

THE ROLE OF BODY SIZE IN THE HABITAT CHOICE AND
FORAGING BEHAVIOUR OF JUVENILE COHO SALMON
UNDER PREDATION RISK

by

ULRICH GEORG REINHARDT

Dipl. Biol., Universität Bonn, Germany, 1992

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

IN FACULTY OF GRADUATE STUDIES

(Department of Zoology)

We accept this thesis as conforming to the required standards

THE UNIVERSITY OF BRITISH COLUMBIA

April 1998

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Abstract

Models of behaviour in trade-off situations between foraging and predator avoidance predict that an animal's decision should depend on dynamic internal states, such as energy or hormonal levels. For example, it is predicted that willingness to risk mortality decreases with increasing assets of the forager. In this thesis, I used a combination of experimental manipulation and computer modeling to examine the influence of various dynamic states, particularly body size, on the risk taking behaviour of coho salmon (*Oncorhynchus kisutch*) fry. I showed that fry in semi-natural stream channels used protective cover opportunistically, associating with it only when it protected them from predators. In the laboratory, I observed habitat choice and agonistic behaviour of groups of coho fry under simulated predation risk. Bigger coho used a risky habitat less than smaller individuals. Bigger fry aggressively monopolized access to food in the absence of predation risk, but in the presence of risk, the size-dependent territorial hierarchy broke down and risk-prone small fish achieved relatively higher growth rates. Using a dynamic optimization computer model with parameters representative of coho foraging, I explored the relationship between body size and optimal foraging effort over the first feeding season. Like earlier dynamic optimization models, my model showed that the willingness to risk predation should decrease with size. In contrast to earlier models, my coho-specific model predicted that risk taking should be highest in the spring. In a final experiment, I examined the influence of feeding conditions, body size, and season on the willingness of individual coho fry to feed under simulated predation risk. As expected, bigger fish were more risk averse than small fish in the summer. This was not the case in the fall when the overall willingness to risk exposure to the predator was lower. I suggest that juvenile salmonids integrate information on their internal state and the environment into their foraging behaviour to a greater extent than previously thought. If increased risk aversion with size is common in nature, it may have important ecological consequences, for example, it may help to explain the widely reported lower mortality rate of bigger juvenile fish.

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Preface

The material presented in Chapter 2 of this thesis has been previously published as Reinhardt, U.G. and Healey, M.C. 1997. Size-dependent foraging behaviour and use of cover in juvenile coho salmon under predation risk. *Can J. Zool.* 75: 1642-1651.

Acknowledgments

The successful completion of this work depended on the contribution of many individuals, whose input, small or big, I greatly appreciated. I cannot list all names here, but I am sure thankful to everybody who helped.

On top of the list of those who I am grateful to, is my supervisor, Mike Healey. Over the last four and a half years without fail, he gave me stimulating and encouraging advice on all aspects of my work. Equally important, I feel, was his understanding and support at those times when I doubted my abilities. I could not have wished for a better supervisor.

I thank the members of my academic committee, Larry Dill, Robin Liley, Tony Pitcher, Lee Gass, and in the late stages of the project, Scott Hinch and Eric Taylor, for helping shape my work through intellectual support and challenge from the early planning stage right through the final write-up. A special thanks to Robin Liley for being my supervisor during Mike Healey's sabbatical leave and allowing me to use his facilities for the experiments in Chapter 2 and 3.

Doing ecological experiments can be hard work. I thank my field assistants, Mark Tiley, Chris Bobinski, Mardel Armsfeld, and Dan Reinders for their enthusiasm, skills, and great work ethic, rain or shine. Jens Oettel, who worked five weeks in the lab for me, deserves particular praise for a great volunteer job done.

Much appreciated logistic support for my field experiments came from the Oyster River Enhancement Society and the UBC Research Farm at Oyster River. The merganser ducks used in those experiments were lent to me by Dave Jenkins; Guy Martel, had painstakingly raised and tamed those birds. I am also grateful to the Rosewall DFO hatchery for providing me with coho salmon for the experiments in Chapter 5. At UBC, the support staff was of great help with everything from paper work to equipment repair; in particular, Alistair Blachford and Lance Bailey saved me out of uncounted struggles with computers.

Thanks also to other people who gave me input on earlier versions of the chapters in this thesis: Jeff Silverstein, Ernest Keeley, Neil Metcalfe, and two anonymous reviewers who commented on the published version of Chapter 2. Ernest also helped me with statistics questions I had. Colin Clark and Ron Ydenberg taught me the dynamic computer programming used in Chapter 4. I am very thankful to Jordan Rosenfeld for discussing my work with me and for support during a particularly rough time in the project.

Major financial support for this research came from a NS.E.RC operating grant to Mike Healey and from a Canada Department of Foreign Affairs and International Trade, Government of Canada Award full scholarship to me. Further financial contributions came from the B.C. Science Council Student Summer Works program.

Without the emotional support of my friends and family, I could not have completed this work. My parents were always there for me when I needed them. I owe my success in life to their loving care. Megumi Segawa gave me her love and affection and sometimes she helped me feed the fish. This thesis is dedicated to her.

Chapter 1 General Introduction

Most animals are preyed upon at some stage in their lives. Since death means loss of fitness, predation exerts a strong selective pressure, which has led to many morphological and behavioural adaptations for reducing the risk of mortality from predation. Many animals behave in the presence of predators in a manner that suggests a trade-off between foraging benefits and mortality risk from predation (Lima & Dill 1990). Models of animal behaviour based on optimality theory and the trade-off between costs and benefits have provided important insights into relationships between predators and their prey (Krebs & Davies 1991). Since optimality theory is based on evolutionary arguments, the major factors that influence the fitness of the organism in question have to be considered when basing a study on optimal behavioural models.

My work in this thesis was guided by the framework of optimality theory. I examine the behaviour of juvenile coho salmon (*Oncorhynchus kisutch*) in situations that pose conflicting demands between foraging and avoidance of predation. Coho salmon can be considered a model animal for a cold-blooded, territorial forager with limited time to gather resources. Previous work on juvenile coho salmon has shown that survival to adulthood is strongly influenced on the one hand by predation in the early life history stages and on the other hand by the ability of the individual to grow quickly (Sandercock 1991). It has been shown that juvenile coho balance short-term foraging benefits against predation risk (Dill & Fraser 1984). Theoretical work and recent experimental studies, however, suggest that juvenile salmonids are also capable of balancing costs and benefits over a longer time period (McNamara & Houston 1986, Bull et al. 1996, Damsgård & Dill 1998). Even though some of the variation in fish behaviour toward predators is clearly due to learning (e.g. Healey & Reinhardt 1995), competitive and probably anti-predator behaviour also has a heritable component (Swain & Holtby 1989, Riddell & Swain 1990).

The purpose of my work was to explore the main factors that determine behavioural decisions of age-0 coho salmon in trade-off situations on various time scales. I focused on the effect of body size on the trade-off but I also addressed aspects of the effect of predation risk on habitat choice in the field and on social interactions among coho salmon. Furthermore, I modeled the effects of various fitness functions and relationships between size, habitat variables, and foraging success on the optimal foraging effort under predation risk. By examining those factors, which I consider important for juvenile coho salmon, I hoped to gain a better understanding of how behaviour in this and similar organisms has evolved through encounters of individuals with situations that pose conflicting demands.

