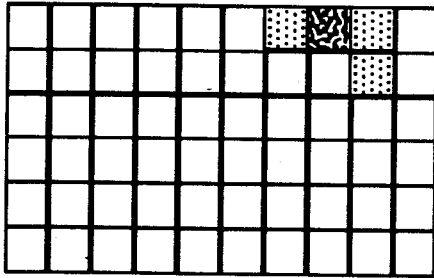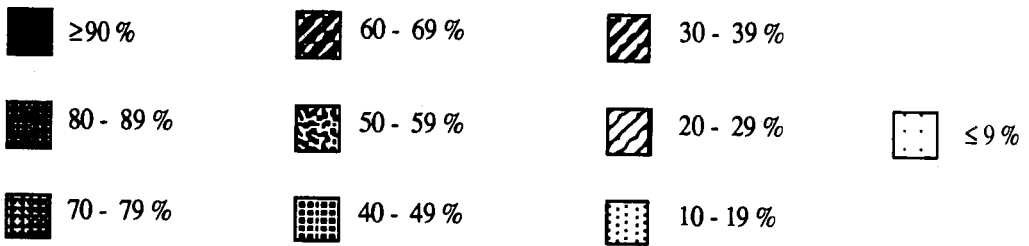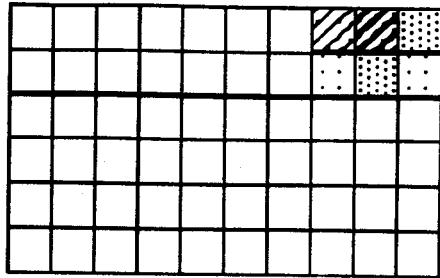
day 30
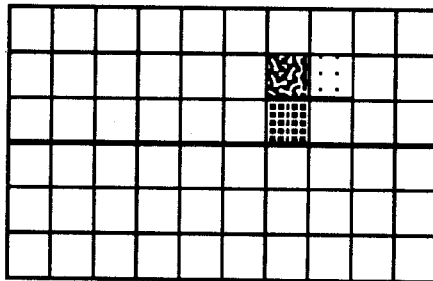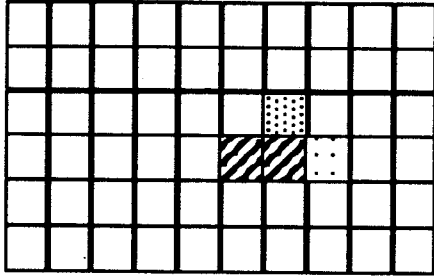
Fish: BW

day 1

day 11
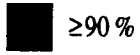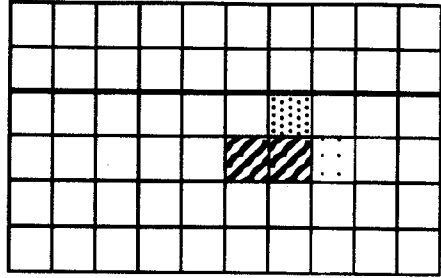
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80 - 89 %	50 - 59 %
70 - 79 %	40 - 49 %

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day 16
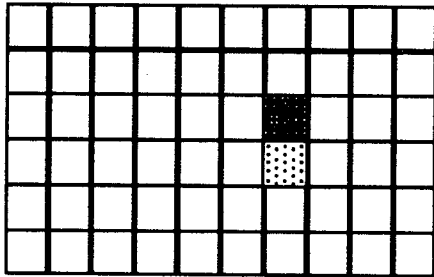
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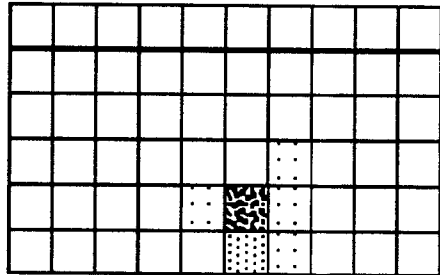
Fish: BW (c'td)

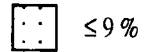day 29

day 32

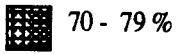|		
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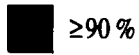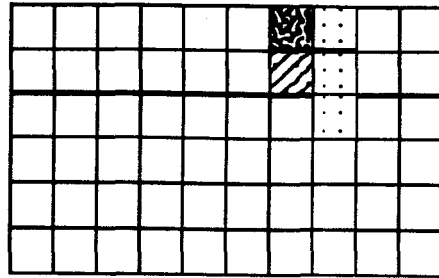
Fish: GG

day 1

day 4

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▦ 80 - 89 %	▨ 50 - 59 %
▦ 70 - 79 %	▦ 40 - 49 %

▨ 30 - 39 %	
▨ 20 - 29 %	⬚ ≤ 9 %
▦ 10 - 19 %	

day 8

day 14

Fish: GG (c'td)

day 20
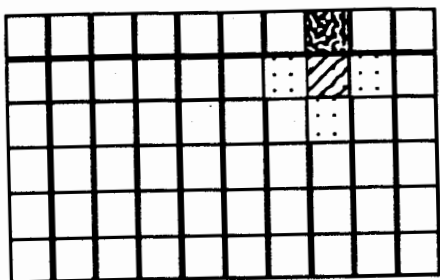
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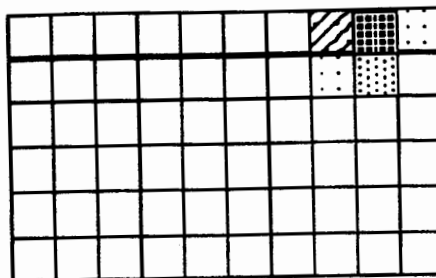
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	80 - 89 %		50 - 59 %		20 - 29 %	≤ 9 %
	70 - 79 %		40 - 49 %		10 - 19 %	

Fish: Ggr

day 1

day 4

≥ 90 %		60 - 69 %		30 - 39 %
80 - 89 %		50 - 59 %		20 - 29 %		≤ 9 %
70 - 79 %		40 - 49 %		10 - 19 %
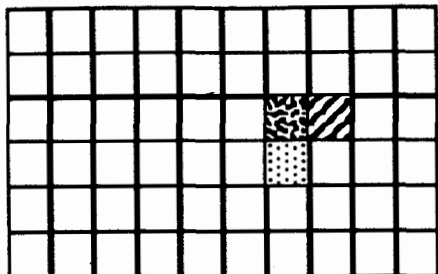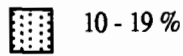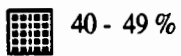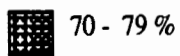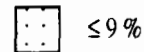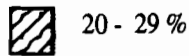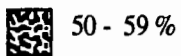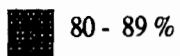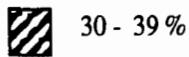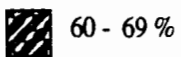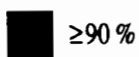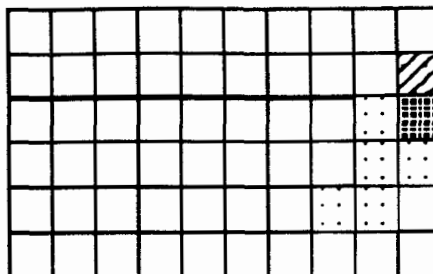
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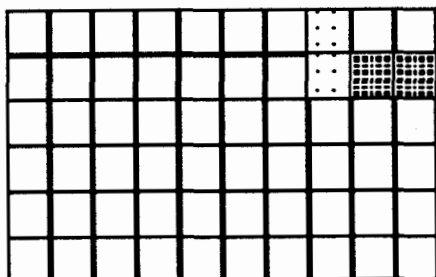
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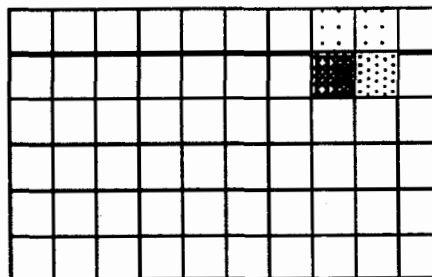
Fish: Ggr (c'td)

day 22
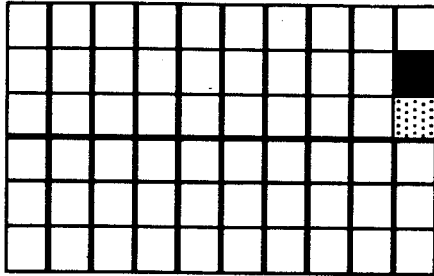
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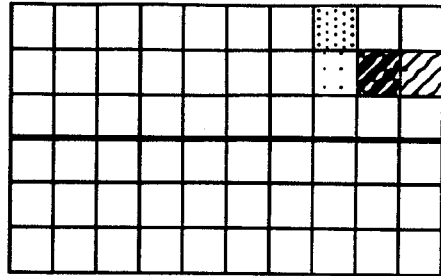
	≥90 %		60 - 69 %		30 - 39 %
	80 - 89 %		50 - 59 %		20 - 29 %		≤ 9 %
	70 - 79 %		40 - 49 %		10 - 19 %

Fish: GO

day 1

day 8

■ ≥90 %	▨ 60 - 69 %	▨ 30 - 39 %
▦ 80 - 89 %	▨ 50 - 59 %	▨ 20 - 29 % ⬚ ≤ 9 %
▦ 70 - 79 %	▦ 40 - 49 %	▦ 10 - 19 %

day 12

day 15

Fish: GrO

day 1

day 3

■ ≥90 %	▨ 60 - 69 %	▨ 30 - 39 %
▦ 80 - 89 %	▨ 50 - 59 %	▨ 20 - 29 %
▦ 70 - 79 %	▦ 40 - 49 %	▦ 10 - 19 %