Little is known about the influence of predation risk on the behaviour of salmonids in natural habitats, despite the fact that predation is a major cause of natural mortality for many juvenile salmonids (Sandercock 1991) and has a strong impact on short-term behaviour in a laboratory environment (Milinski 1993). Many studies have tried to assess the habitat requirements and preferences of coho salmon and, in particular, their behaviour in relation to cover structures that are supposed to protect the fish from predators (e.g. Bisson et al. 1987, Lonzarich & Quinn 1995, Peters et al. 1993). These empirical studies, which usually did not incorporate measurements of predation pressure, have yielded contradictory findings with regard to coho's use of cover during the summer months. In my initial experiments, I tested whether the presence of predators may be responsible for variation in cover use in the field. I made detailed observations of the use of cover by coho, movement between habitats, and foraging behaviour under experimentally manipulated levels of predation risk. I hypothesized that juvenile coho would avoid cover in the absence of predation risk and increase their use of cover if it helped to protect them from predators.

The main part of my thesis focuses on the question of how body size influences trade-off behaviour in coho salmon. The trade-off arises if a prey increases its future survival probability by growing, but the foraging activity necessary renders it more susceptible to detection by predators in the present. If the costs and benefits depend on the body size of the forager, then larger foragers may be more or less risk averse than smaller ones. Body size of a prey as a modifier of its behaviour under predation risk has attracted the attention of biologists in the past. A number of studies on non-salmonid fish (e.g. Power et al. 1985, Werner & Hall 1988, Mittelbach 1986, Eklöv & Diehl 1994, Schlosser 1988) have demonstrated that size-dependent susceptibility to predation and predator avoidance behaviour can influence inter- and intra-specific interactions sometimes across trophic levels (Powers et al. 1985). At present, there are no similar studies on salmonid fish. Grant & Noakes (1987), however, found that the apparent willingness of age-0 brook trout (*Salvelinus alpinus*) to risk predation under field conditions was negatively related to body size.

Coho and other anadromous salmonids derive a number of advantages from a large body size including greater over-winter and marine survival of larger juveniles (Bilton et al. 1982, Holtby 1987, Holtby et al. 1990), better escape abilities in encounters with pursuit predators (Parker 1971, Healey & Reinhardt 1993), and higher reproductive success (Sandercock 1991). Additionally, in juvenile Atlantic and coho salmon, size relative to conspecifics in the cohort is important since the biggest fish gain the great advantage of territorial dominance over food sources (Holtby et al. 1993, Metcalfe et al. 1989). This has the effect that, in natural populations, the size difference between small and large fish typically increases over the feeding season (Thorpe et al. 1992).

However, bigger fish also face fundamental disadvantages related to their size that may influence their foraging behaviour under predation risk. The first disadvantage stems from a slowing down of metabolism with increasing size which results in a lower maximum growth rate of larger

fish (Brett 1979). The second disadvantage has to do with the relationship between the increase in expected fitness from growing (the marginal fitness value of a unit growth) and the fitness value already accrued. The same absolute weight increase under the same risk of mortality may be less 'attractive' to the larger animal if fitness is a decelerating function of size (McNamara & Houston 1986). Furthermore, the larger animal has already accumulated assets that help to increase its fitness and, therefore, its potential loss will be greater (Clark 1994). The optimal choice for the larger animal may be to forego a small increase in fitness so as to protect the fitness it expects given its current state. This simple concept was termed the Asset Protection Principle by Clark (1994). Based on these theoretical considerations and Grant & Noakes' (1987) observations of lower apparent risk taking of larger fish, I hypothesized that larger juvenile coho salmon would be more risk-averse under predation threat. I explored the effect of body size on the willingness of coho salmon to take risks using a combination of laboratory experiments and a dynamic optimization computer model.

My first series of laboratory experiments examined in detail the behaviour of fish of different sizes under predation risk, in particular their habitat choice, social interactions, and the consequences of their behaviour on growth rates. I observed habitat choice, aggressive interactions, and growth rates of individual fish in the absence and presence of simulated predation risk. I expected that larger fish under risk would use a refuge to a greater extent than smaller fish. Based on Werner et al.'s (1983a) finding of reduced food competition in bluegill sunfish (*Lepomis macrochirus*) due to predator avoidance behaviour of some size classes of the prey, I also expected that predator avoidance behaviour of large fish would lead to small fish being able to gain better access to food than in the absence of a predation threat.

To explore what effect the Asset Protection Principle (Clark 1994) may have on risk taking of coho during their first feeding season, I constructed a dynamic optimization model based on known relationships between size and subsequent survival probability in coho and incorporating size-dependent bioenergetic constraints on growth and feeding. I also used the model to explore the effect of seasonal trends in water temperature and food production available to coho salmon on their optimal foraging effort.

The main assumption of dynamic optimization models (also called Dynamic Programming Models - DPM's) is that the animal incorporates fitness consequences of its current state (e.g. body size) into a flexible behavioural pattern which varies with changes in time and state. Despite extensive use of dynamic modeling to explore and analyze behaviour (e.g. Mangel & Clark 1988), direct experimental evidence that animals respond to changes in their state as predicted by dynamic models is still fairly scarce. In one recent study, Bull et al. (1996) developed a DPM to predict changes in appetite in over-wintering juvenile Atlantic salmon (*Salmo salar*) and confirmed their prediction of higher appetite in early versus late winter in a manipulative experiment. In the case of juvenile coho salmon, we don't know yet whether foraging under predation risk is influenced by long-term strategies which depend on states such body size or season, or whether willingness to take risks only depends on short-term variables such as size of food particles (Dill & Fraser 1984), stomach fullness (Dill et al. 1980) or recent experience of a predation threat (Healey & Reinhardt 1995). A recent study by Damsgård & Dill (1998), however, showed that long-term energy deficits also increased the willingness of coho salmon to feed under risk.

The objective of my second set of laboratory experiments was to examine specifically how short-term foraging gains, accumulated fitness assets (body size), and season affect the response of coho to a predation threat. I observed the response of fish of different body sizes that were fed

different rations to a simulated predation threat in the summer and fall. Based on previous experimental work (e.g. Damsgård & Dill 1998) and my and Clark's (1994) DPM, I expected that risk taking would decrease with increased feeding ration and body size, and that there would be differences in the risk taking between summer and fall.

The thesis is organized in the following way :

- in Chapter 2, I describe experiments designed to assess the importance of predation risk for habitat choice and foraging behaviour in a semi-natural field setting and in laboratory stream tanks,
- in Chapter 3, I analyze observations from the first laboratory experiment that relate to the effects of predation risk on size-dependent social interactions and growth patterns,
- in Chapter 4, I present a dynamic programming model that explores optimal foraging effort under predation risk by juvenile coho salmon under realistic physiological constraints and given various relationships between size in the fall and fitness,
- in Chapter 5, I describe experiments that test specific predictions arising from my own and other dynamic optimization models about changes in risk-taking with increasing body size and progression of the season, and
- in Chapter 6, I conclude with an evaluation of the ecological consequences of the findings of this study.

Chapter 2 **Size-dependent foraging behaviour and use of cover under predation risk in field and laboratory experiments**

Introduction

When an animal chooses its foraging mode, it often has a choice between risky, but energetically rewarding and safe, but energetically less rewarding behaviour. When it chooses among habitats, this trade-off situation often arises either because the physical structure that protects from predation (i.e. refuge) also impedes the animal's own foraging or because a safe habitat attracts conspecifics which compete for resources. The habitat choice of animals in trade-off situations has been the focus of many theoretical studies and manipulative experiments (e.g. McNamara & Houston 1986, Gilliam & Fraser 1987, Lima & Dill 1990, Clark 1994). Studies on habitat use by salmonid fishes, however, have often been restricted to correlating fish densities with habitat characteristics. For example, studies comparing the density of fish in reaches with and without large instream woody debris ("LWD": wood pieces with > 10 cm diameter), found that coho salmon are more abundant where LWD is present (House & Boehne 1986, Bisson et al. 1987, Fausch & Northcote 1992). Similarly, the addition of fine woody debris to streams (brush bundles, small trees with branches) has been shown to attract coho juveniles (Nickelson et al. 1992, Peters et al. 1993, Lonzarich & Quinn 1995, Giannico 1995). The impact of this research has been such that now those concerned with fish habitat almost universally assume that salmonids need cover (Meehan 1991, Bjornn & Reiser 1991) and stream improvement projects should aim at providing fish with such cover (Reeves et al. 1991, Peters et al. 1993). By contrast, many studies that have observed the use of cover by salmonids closely (i.e. at a microhabitat scale), show that cover structures are either little used (Bugert et al. 1991, Bugert & Bjornn 1991, Fausch 1993), or, as in the case of overhead structures, ignored or even avoided (Ruggles 1966, Fausch 1993, Giannico 1995). Cover may be used by salmonids as protection against strong

currents (Shirvell 1990, Fausch 1993), or it may protect the fish from predators (Sandercock 1991). However, the assumed positive effect of cover on survival rates is sometimes confirmed in manipulative experiments (Lonzarich & Quinn 1995), whereas other times it isn't (Spalding et al. 1995). Thus, the significance and value of cover remains somewhat controversial.

In this Chapter, I examine the use by juvenile coho salmon (*Oncorhynchus kisutch*) of one type of cover, brushy in-stream debris, and one important role of it, protection against predators. I explored whether and how juvenile coho salmon use in-stream brushy debris during their first summer, what impact the threat of predation has on the response of salmon to cover, and finally how their behaviour in relation to cover and predation risk affects growth and survival during their first summer.

Materials and Methods

I approached the problem using a combination of field and laboratory experiments and manipulating levels of predation risk. The field experiments were designed to allow me to observe how coho distribute themselves in natural habitats in the presence and absence of real predators. Such observations are relatively rare in the literature. In consideration of the conflicting observations in the literature noted above, I used these experiments to address the following questions:

1. How do coho distribute themselves in relation to cover both within and between pools in a stream?
2. How does the presence of a predation threat affect the distribution of coho, their use of cover, and their foraging behaviour ?
3. How does the presence of cover influence the hunting and capture success of an avian predator of coho ?

My field experiments suggested that coho behaviour in relation to cover and predation threat was strongly size-dependent. A similar observation has been reported by Grant & Noakes (1987) for juvenile brook trout. To explore the effects of size and individual behaviour in more detail, I conducted further experiments in the laboratory where I could monitor the behaviour of fish more easily. The laboratory experiments were designed to address questions 1 and 2 above as well as the following question:

4. How is the growth rate of coho affected by predation threat ?

Field Experiments

I carried out field experiments at the Oyster River Enhancement Society's spawning channels, Vancouver Island, British Columbia from July - August of 1994. Juvenile young-of-the-year coho salmon used in the experiments were netted from the channels. I fenced off 10 m sections of the spawning channel and moved gravel to create 6 sections with equal areas of upstream riffles (depth 5-10 cm) and pools (depth 50 cm). (Figure 2.1). Brushy in-stream cover was provided by 3 or 4 defoliated small alder trees (trunk diameter about 5 cm) tied together into spindle-shaped bundles of about 1 m diameter and 3.5 m length and submerged into the pools by weighing them down with boulders. The sticks in the bundles were arranged parallel to the waterflow so that the current-shielding effect of the cover was kept to a minimum. One bird at a time from a pair of tame merganser ducks (*Mergus merganser*), a common predator of juvenile salmon during the summer months (Wood & Hand 1985), was released into the stream channels as the experimental predator where it would actively search for and pursue fish.

Three-pool experiment

The purpose of the first experiment was to explore the distribution pattern of coho salmon on a stream-reach scale in relation to the density of in-stream cover and presence and absence of predators. I opened small (35 cm wide) passageways between 3 adjacent channel sections, thus creating a 30 m long section of stream consisting of 3 riffle-pool combinations. I placed 3 cover bundles so that one pool had no cover, one contained one cover bundle ("medium cover" treatment), and the third contained two bundles ("high cover" treatment) (Fig. 2.1a). Three hundred juvenile coho salmon were measured, marked in groups of 100 by clipping a piece off one or both pelvic fins, and each group was released into one of the three stream sections, resulting in a starting distribution of 100 fish per section. After 7 days, I closed the passages between sections, netted out the fish, verified the section in which they had originally been released, measured, and counted them. The cover bundles were then moved such that, after three weeks, each of the three pools had contained each cover density once. After replacing missing fish in each marked group to maintain a group size of 100, each fish group was released into a different section. Three weeks without predation threat (last three weeks of July) were followed by three weeks of predator treatments runs with a new set of 300 fish. Counts were made 3 times each with and without predation. Water temperature in the channels ranged from 14.5° C to 18° C in the afternoon. For predation treatments, one randomly chosen merganser duck was released into one of the sections on the third day of each week and allowed to hunt freely until it stopped search behaviour (search behaviour indicated by dipping the head underwater, Wood & Hand 1985) for more than 3 minutes, or 25 minutes had passed. This was repeated once or twice a day for a total of 4 days. I recorded the total time spent by the duck in active hunting (swimming with frequent dips of the head underwater) in each section, the number of head dips, the number of diving pursuits (characterized by submergence of the whole body and a quick acceleration movement; Wood and Hand 1985), and the incidence of fish capture. The two ducks sampled all areas of the experimental stream reach by frequently switching

among pools and dipping the head underwater in search for prey as well as trying many diving pursuits of fish.