☐ ≤ 9 %
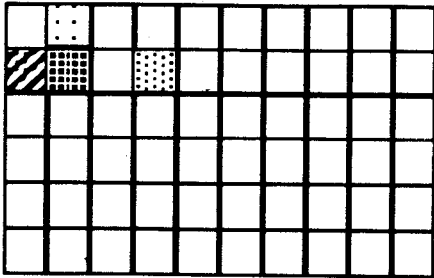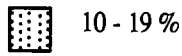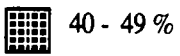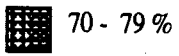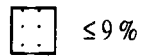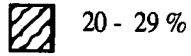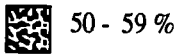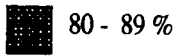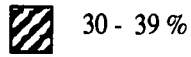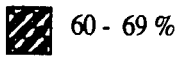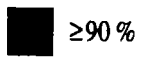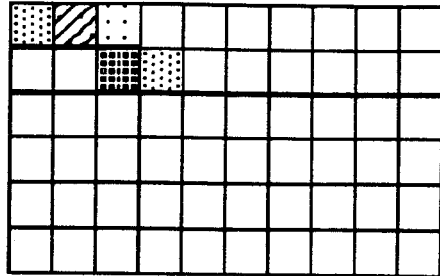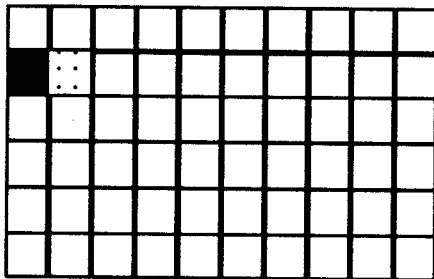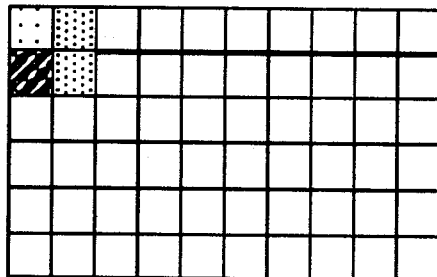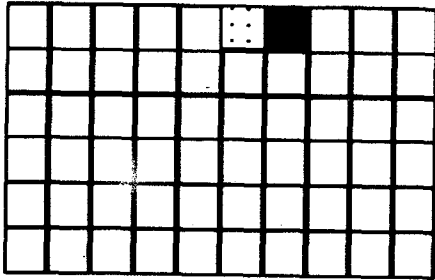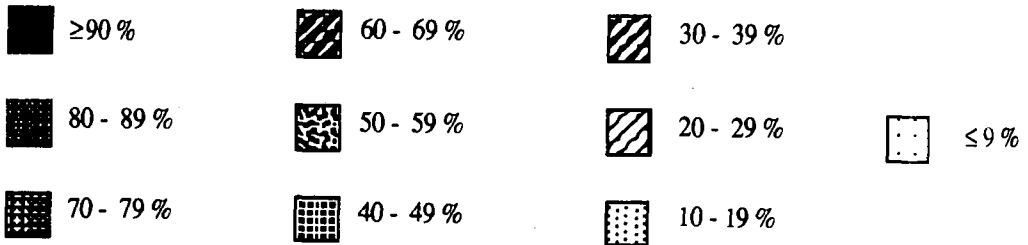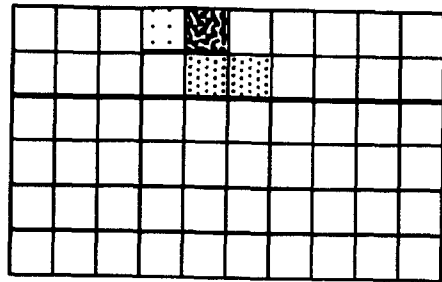
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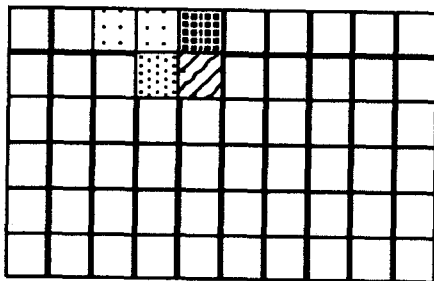
day 12

Fish: GrO (c'td)

day 13

day 14

	≥90 %		60 - 69 %		30 - 39 %
	80 - 89 %		50 - 59 %		20 - 29 %
	70 - 79 %		40 - 49 %		10 - 19 %

≤ 9 %

Fish: GW

day 1

day 15

■ ≥90 %	
▨ 80 - 89 %	
▦ 70 - 79 %	

◪ 60 - 69 %	
▨ 50 - 59 %	
▦ 40 - 49 %	

|	
▨ 30 - 39 %	
▨ 20 - 29 %	▫ ≤ 9 %
⋮ 10 - 19 %	
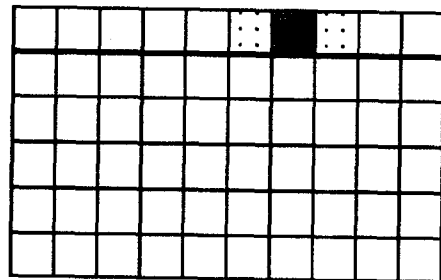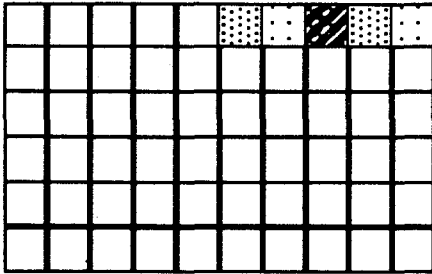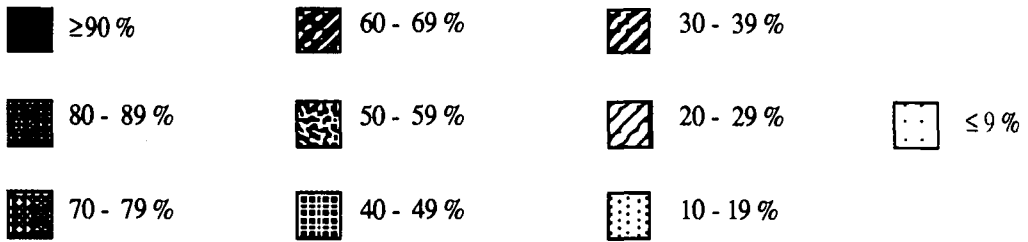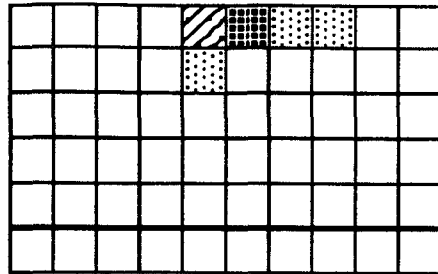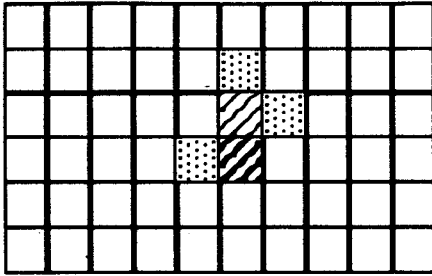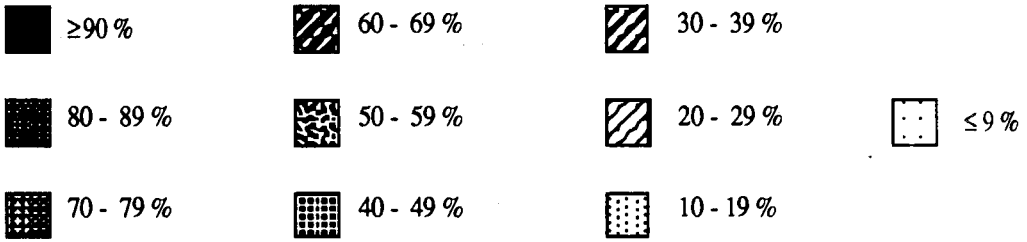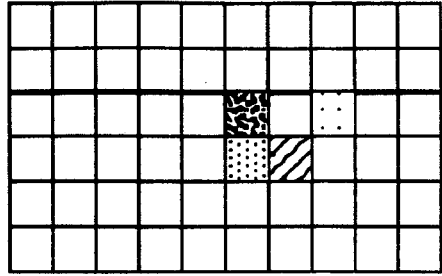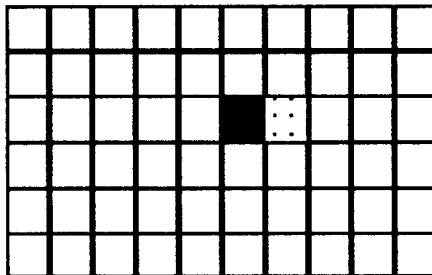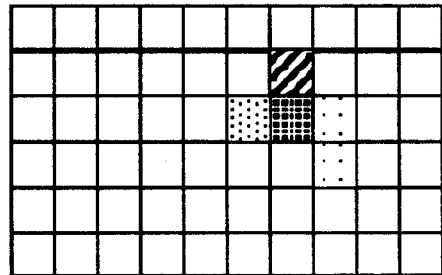
day 20

day 22

Fish: GW (c'td)

day 28
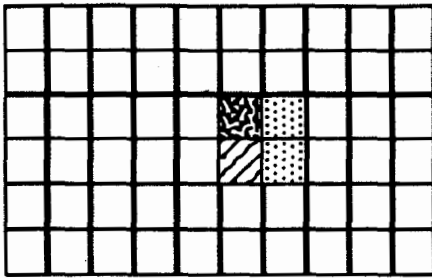
day 30
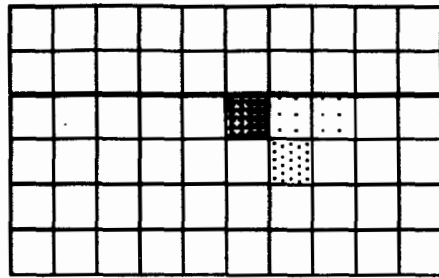
■ ≥90 %	▨ 60 - 69 %	▨ 30 - 39 %
▓ 80 - 89 %	▨ 50 - 59 %	▨ 20 - 29 % · · ≤ 9 %
▓ 70 - 79 %	▦ 40 - 49 %	▦ 10 - 19 %