One-pool experiment

A second experiment was designed to permit observations of the behaviour of coho in a single pool in relation to the presence of cover and presence or absence of a predator. I used three unconnected 10-m sections of the stream channel as replicates for underwater observation of fish behaviour. Observations were made by snorkeling and lasted through the first three weeks of August. I divided each pool with marking tape into 12 squares of roughly equal bottom area and submerged two cover bundles into each pool: one at the centre, the other at the side (Fig. 2.1b) so that each pool had six squares with cover. Each section was then stocked with 100 fish that were allowed a minimum of 3 days to settle into the new environment before I started observations. For daytime observations (between 0800 and 1900 hrs), I entered the pool from the downstream end and remained motionless for 3 min. before starting to take notes on a slate. The fish did not seem disturbed by the presence of the observer; they were often feeding right in front of the diver's face. In each observation period (12- 15 min.), I first counted the number of fish in six randomly selected squares and then recorded the behaviour of five arbitrarily chosen focal fish in each of the six squares. A focal fish was observed for three 5-s periods and behaviour characterized in one of four categories (see Table 1). I considered feeding or aggressive action to dominate any 5-s period in which it occurred although such events were usually of shorter duration. I waited for a minimum of 2 h before snorkeling again in a section. No observations were done in the riffle areas. I completed 10 observations per section (spread over 5 - 8 days) without predator ("before" observations), followed by an average of 25 observation periods with one of the two hunting merganser ducks present. I also did observations between duck hunting periods (2 to 24 h after hunting). In this experiment, the ducks avoided getting too close to the observer and did not often pursue fish (2 fish caught in 269 min. total time in pools). Therefore, although the ducks were

active in the pools, their behaviour may not have mimicked that of a hunting predator as well as in the 3-pool experiment. Water temperatures during the day ranged from 16.5° C to 19° C. As this procedure was conducted independently in each of three pools, there were three replicates in each treatment.

Laboratory Experiment

I designed a laboratory experiment to allow observation of interactions between fish and individual differences in behaviour under the threat of predation. I conducted this experiment at the University of British Columbia during July and August of 1995 using young-of-the-year coho salmon seine-netted from the Salmon River near Langley, British Columbia. I assumed that, even though the fish in the field and laboratory experiments were from different populations, potential differences in anti-predator behaviour (Rosenau & McPhail 1987) would be small enough to permit comparison of behaviour between field and laboratory experiments. Both river systems are similar physically and have similar resident predator populations (potential salmon fry predators observed at both rivers were: minks, belted kingfishers, great blue herons, green-backed herons, common mergansers and adult cutthroat trout; personal observations and G. Giannico, Westwater Research Centre, University of B. C., pers. comm.). The fish were held in 800-L oval Plexiglas tanks and fed freeze-dried euphausiid shrimp, *Euphausia pacifica* (Murex Fish Foods, Langley, B.C.) prior to the experiment. Water temperatures ranged from 14 - 16° C.

I simulated predation threat to the fish by using an electrified model of a kingfisher made from wood and Plexiglas and painted in realistic colours. A kingfisher model was chosen for this experiment because it is easier to arrange for a brief realistic presentation and because it is a commonly employed predator model in laboratory studies involving salmonids and other small fish (e.g. Milinski 1993, Gotceitas & Godin 1991). The model was 35 cm long and had wings which extended 5 cm from either

side of the body; it contained a metal core with a metal protrusion in place of the beak and a connection to a backpack-type electrofishing device. By briefly (about 1 s) plunging the model into a tank containing fish and applying a shock (300 Volt/75hz), I scared the fish. Before using the fish in the experiments, they were conditioned to the model in the holding tanks by two short presentations by the electrified model. This ensured recognition of the model as a threat later in the experiments.

On rare occasions, fish that were closer than 5 cm to the head of the model were stunned by the electric shock, but no mortalities could be attributed to the use of the shock. I decided to use an electrical current with the model in order to provide a strong negative association with the model. Preliminary trials revealed that visual presentation of the model alone or plunging it into the pool only elicited a startle response and the fish resumed foraging quickly after model presentation (see also Gotceitas & Godin 1993). By combining the electric shock with the experience of plunging the model in the water, I hoped to achieve a simulation of the traumatizing experience of a failed predation event. As in other studies that employed predator models for reasons of simple handling and standardizable procedure, I hoped that the reaction of the study species to the model would be similar to the reaction it would show to a real predation experience. For a discussion of impact of electric shocks on fish of different sizes, see Methods section in Chapter 5.

I divided each of three oval re-circulating stream tanks into 2 pools (length 1.7 m, width 0.45m, depth 0.28 m), separated by a riffle of about 2.5 m length and 2 cm depth (Figure 2.2). A pump submerged at the head of one pool and a hose delivering de-chlorinated city water (containing 10 ppm sodium thiosulfate solution) at the head of the other pool produced a surface current velocity of about 0.25 m/s at the head and 0.06 m/s at the tail of each pool. One of the pools ("covered pool") contained six transparent Plexiglas plates (dimensions 0.10 m x 0.22 m) with a "branch" pattern painted on them which were installed beneath the water surface as simulated overhead cover. They partially blocked

access to food floating at the surface and occupied about 1/3 of the surface of that pool (Fig. 2.2). The fish in the pools could be observed through glass windows from a darkened observation space in the centre of the tanks.

Freeze-dried shrimp were delivered from an automatic disc feeder at the head of each pool (Fig. 2.2). A stream of pressurized air carried the particles for a variable distance (up to 40 cm) downstream from the feeder. By feeding this way, no single fish could dominate the whole food delivery area. Uneaten food floated to skimmers at the tail of the pool and was removed from the tanks. The dry weight of the food ration was 5% of the combined live weight of a group of fish divided equally between the 2 feeders.

For each replicate of the experiment, I netted 20 coho juveniles from the holding tank, anaesthetized them in a solution of sodium bicarbonate and acetic acid (Prince et al. 1995), weighed them to the nearest 0.1 g, and marked them individually by tattooing a simple code with ink into the skin on both sides of the body. The 20 fish were released into a stream tank and allowed 60 h to choose between pools and establish a dominance hierarchy. On day 3 of each replicate week, I recorded the pool which each fish had chosen. After the first observation, I simulated predation threat in the pool without cover ("open pool") by dipping the electrified kingfisher model as described above. This procedure was repeated 3 times per day at random times between 0800 and 1800 hrs each time dipping the model 1-4 times at 30-s intervals. The fish in the covered pool were spared the predation simulation and these fish showed no sign that they were aware of the electrified model being dipped in the open pool. For 3 days of simulated predation threat, I assessed the position of all visible fish 5 times per day. For two days after predation, I recorded the location of all fish three times per day. On the 7th day of each replicate, all fish were removed, anaesthetized, weighed to allow calculation of growth rates over the previous week, and discarded. Twelve replicate treatments over 4 weeks preceded 2 weeks (6

replicates) of control treatment in which no simulated predation was performed. Different fish were used in each replicate trial.

Data Handling and Statistics

I analyzed the distribution of fish in the Three-Pool-Experiment using Chi-square tests on counts of fish in each stream section, summed up over the three replicate weeks. This test assumes that each observation of a fish in one of the habitats constitutes a statistically independent observation. I analyzed hunting time and capture success of the merganser ducks in this experiment by pooling the observations for the two ducks, again assuming that each capture of a fish by a duck was an independent observation. I analyzed data from the One-Pool-Experiment using repeated-measures ANOVA's. For the analysis of distribution of fish within the pools, I averaged the results from the repeated counts of fish in the 12 squares in each pool into a mean number of fish for each of six areas (see Fig. 2.4 for the six areas). The ANOVA was done considering each of the six areas and three replicates independent observations (for a total $n = 18$) and considering observations in the absence and presence of a merganser duck repeated measures. I did the statistical analysis of behavioural patterns in this experiment in a similar way: I summed up the observations in each of the four behaviour categories so that I obtained four frequency data for each of the three replicates (for a total $n=12$). In one ANOVA, I considered observations in predator presence and absence repeated measures, in the analysis of behaviour of fish inside and outside of cover, I treated the observations in the two locations as repeated measures. I used the interaction term between the repeated and other factor as an indication of significant differences in the patterns of numerical distribution and behaviour. In the Laboratory Experiment, I considered each tank with 20 fish a replicate with the exception of the analysis of growth rates by size, where I considered the growth rate of each individual fish an independent observation. I divided the five days of observation in each replicate into five observation periods: Day 1 before simulated predation ("before"), day 2 and 3 during simulated predation ("during predation"), and two

days after predation simulation ("1 day after" and "2 days after"). Repeated observations in each time period were combined into means. I compared observations between the two locations ("open pool" and "covered pool") using paired t-tests. Reported P-values are two-tailed with $\alpha = 0.05$ as significance criterion.

Results

3-Pool Experiment

In the 3-pool experiment without predation, the amount of cover did not influence the distribution of fish after one week (Chi-square contingency test on counts of fish in each cover density against expected even numerical distribution among pools; $X^2 = 0.19$; d.f.= 2, n.s.), but significantly fewer fish than expected by chance were found in the downstream section of the reach ($X^2 = 7.88$; d.f.= 2, $p < 0.05$). Fish apparently sampled the available habitats: the average chance of removing a marked fish from the same section in which it was released was 35%.

The distribution of fish after one week of daily hunting by a duck deviated significantly from the control distribution (Fig. 2.3). Most fish were in the pools with cover (Chi-square contingency table comparing control and treatment distributions; $X^2 = 189.3$; d.f.= 2, $p < 0.0001$). In predation trials, only 7% (range from 1.5% to 13%) of all fish were seined from the section lacking cover. Since the fish had to redistribute themselves each time the cover was moved to match the previous pattern, distribution relative to cover clearly was an active behaviour. The sections containing two cover bundles consistently had more fish (54%, range 49-60%) than the section with medium cover (39%, range 33-46%) (Fig. 2.3, Chi-square test on counts in medium versus high cover sections; $X^2 = 10.47$, d.f.= 1, $p < 0.01$). Treating each week of residence of a group of fish as replicates yielded a significant difference in the proportion of fish in the pool without cover in presence and absence of predation risk

by the merganser duck (t-test on arc-sine square root transformed proportions: $t = 4.92$, $d.f. = 2$, $p < 0.01$).

Additionally, I did a single set of daily underwater counts after the last predator treatment in the experiment. After being released again in equal proportions into the three sections, only 16 % of all fish were counted in the section without cover after one day, although the cover bundles had been shifted to a different stream section; the fish then gradually returned to an even numerical distribution among the sections within five days.

The two merganser ducks combined caught 32 fish during a total hunting time of 333 min. over 20 introductions to the stream sections (Table 2). The ducks spent a large proportion of their hunting time (42%), tried more than half of their pursuit dives (52%), and caught 66% of all fish in the open section. (Table 2). The ducks caught significantly more fish in the open section in relation to time spent hunting, but not in relation to frequency of diving pursuits (Chi square test on number of captures in open versus cover; in relation to hunting time $X^2 = 7.3$, $d.f. = 2$, $p < 0.05$; in relation to pursuits; $X^2 = 1.8$, $d.f. = 2$, n.s.). The differences in hunting effort and success between medium and high cover were small. (Chi-square test on captures in relation to hunting time; $X^2 = 0.26$ and captures in relation to pursuits ; $X^2 = 0.2$, $d.f. = 1$, both tests n.s.).

One Pool Experiment

The introduction of a merganser duck changed the behaviour of the fish in the single pool in several ways. Firstly, before introducing the predator, the fish were fairly evenly distributed over the pool (Fig. 2.4), but on introduction of the predator, fish proportions decreased at the marginal areas of the pool and increased at the central and head areas (Fig. 2.4). The difference in fish distribution between before and during predation was significant (repeated-measures ANOVA on log-transformed

mean number of fish in the six areas and 3 replicates, interaction term between area and predation treatment: $F_{5,11} = 9.7$, $p < 0.001$). Secondly, the behaviour of the fish during predation changed with the introduction of the predator (repeated-measures ANOVA on log-transformed frequencies of observations in the four behaviour categories shown in Fig. 2.5 and three replicates, interaction between behaviour and predation treatment: $F_{3,7} = 4.12$, $p < 0.05$). During predation, more fish were moving than before predation and slightly fewer aggressive acts were observed (Fig. 2.5). The ducks disturbed the substrate when swimming in the riffle area, and a large group of fish (up to 35) fed opportunistically on the drifting particles despite the presence of the predator. These fish would move temporarily into the brushy cover whenever the duck approached closer than about 1 m.

Before predation, fish in cover tended to move less, tried fewer feeding attempts, and were less aggressive compared with those in the open (Fig. 2.6a; repeated-measures ANOVA on log-transformed frequencies of observations in the four behaviour categories shown in Fig. 2.6 and three replicates, interaction between behaviour and predation treatment: $F_{3,7} = 10.2$, $p < 0.01$). Between predation events, there were qualitatively similar differences in behaviour between fish in the open and in cover, but the magnitude of differences was reduced (Fig. 2.6b; repeated-measures ANOVA on log-transformed frequencies of observations as above: interaction term $F_{3,7} = 0.4$, n.s).

Laboratory Experiment

Before simulated predation in laboratory stream channels an average of 47 % of the fish chose the covered pool (Fig. 2.7a) as habitat, whereas once simulated predation began, an average of 57-64% of observed fish chose the covered pool (Fig. 2.8a). The proportion of fish in the open pool dropped from before predation to 1 day after predation in 10 out of 12 replicates (binomial test, $p < 0.05$). The counts of fish in the open and covered pool were only significantly different 1 day after the end of simulated predation (paired t-test on arcsine-sqrt. transformed proportion of fish in open versus

covered pool, $t = -2.42$, $p < 0.05$, $n=12$). The fish in the open pool were also smaller than their counterparts in the covered pool (Fig. 2.7b), a difference that was significant 1 and 2 days after simulated predation was stopped (paired t-tests on log-transformed mean weights in open versus cover; one day after: $t = -3.26$, $p < 0.05$, two days after: $t = -2.36$, $p < 0.05$, both $n=12$). The average weight of fish in the open pool dropped from before predation to 1 day after predation in 11 out of 12 replicates (binomial test, $p < 0.01$). In the control trials (without predation), I found no consistent differences between numbers and weights of fish in open and covered pools (% of fish in cover: mean 40%, range 25 - 57%, S.E. 8.6; mean weight in cover 2.39g, S.E. 0.10, in the open 2.46g, S.E. 0.22, $n = 6$).

I analyzed growth rates of individual fish for each treatment (control versus predation) group by separating fish into two size categories by tank (i.e. the 10 biggest fish of each tank comprising the "Large" group) and tested for effects of fish size category and treatment on daily growth rates using a two-way ANOVA (Table 3). Overall, the growth rates of all fish were significantly depressed under the predation treatment (0.40 % per day in predation trials versus 0.73 % in control trials). This was due to fish in the large size class having significantly lower growth rates under predation treatment (Fig. 2.8, Tukey's test; $p < 0.05$ for large fish; n.s. for small fish). Average growth rates differed between the small and large group in the control, but not predation treatment (Fig. 2.8, Tukey's test; control: $p < 0.05$; predation: n.s.). When the analysis of growth rates was done using mean daily growth rates by tank (i.e. considering the mean of 10 small or large fish an independent observation), large fish grew significantly better than small fish in the control, but not predation treatment (paired t-tests comparing mean growth rates of large vs. small fish, control: $t = 3.37$, d.f. = 5, $p < 0.05$, predation: $t = -0.12$, d.f. = 11, n.s.), but other growth rate differences were statistically insignificant (Tukey tests after ANOVA with size class and experimental tanks as blocks, $F_{17,17}$ (for blocks) = 2.47, $p < 0.05$, all pairwise comparisons, n.s.).