Fish: PW

day 1

day 8

	≥90 %		60 - 69 %		30 - 39 %
	80 - 89 %		50 - 59 %		20 - 29 %	≤ 9 %
	70 - 79 %		40 - 49 %		10 - 19 %

day 14

day 26

Fish: PY

day 1

day 6

≥ 90 %	60 - 69 %	30 - 39 %
80 - 89 %	50 - 59 %	20 - 29 %
70 - 79 %	40 - 49 %	10 - 19 %

≤ 9 %
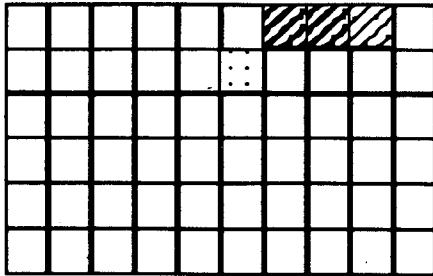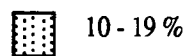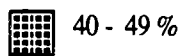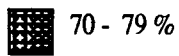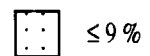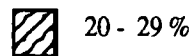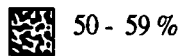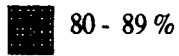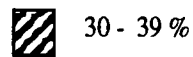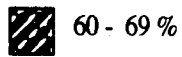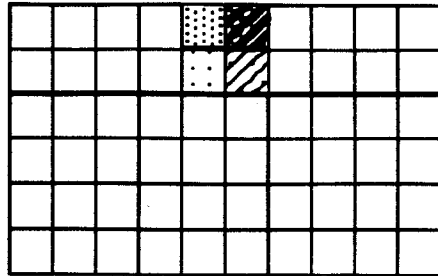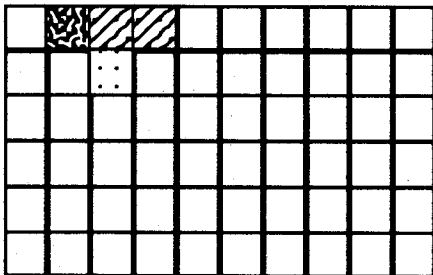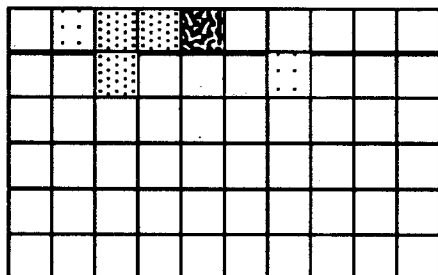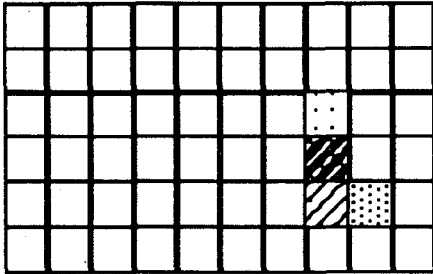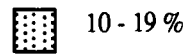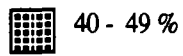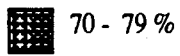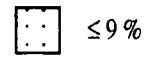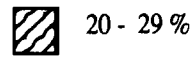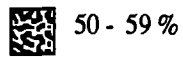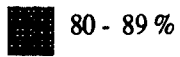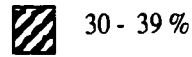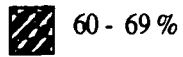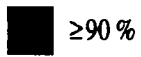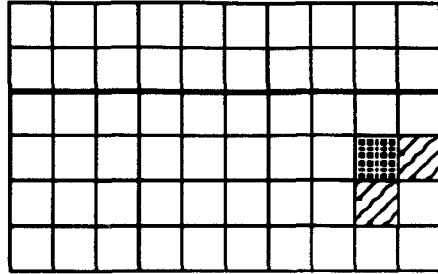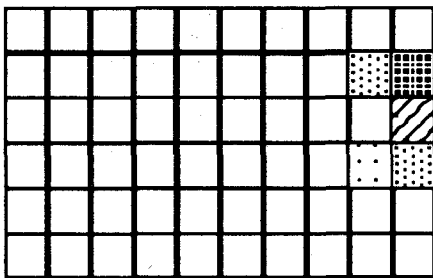
day 18

day 21
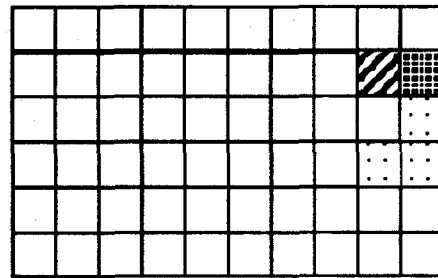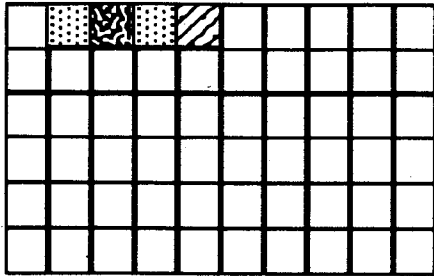
Fish: WO

day 1

day 18
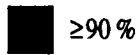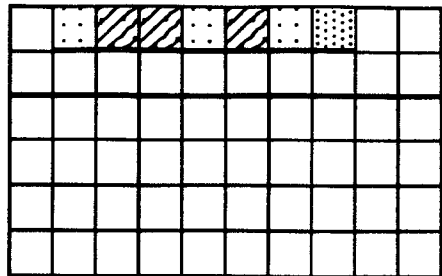
▪ ≥90 %	▨ 60 - 69 %	▨ 30 - 39 %
▨ 80 - 89 %	▨ 50 - 59 %	▨ 20 - 29 %
▦ 70 - 79 %	▥ 40 - 49 %	▨ 10 - 19 %
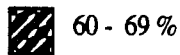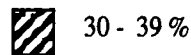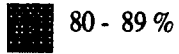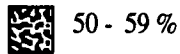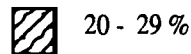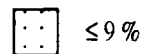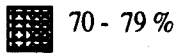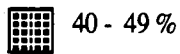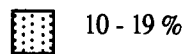
⬚ ≤ 9 %

day 22

day 25

Fish: WY

day 1

day 5

≥ 90 %

80 - 89 %

70 - 79 %

60 - 69 %

50 - 59 %

40 - 49 %

30 - 39 %

20 - 29 %

10 - 19 %

≤ 9 %
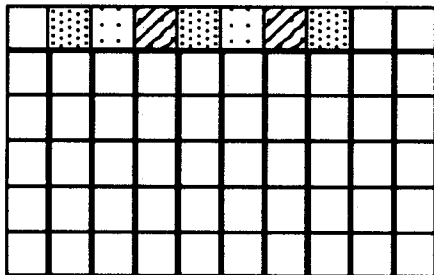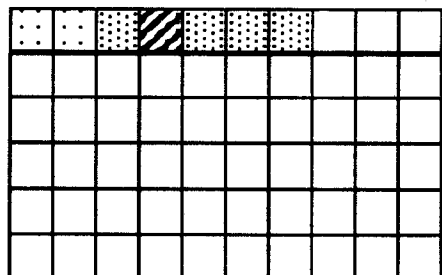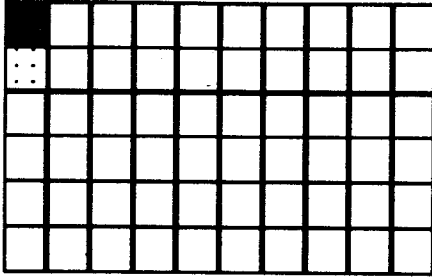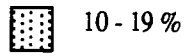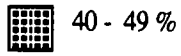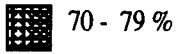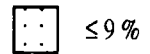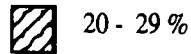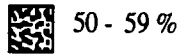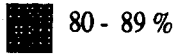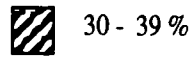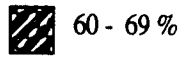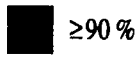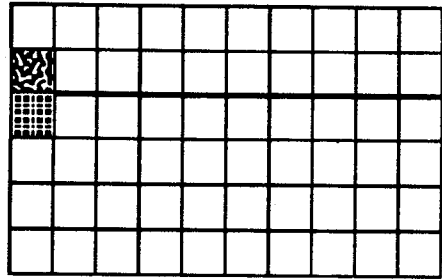
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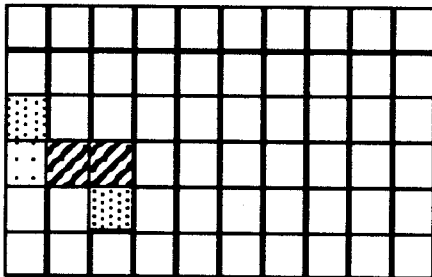
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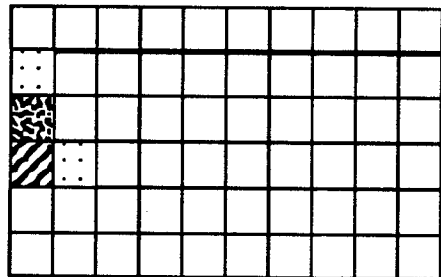
Fish: WY (c'td)

day 20

day 23

	≥90 %		60 - 69 %		30 - 39 %
	80 - 89 %		50 - 59 %		20 - 29 %
	70 - 79 %		40 - 49 %		10 - 19 %