Discussion

The results of my field and laboratory experiments suggest that juvenile coho salmon use cover in a flexible manner, so that the association with cover depends on the benefit the animals derive from its use. Before predation threat, the fish seemed indifferent to the presence of cover or used it less actively for foraging. But, after being threatened by a real or simulated predator, some coho increased their use of cover whereas others changed their foraging behaviour. It should be noted, however, that in the field experiment this conclusion arose from the observation of a large number of individual fish, but a fairly small number of replicated treatments. Potential interactions between fish in a group (see Chapter 3) may limit the generality of some of the conclusions from the field experiments. Based on the laboratory experiment, it appears that the larger fish were more likely to seek cover and the small fish to seek foraging opportunities when the predator was present. Indifference toward or avoidance of cover by juvenile coho on a micro-habitat scale has been reported by several authors (Bugert et al. 1991, Fausch 1993, Giannico 1995). Giannico (1995), for example showed that juvenile coho were indifferent toward cover in absence of food and avoided cover when food was offered. Fausch (1993) and Shirvell (1990) concluded that if in-stream cover was used, it mainly served for protection against strong currents. Since those studies did not manipulate predation risk for the fish, it can't be determined whether predation would have resulted in an increase in use of cover similar to that which I observed. Tabor & Wurtsbaugh (1991) showed that juvenile rainbow trout in ponds shifted to near-shore habitats that provided protection from predation when piscivorous predators were introduced, whereas Bugert et al. (1991) did not find different habitat use by juvenile coho salmon in streams in presence or absence of predators. My observation that coho in absence of predation also distributed themselves independently of cover on a reach scale contrasts with Giannico's work (1995), who found that coho preferred pools containing cover even in artificial stream channels with no predators. At present, I have no satisfactory explanation for the differences between Giannico's (1995) and my findings. Other field studies (Lonzarich and Quinn 1995; Peters et al. 1993) on similar spatial scales to my study have generally

found that juvenile coho were attracted to pools containing in-stream cover, but no direct information was gathered on the level of predation risk. In Lonzarich and Quinn 's (1995) study, coho juveniles also had higher survival in pools containing brushy instream cover. However, in a similar experiment, Spalding et al. (1995) found that juvenile coho were distributed independently of the amount of brushy cover structures in a stream channel, which also did not influence survival of fry over several weeks. Giannico (1995), found a temporal trend toward increased use of cover by coho fry over the summer and argued for an ontogenetic change in habitat use to explain contradictory results in the above mentioned studies. Although predation treatment followed control treatment in time in my experiment, there did not appear to be any ontogenetic change in behaviour that could account for my results as, following removal of the predators in the predation treatment, coho gradually assumed an even distribution among the pools. Nor can ontogeny explain differences in response to cover and predation in my laboratory experiments where both types of control (pre-treatment before the predator model was introduced and post-treatment in the replicates where I did no predator simulation) showed no preference for open or covered pools. Based on my results, I argue that an examination of predation pressure and protection of the juvenile fish provided by the cover structures is necessary in field studies of habitat use.

The observation that more fish were feeding at the head of the pool in the single pool experiment when the predator was present conflicts with the expectation that fish should attempt to minimize exposure to predation. Although I do not know the size of the fish in that experiment precisely, my observations suggest that it was the smaller fish which previously had occupied marginal positions in the pool that increased their feeding activity at the head of the pool. It is possible that the risk averse behaviour of the larger (presumably dominant) fish creates a feeding opportunity for the smaller fish, provided they are prepared to risk exposure to the predator. A similar pattern was observed by Hegner (1985) in blue tits (*Parus caeruleus*), where smaller, subordinate members of a flock

resumed feeding after a predation threat earlier than dominant individuals. In Grant and Noakes' (1987) study, smaller juvenile brook trout in streams resumed feeding earlier than larger individuals after being scared. Overall, the results of this and previous studies suggest that, if one wants to predict habitat use by juvenile coho salmon under various conditions of feeding and predation risk, it will be necessary to evaluate the costs and benefits for individual fish associated with the use of available habitats.

My laboratory experiments showed that there were differences among individuals in their response to simulated predation risk which lead to a spatial segregation of fish by size. The cause for this segregation was probably a risk-avoidance reaction by larger fish, which showed a preference for the pool offering refuge from predation after predation simulation was begun. Since larger coho tend to be dominant over smaller conspecifics (Chapman 1962; Sandercock 1991), the small fish were probably left with the choice of marginal positions in the safe pool or occupation of the risky pool. Facing this dilemma, many small fish choose the risky pool to the effect that a small difference in number of fish between the pools resulted compared to the field experiment where the overall density of fish was smaller and territorial aggressiveness, therefore, probably less intense. The large fish in the refuge traded off safety from the perceived predator for reduced growth rates compared to control treatments, whereas the smaller fish on average had similar growth rates under both treatments, to the effect that under predation, small and large fish experienced similar mean growth rates.

Size-specific responses to predation risk as a result of size-dependent susceptibility to predators have been shown for various fish species (e.g. Werner and Gilliam 1983, Werner et al. 1983, Eklöv and Diehl 1994). However, increased susceptibility to predation of larger coho (e.g. Wood and Hand 1985, but see Feltham 1990) seems an insufficient explanation for the greater risk avoidance of larger fish in my study since other studies also reported improved predator evasion capability with size (e.g. Healey & Reinhardt 1995) and Martel & Dill (1995) showed that movement, and not body size, was a predictor

of susceptibility of coho fry to capture by a bird predator. Higher satiation levels (i.e. greater stomach fullness) of larger fish (due to territorial dominance) as a cause of greater risk avoidance (e.g. Gotceitas and Godin 1991) may have contributed to the formation of the observed distribution pattern in my laboratory experiment, but cannot account for its persistence after predation was stopped. Since fish were fed evenly in the laboratory for several weeks prior to the experiment, long-term difference in level of nutrition between small and large fish as a cause for observed greater risk avoidance in larger fish (Damsgård & Dill, 1998) were unlikely in my experiment. Instead, I argue that the "Asset-Protection-Principle" (Clark 1994), which I discuss in Chapter 5 and 6 in more detail, is responsible for the observed size-dependency of risk taking behaviour.