≤ 9 %

Fish: yW

day 1

day 14

Pattern	Range	Pattern	Range	Pattern	Range
■	≥90 %	▨	60 - 69 %	▨	30 - 39 %
▦	80 - 89 %	▨	50 - 59 %	▨	20 - 29 %	□ ≤ 9 %
▦	70 - 79 %	▦	40 - 49 %	▦	10 - 19 %

day 17

day 22
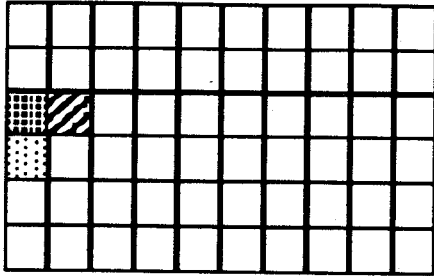
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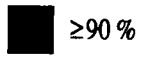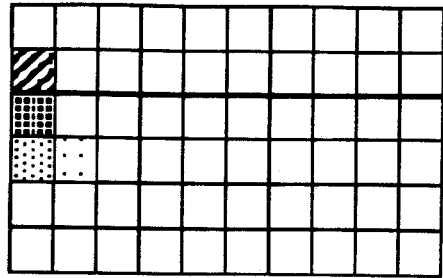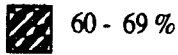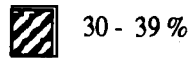
day 23

day 32
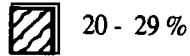
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	80 - 89 %		50 - 59 %		20 - 29 %		≤ 9 %
	70 - 79 %		40 - 49 %		10 - 19 %
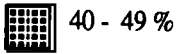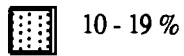
Fish: YW

day 1

day 3
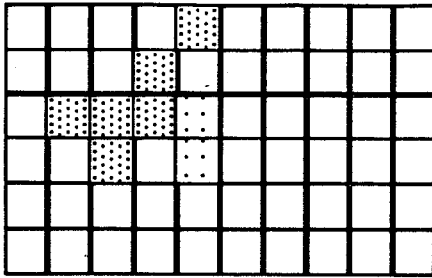
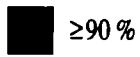|	≥ 90 %		60 - 69 %		30 - 39 %
	80 - 89 %		50 - 59 %		20 - 29 %		≤ 9 %
	70 - 79 %		40 - 49 %		10 - 19 %
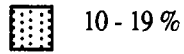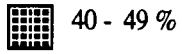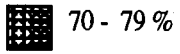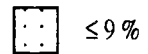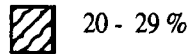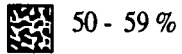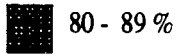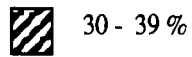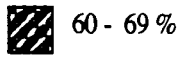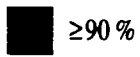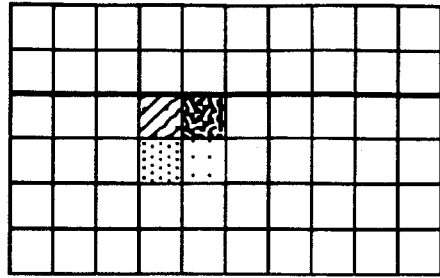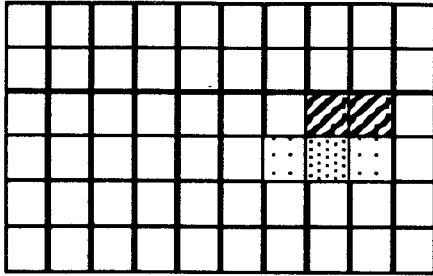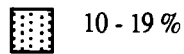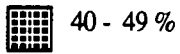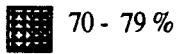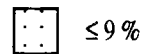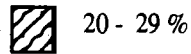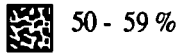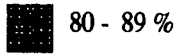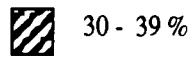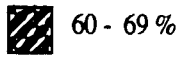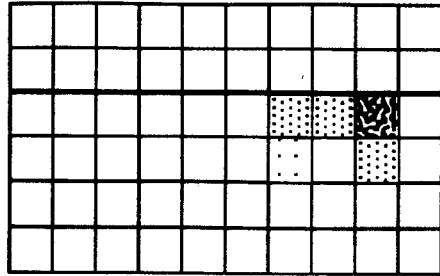
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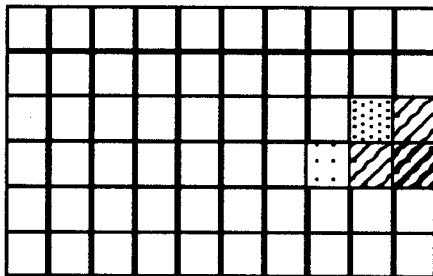
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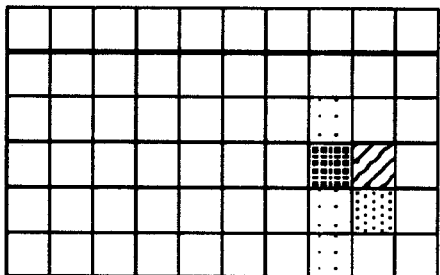
Fish: YW (c'td)

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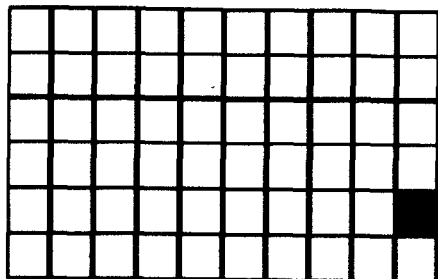
day 19

≥90 %		60 - 69 %		30 - 39 %
80 - 89 %		50 - 59 %		20 - 29 %		≤ 9 %
70 - 79 %		40 - 49 %		10 - 19 %

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Dill, L. M., R. C. Ydenberg, and A. H. G. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (Oncorhynchus kisutch). Can. J. Zool. 59: 1801-1809.

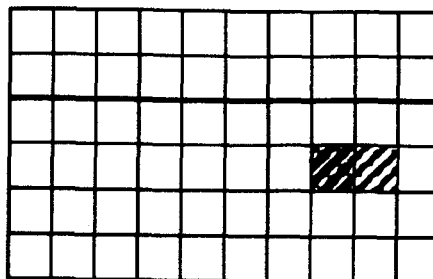Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). J. Fish. Res. Board Can. 22: 1035-1081.

Mason, J. C. 1966. Behavioral ecology of juvenile coho salmon (Oncorhynchus kisutch) in stream aquaria with particular reference to competition and aggressive behavior. Ph.D. thesis, Oregon State University, Corvallis.

Nielsen, J. L. 1992. Microhabitat specific forage behavior, diet and growth rates in juvenile coho salmon. Trans. Am. Soc. Fish. (in press)

Puckett, K. J., and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (Oncorhynchus kisutch). Behaviour 92: 97-111.

Appendix B:
Floater behaviour

Methods

Three floaters were observed: one in the control enclosure on October 15, 1989, and two in the enclosure submitted to two merganser presentations per day (enclosure 2), one on each of October 14 and 15. The methods were identical to those described in Chapter 2. The behaviours observed were also similar to those observed for territorial fish, with the addition of submissive behaviours. These included slow retreat from approaching fish (avoidance) and overt flight from chasing fish. One floater in enclosure 2 could not be observed during the 180 min period (three hours after removal of the merganser) due to low light intensity. The experiment had to be ended earlier than planned because of adverse weather conditions, flooding of the area, and the return of some spawning chum salmon (*O. keta*), precluding a more complete data set.

Results and Discussion

Because of the small sample size, no statistical analysis was carried out on the data. Floaters were occasionally involved in aggressive interactions, but the average percentage of their time budget taken up by these interactions was less than that for territorial fish ($< 2\%$ for floaters (Fig. B.1) vs. ≈ 3.5 to 6 % for territorial fish (Fig. 2.4); data for the period preceding introduction of the mergansers). The following trends in the floater data contrast sharply with those observed in territorial fish: when the birds were present, the average duration of swimming behaviours increased and the average duration of station holding bouts decreased (Fig. B.2); in addition, the

number of feeding behaviours increased (Fig. B.3) . Similar trends can be seen in the percentages these behaviours made up of the total time budget (Fig. B.1)

Territorial fish reduced their overall movements and their aggression level, and tended to feed less, when mergansers were present (Chapter 2). This would have reduced the level of competition for food faced by floaters. If movement increases risk of detection by mergansers (Chapter 3), the present results may indicate that floaters trade off an increased risk of mortality for opportunistic energy gains. Also, the floaters' increase in movement should have increased their opportunity for contact with territorial fish. The fact that the latter actually decreased their aggression level reinforces my conclusion that territorial behaviour was affected directly by the presence of predators.
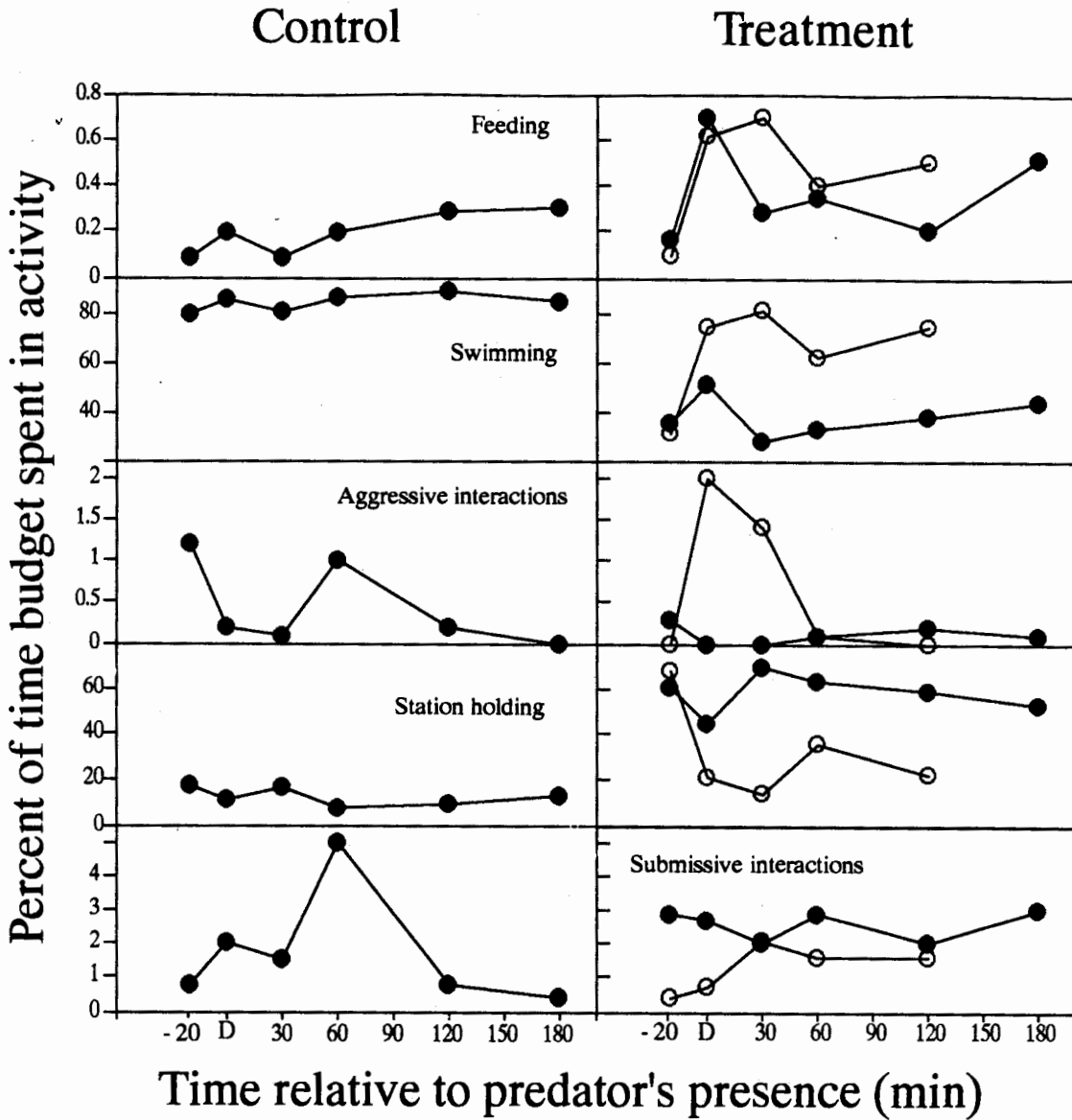
Figure B.1 . Percent of total time budget spent in each behaviour category by floating juvenile coho as a function of the time elapsed relative to a merganser's presence upstream (D = time during which predator present). Different symbols represent different individuals.
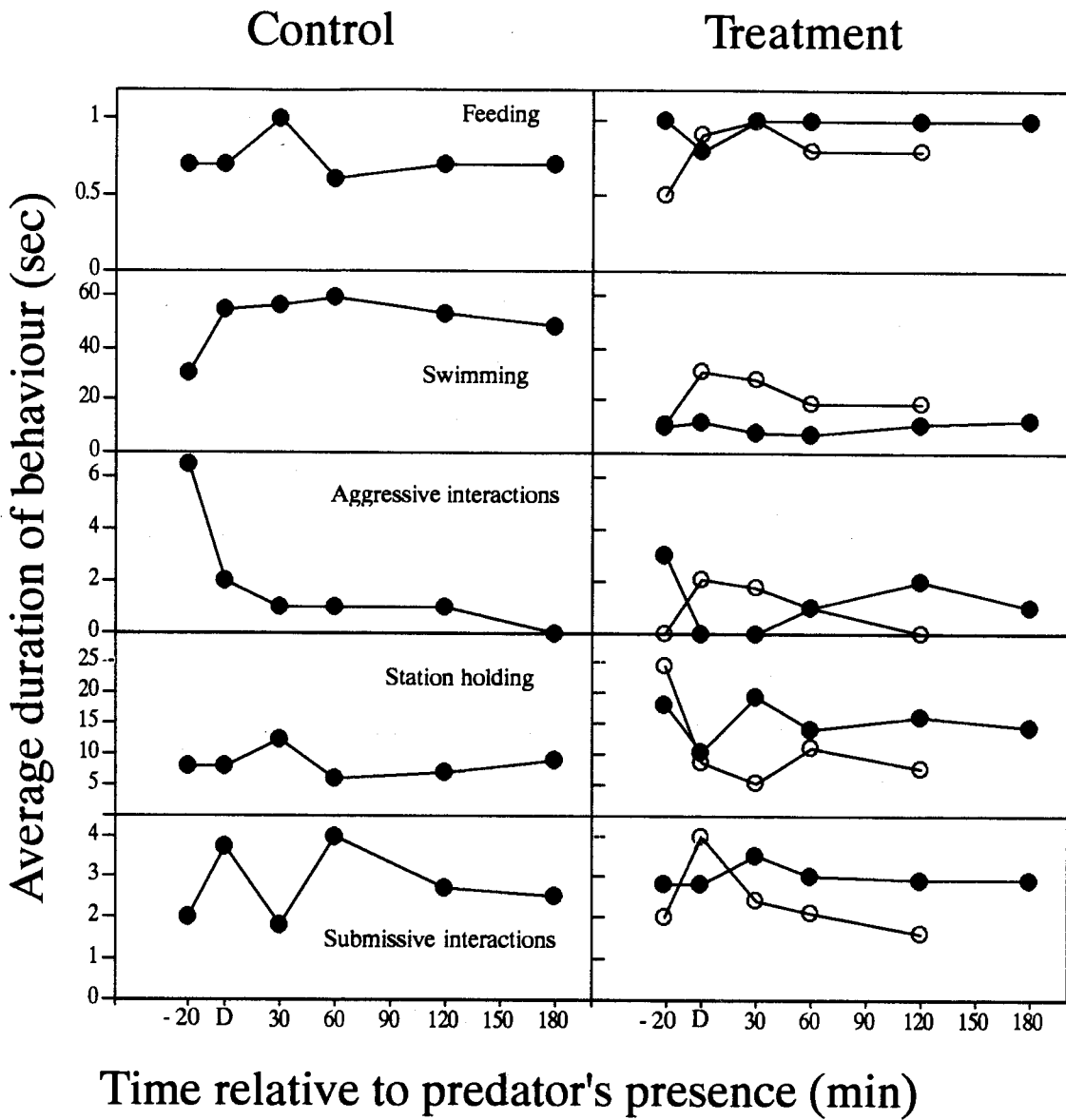
Figure B.2 . Mean duration of behaviour categories recorded for floater juvenile coho as a function of the time elapsed relative to a merganser's presence upstream   Legend as in Fig. B.1.
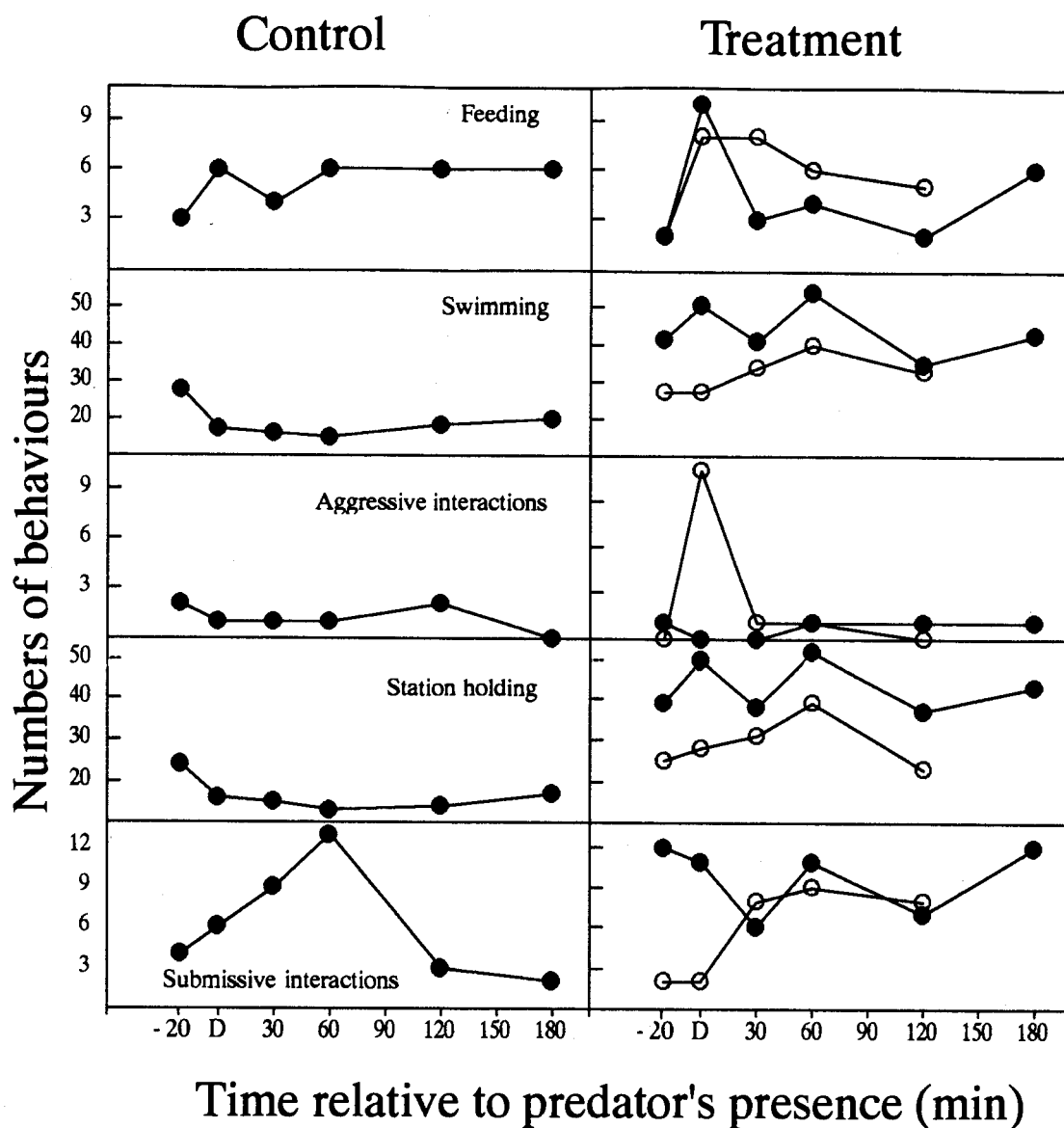
Figure B.3 . Total number of behavioural acts recorded for floater juvenile coho as a function of the time elapsed relative to a merganser's presence upstream.   Legend as in Fig. B.1.