The observations by Grant and Noakes (1987) suggest that size-determined risk taking by salmonids also occurs in natural streams. The scenario I invoke for natural streams is that risk aversion by larger members of a cohort may lead to reduced overall growth rates under frequent predation risk with drifting food particles potentially being lost to competitors or other trophic levels. In Tabor and Wurtsbaugh's (1991) study, rainbow trout experienced reduced growth rates as a consequence of their moving from pelagic to near-shore habitats in response to introduction of predators to a reservoir. At a cost of greater exposure to the predator, smaller fish may gain access to better feeding opportunities because of greater willingness to feed under risk. In this way, growth rate differences between small and larger members of the cohort due to territorial dominance of larger fish may be reduced or, at sufficiently high frequencies of predation events, even reversed. Through individual, size-mediated differences in risk-taking the population dynamics of a cohort and possibly on other trophic levels may be affected. Several workers (e.g. Abrams and Matsuda 1993; Mittelbach and Chesson 1987; Sih 1987; Werner 1992) have suggested that such wide-ranging effects can be the outcome of the sum of behaviours of individuals.

Table 1. Behaviours of juvenile coho salmon recorded in the One-pool Experiment.

Behaviour Category	Description
Still	holding position in the current or sitting on bottom, no movement apart from slow (< 1 bl/s) drifting with the current
Moving	any swimming motion resulting in displacement from a position
Feeding	interception of particle from the surface or water column, feeding attempt (directional movement for > 3 bl and return to a holding position)
Aggression	charges, nips, chases and lateral displays (Swain and Holtby 1989)

Table 2. Hunting effort and success of the merganser ducks in the Three-pool Experiment

	No Cover	Medium Cover	High Cover
Total Minutes in Section	143	86	109
No. of Dive Pursuits	98	24	58
No. of Captured Fish	21	4	7

Table 3. Results of 2-Way ANOVA on daily growth rates in the Laboratory Experiment.

Source	d.f.	Mean Square	F-Ratio	P (alpha)
Predation/ Control	1	7.97	3.97	0.047
Size Group	1	5.62	2.8	0.095 (n.s.)
Interaction	1	7.43	3.7	0.055 (n.s.)
Error	332	2.01	n= 336	

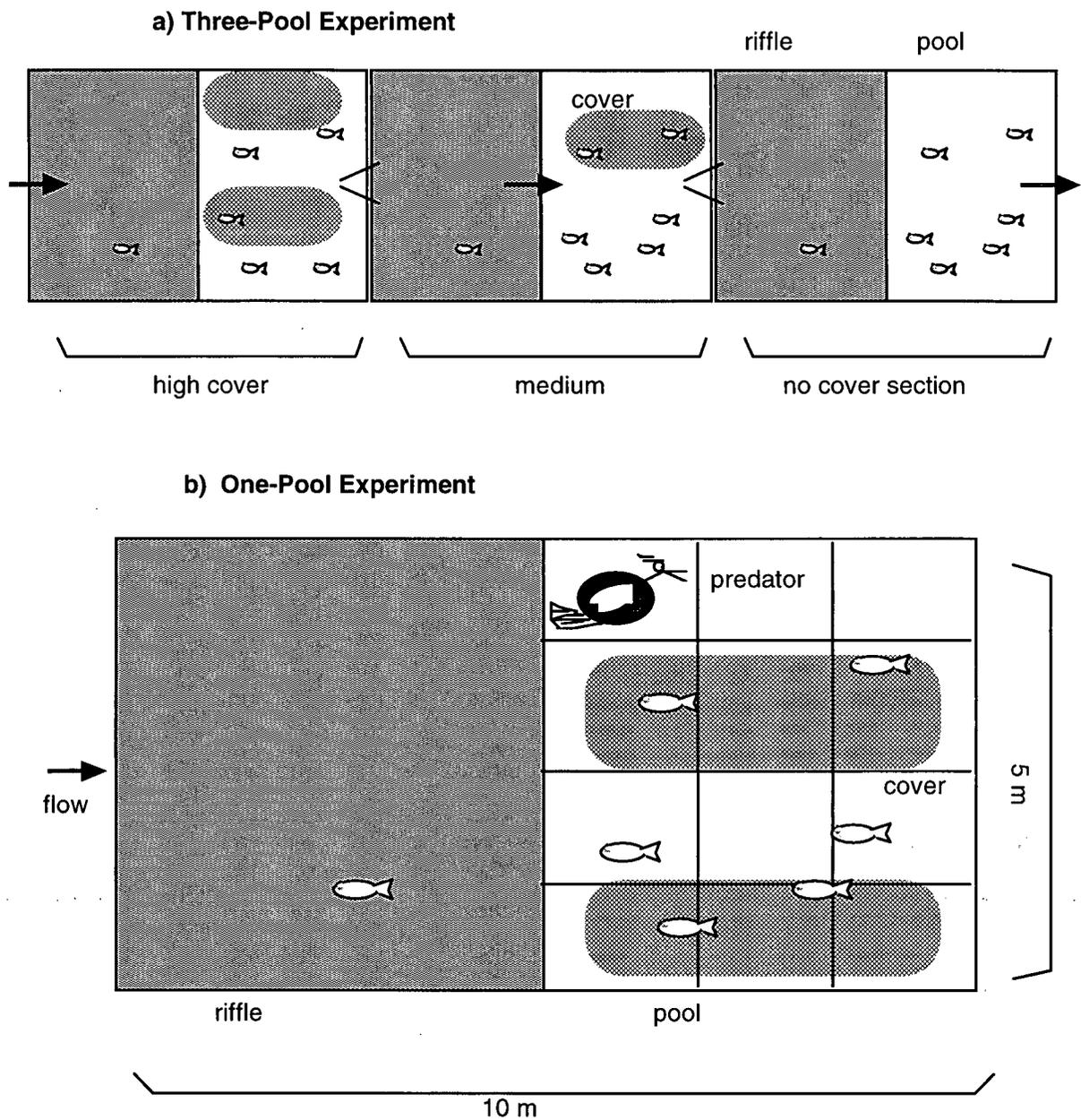


Fig. 2.1 Experimental set-up of a) the Three-pool Experiment and b) the One-pool Experiment. Distribution of cover treatments was changed between repeated observations in the three-pool-experiment.