Appendix C:
Size selective feeding by mergansers

Introduction

Most predators have to detect their prey, approach and capture it . Selection should consequently favour potential prey who can break this chain of events. Juvenile coho are cryptic over their natural substrate (Donnelly and Dill, 1984), and territorial coho may further escape detection by common mergansers because they decrease their rate of movement when in the presence of these birds (Chapters 2, 3 and 4). However, field results indicate that territorial juvenile coho are larger than their non-territorial conspecifics (Chapter 2; Puckett and Dill, 1985), and many predators have been shown to select prey at least partially on the basis of size (e.g., Crowl, 1989; Michaletz *et al.*, 1987; Molles and Pietruszka, 1987; Parker, 1971). Wood and Hand (1985) showed that common mergansers preferentially selected large coho smolts (40 g) over small fry (2 g) in stocked enclosures. Such a large size difference is unlikely to be found among fish cohabiting in natural streams, since smolts migrate to saltwater. Nevertheless, even within a narrower size range, large fish may be more prone to detection than small ones. Territoriality, and concomitant large size, may thus carry a cost in terms of increased probability of detection, even though this cost may be attenuated by territorial fish behaviour, as noted above. On the other hand, a larger size may make prey less profitable by increasing handling time. In this Appendix I report the results of an experiment designed to test whether size differences of the magnitude of those observed in natural populations of juvenile coho influence their probability of surviving once they are detected by common mergansers.

Methods

In juvenile coho, size covaries with behaviour: larger fish are more likely to be territorial (Chapter 2) and territorial fish may behave differently than smaller fish (floaters) when they sense mergansers (Appendix B). To minimize the influence of behaviour on detection, I used hatchery fish, who are not territorial and have probably never been exposed to mergansers. Their size distribution approximated that of a wild population of territorial fish and floaters in early October (Chapter 2). Fish were chosen to correspond in size to wild fish at that time of year because hatchery fish of that size range were most common.

The experiments were conducted in an outdoor pool (4 m diameter, 0.5 m depth) at the Animal Care Facility at SFU from June - October, 1990. Each test involved 14 fish (to roughly correspond to coho density in Moody's Channel). Prior to the start of the experiment, the fish were measured (total length) and weighed. They were subsequently introduced into the pool and left to acclimate for an hour, after which time a bird was introduced and left for 20 min or until it was estimated that about half the fish had been eaten. The bird was then removed and the fish seined, re-measured and re-weighed. This enabled me to determine which fish had been eaten.

Three male mergansers were tested in June and July and one female was tested from mid-September to mid-October. The female was tested later because she had problems acclimating to the test pool. Because of this delay, the fish size distribution with which she was presented could not be made to match as closely that of territorial fish and floaters as had been the case for males.

Results

The distribution of fish lengths presented to the female differed significantly from that presented to the other birds (Kruskal-Wallis H = 13.631, P < 0.01). The three males, however, faced fish populations with similar size distributions (Kruskal-Wallis H = 0.838, P = 0.65). The results are therefore presented separately for the female but are pooled for the males . For the three males, there were no differences between the size of fish eaten and those left alive, in terms of either total length or wet weight (Fig. C.1a & C.1b). But the female did discriminate: the fish she left alive were significantly longer and heavier than the fish she ate (Fig. C.2a & C.2b).

When the only fish considered were those whose sizes corresponded to average territorial fish and floaters, males did not discriminate between the two size groups (Fig. C.3) but the female ate proportionally more smaller fish than larger ones, at least when fish length was considered (Fig. C.4a). She did not, however, appear to discriminate on the basis of fish wet weight (Fig. C.4b).

Discussion

Once a prey is detected it has to be caught, then subdued. These last two steps are where the fish's size may be important for some mergansers. The female ate fish significantly smaller than the ones she left alive. Because the experimental conditions precluded crypsis, fish size is assumed to have little influence on their probability of detection by mergansers, so small fish might simply have been easier for her to catch. In salmonids, size is positively correlated with

swimming speed (Bainbridge, 1958; Wardle, 1975) and larger fish could thus escape more easily

than smaller
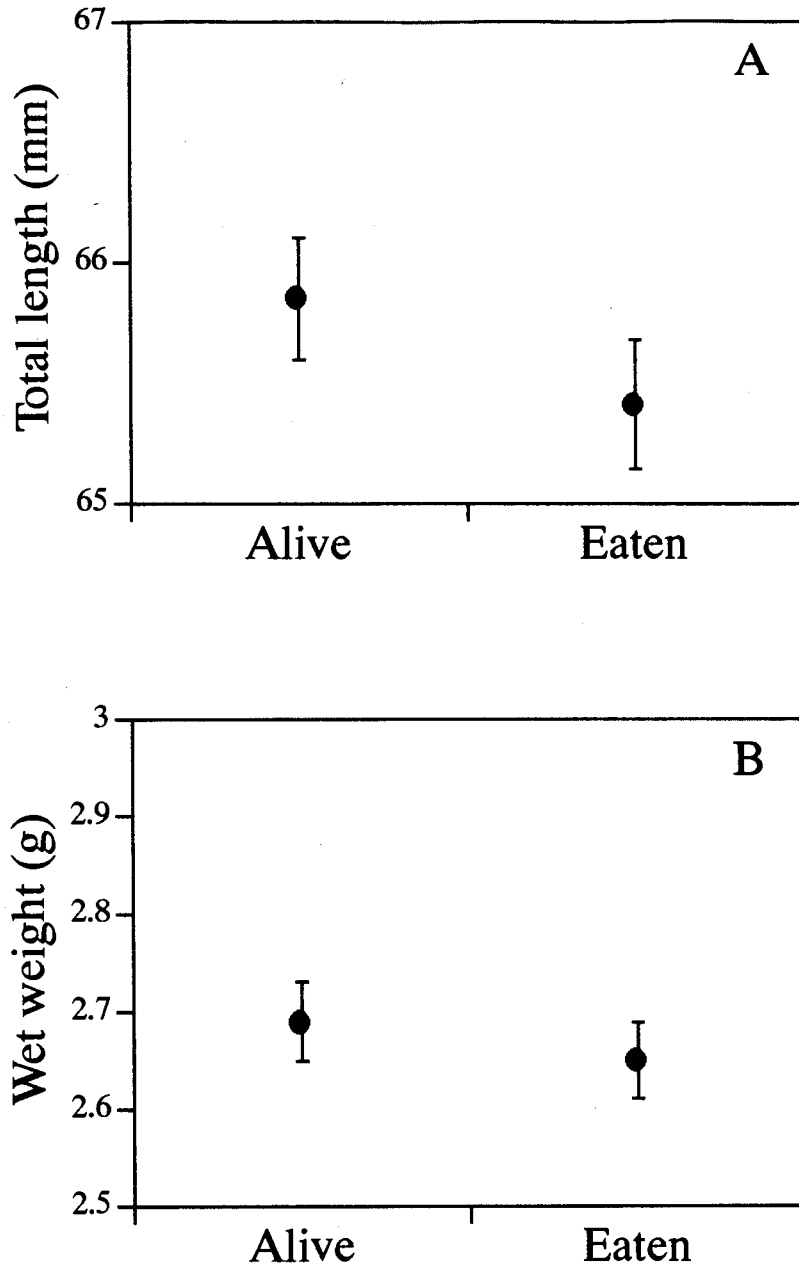
Figure C.1. Mean size (± s.e.) of fish eaten vs. left alive by three male common mergansers. N = 160 (alive) and 126 (eaten). There are no significant difference between pairs.
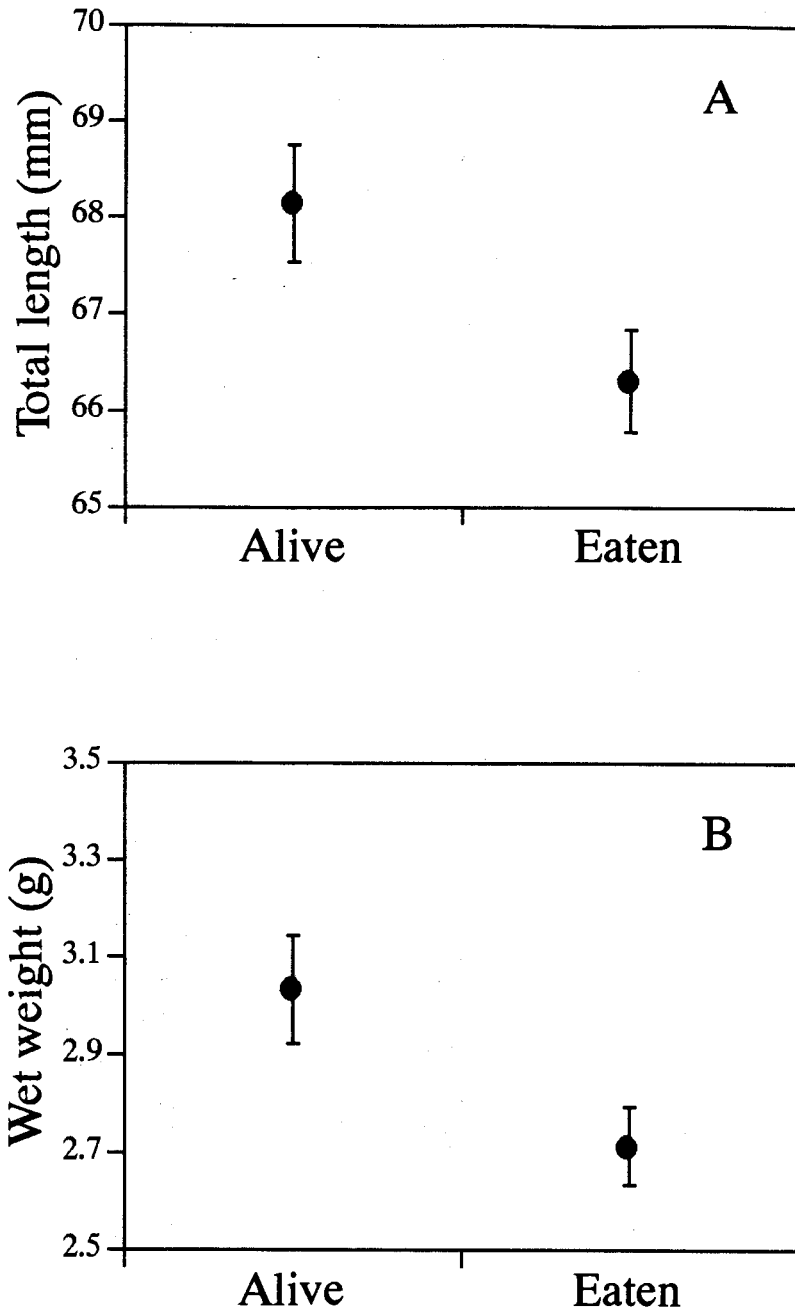
Figure C.2. Mean size (± s.e.) of fish eaten vs. left alive by one female common merganser. N = 33(alive) and 51 (eaten). Both pairs are significantly different (t-tests, P < 0.05).
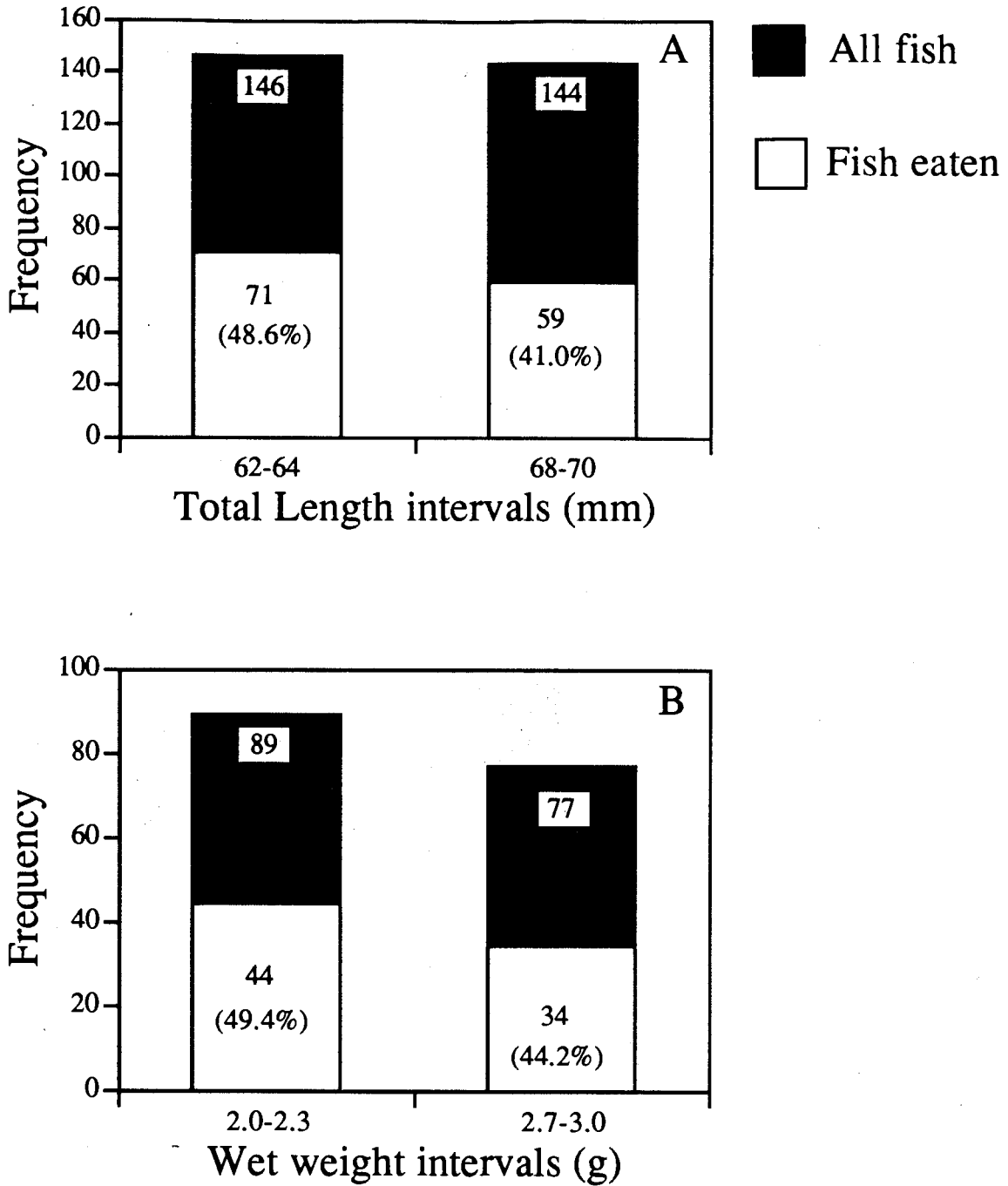
Figure C.3. Number of fish eaten by three male mergansers in relation to the number of fish presented in the two size classes corresponding to floater and territorial fish. A. Total Length B. Wet weight . There were no significant differences between groups (X^2 tests, 1 df, P = 0.19 and 0.49).
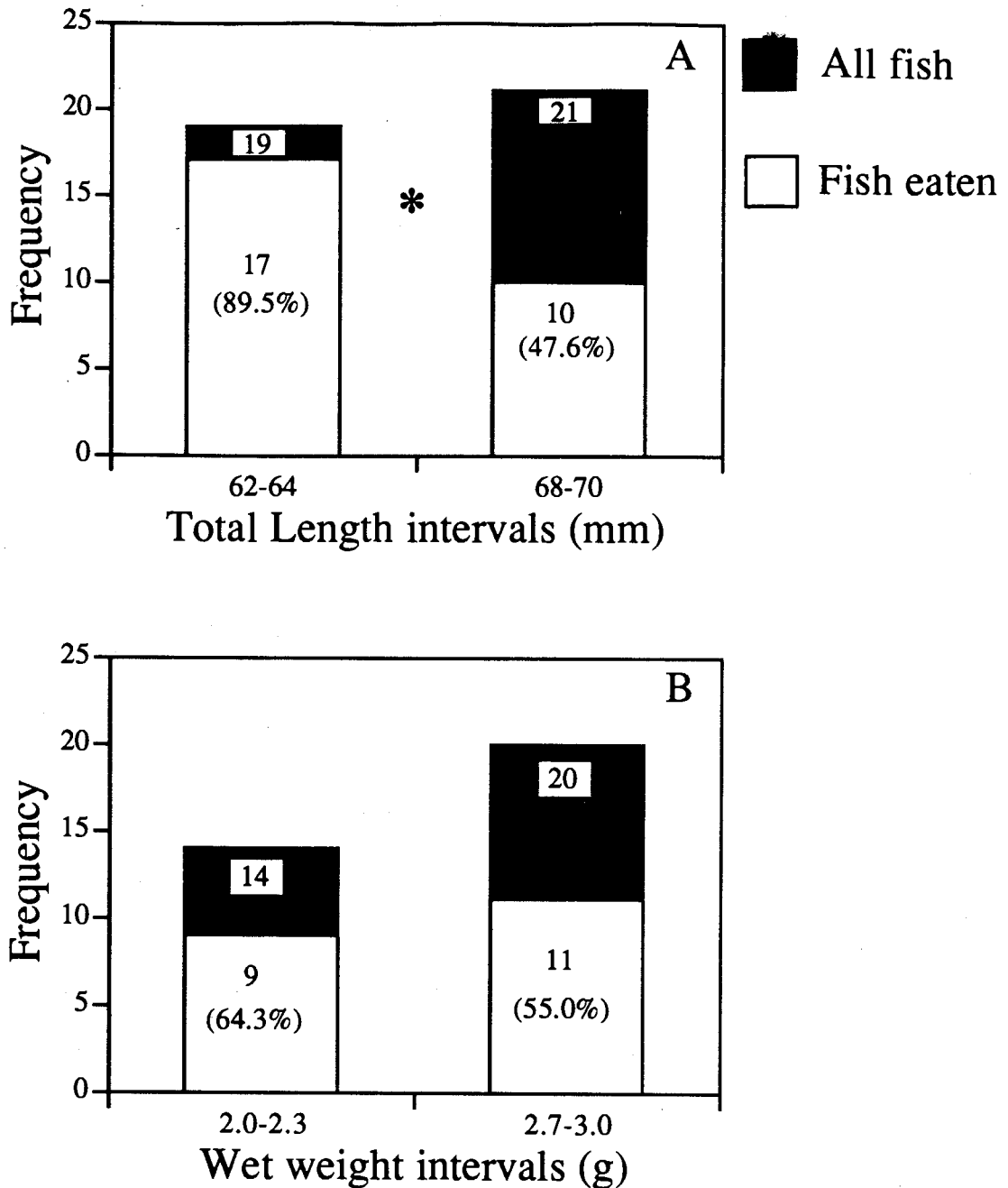
Figure C.4. Number of fish eaten by the female merganser in relation to the number of fish presented in the two size classes corresponding to floater and territorial fish. A. Total Length *: the two percentages eaten are significantly different (Fisher exact test, P < 0.007). B. Wet weight (no significant difference between groups, Fisher exact test, P = 0.73).

ones. This would preclude the necessity for any active selection on the part of the mergansers. To provide evidence of active selection, one would need to ascertain whether the female failed to attack any of the fish she detected or rejected any of the fish she caught. Another possibility is that small fish are easier to handle than large ones, as was the case for one male presented with a much broader range of prey sizes (Fig. C.5).

The birds' size and morphology may influence their selection of fish: none of the males discriminated among the fish with which they were presented, and the males were on average 30 % heavier than the female (1200 vs 900 g), who did discriminate. The female ate proportionally more small fish than did the males, and length rather than weight seemed to be her discrimination criterion. Latta and Sharkey (1966) suggested from feeding experiments with mergansers that girth rather than length of fish is critical in determining prey selection. However, their results were based on fish longer than 180 mm.

The female discriminated between fish whose size difference was 3% in total length; the fish she ate were on average 1.8 mm shorter than the fish she left alive. Territorial fish measured in September in a natural stream were on average 9% longer than floaters (Chapter 2). In this experiment, fish of floater length were twice as likely to be eaten by the female as were fish of territory holder length. Merganser broods usually remain in streams from June to September-October (Munro and Clemens, 1937; Erskine, 1972; Bellrose, 1976). By late September - mid-October, the chicks are about the size of adult females (Palmer, 1976). There should therefore be considerable selection pressure on juvenile coho to grow to a size beyond which they are less acceptable (or catchable) to mergansers. If the results of this experiment can be generalized to other female mergansers, I would predict that juvenile coho from streams where merganser predation is important will be larger than juveniles from streams where merganser predation is

absent. Territoriality, as shown in Chapter 2, is a foraging tactic which increases coho growth

rate. Thus, a long-term consequence of territorial behaviour may be a reduced risk of predation.
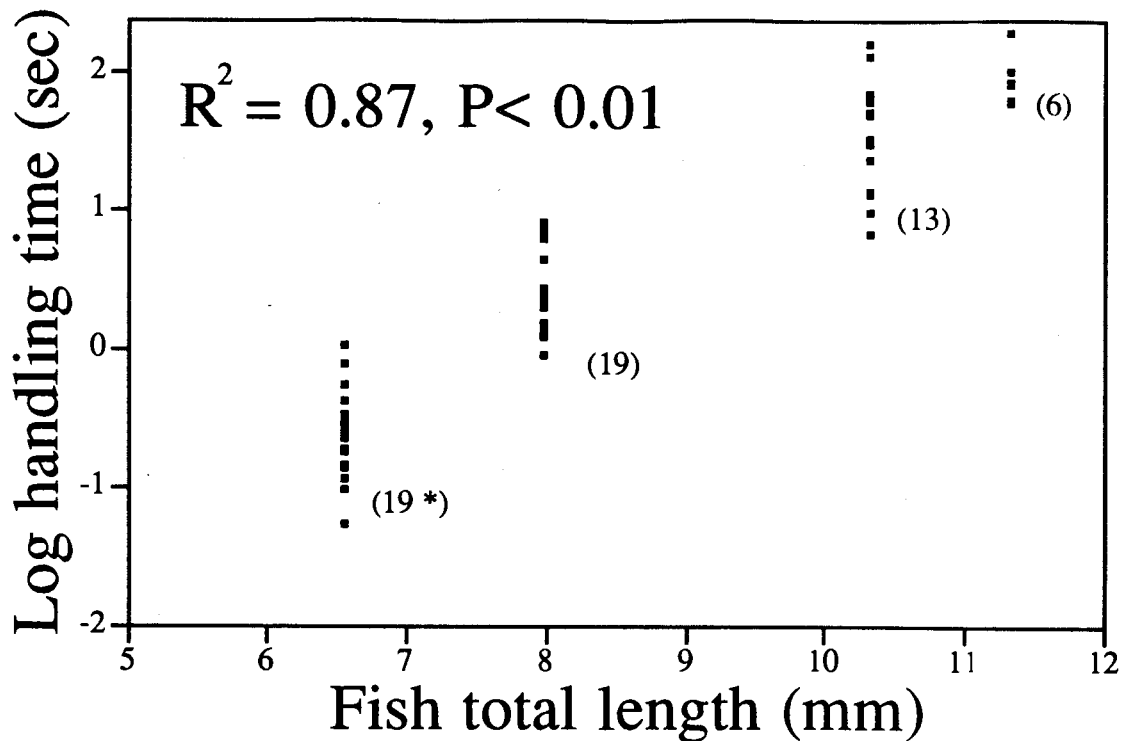
Figure C.5. Handling time of a male merganser as a function of juvenile coho size (Total Length, TL). During each trial, one male merganser was introduced into a 3.8 x 1.9 x 1.9 m enclosure (water depth 0.5 m) in which 60 juvenile coho had been left 30 min to acclimate. These fish had all previously been measured and weighed. The bird was left with the fish until he ceased to attack them, then was removed. The remaining fish were then seined, measured and weighed again, allowing me to determine the size of the fish eaten. Each trial was videotaped from approximately 2 m above the enclosure, and handling times for each fish eaten were measured from the tapes. Handling time consisted of the time elapsed from the moment the bird made first contact with a fish until he swallowed it. Four groups of coho parr were thus tested: 5.1-7.0 cm TL ($\overline{x}$ = 6.58 ± 0.32 s.d), 7.1-9.0 cm TL ($\overline{x}$ = 7.9 ± 0.61 s.d.), 9.1-11.0 cm TL ($\overline{x}$ = 10.1± 0.59 s.d.) and 11.1-13.0 cm ($\overline{x}$ = 11.6 ± 0.46 s.d.). Number of fish eaten per trial is between parentheses. *: although 57 fish were actually eaten in this trial, only 19 could be filmed due to an equipment malfunction.

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