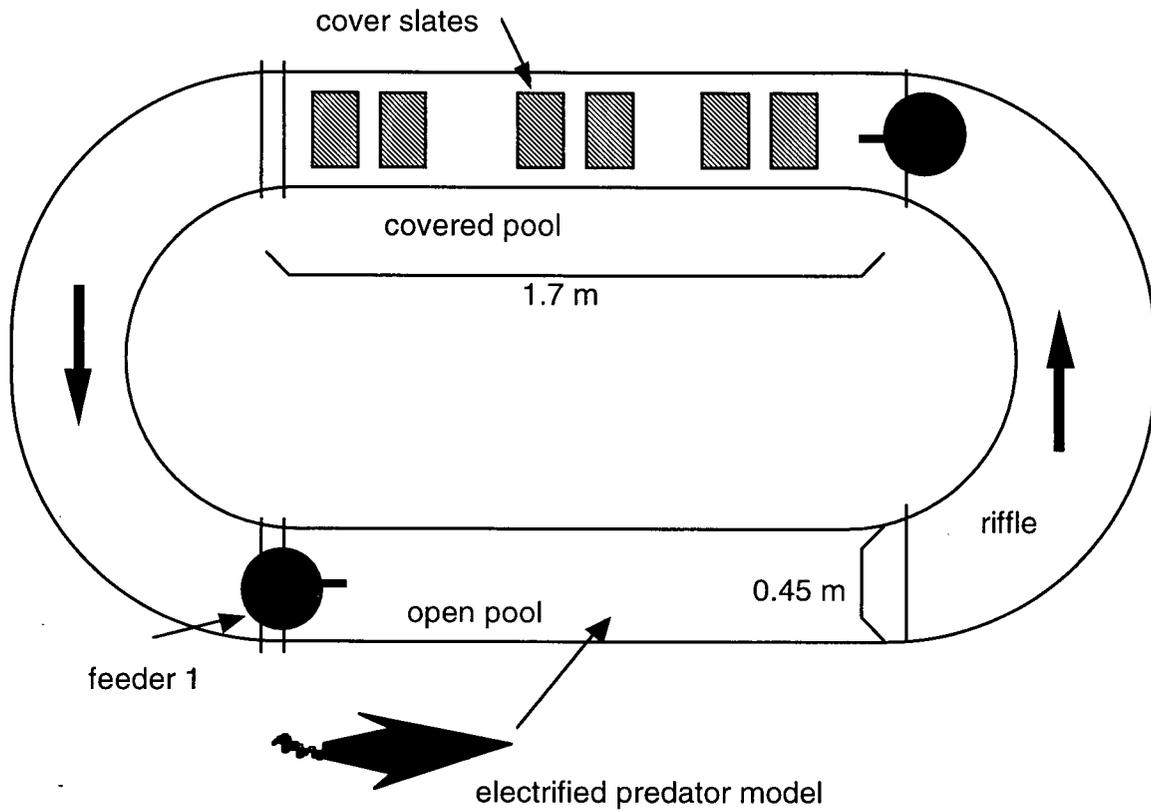


Fig. 2.2 Experimental set-up of the Laboratory Experiment. Fish in the open pool were subjected to simulated predation risk by dipping an electrified predator model.

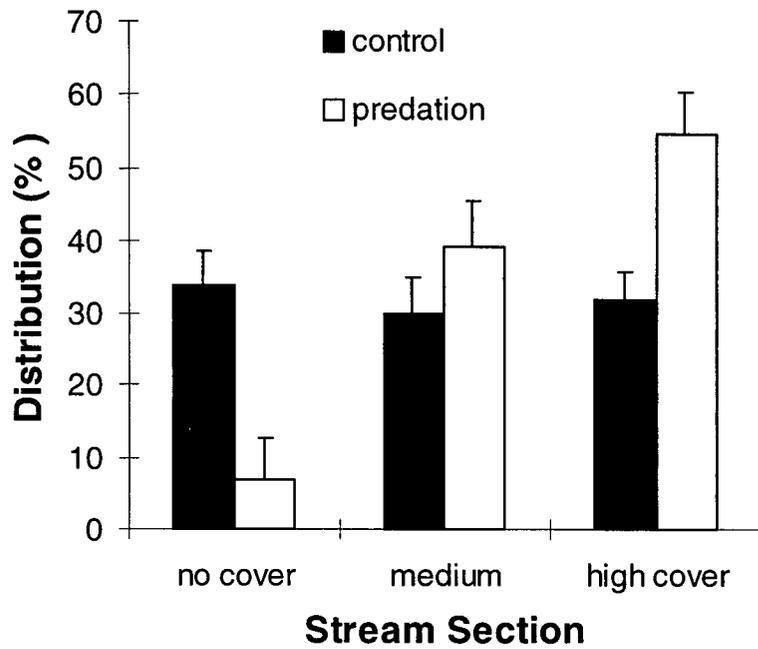


Fig. 2.3 Distribution of fish among three stream sections in the Three-pool Experiment. Each bar represents the mean (+ 2 S.E.) of three replicate weeks. Control and treatment distribution were significantly different in a X^2 comparison.

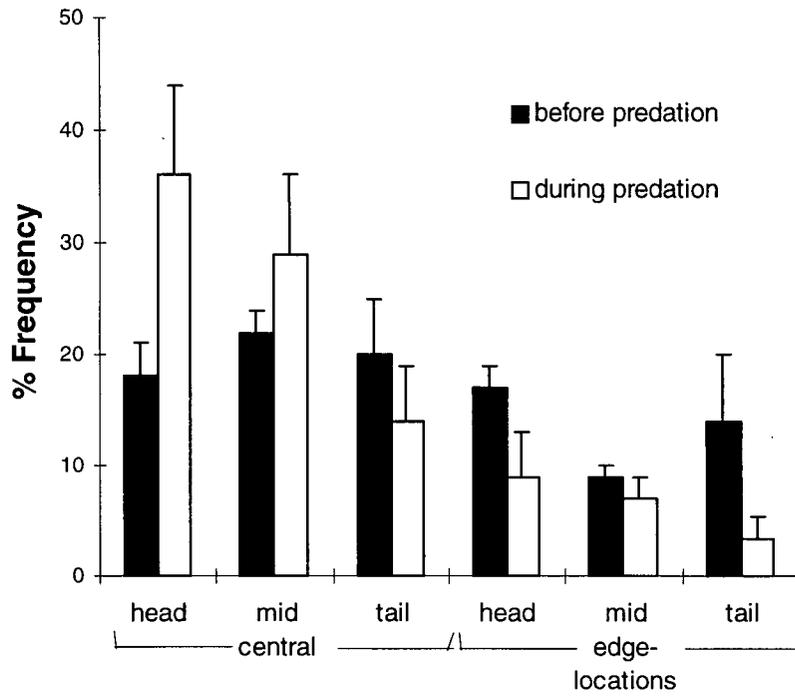


Fig. 2.4 Distribution of fish among 6 areas within a pool in the One-pool Experiment before any predation event and during foraging by a merganser duck. Bars represent mean (+ 2 S.E.) of three replicates. 'Head' refers to the areas of the pool depicted in Fig. 2.1 directly downstream of the riffle, 'mid' and 'tail' areas are further downstream; 'edge-locations' refers to the squares in the pools closest to the bank of the stream, whereas the squares away from the edge were called 'central' locations.

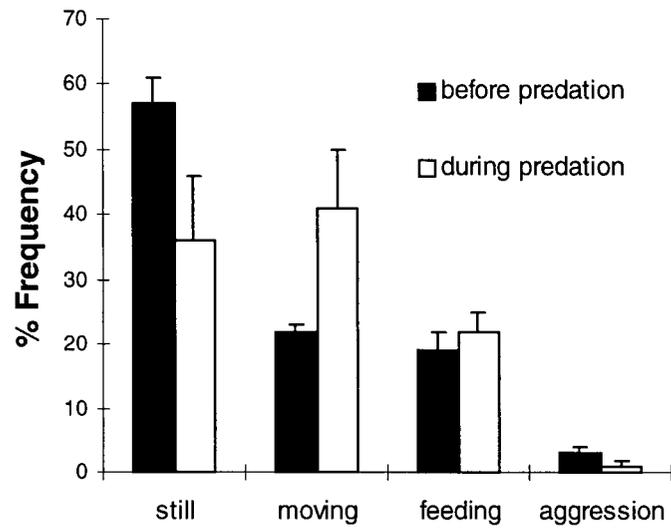


Fig. 2.5 Mean frequency (+ 2 S.E.) of coho behaviour in the One-pool Experiment before and during foraging by a merganser duck. The two behaviour patterns were significantly different.

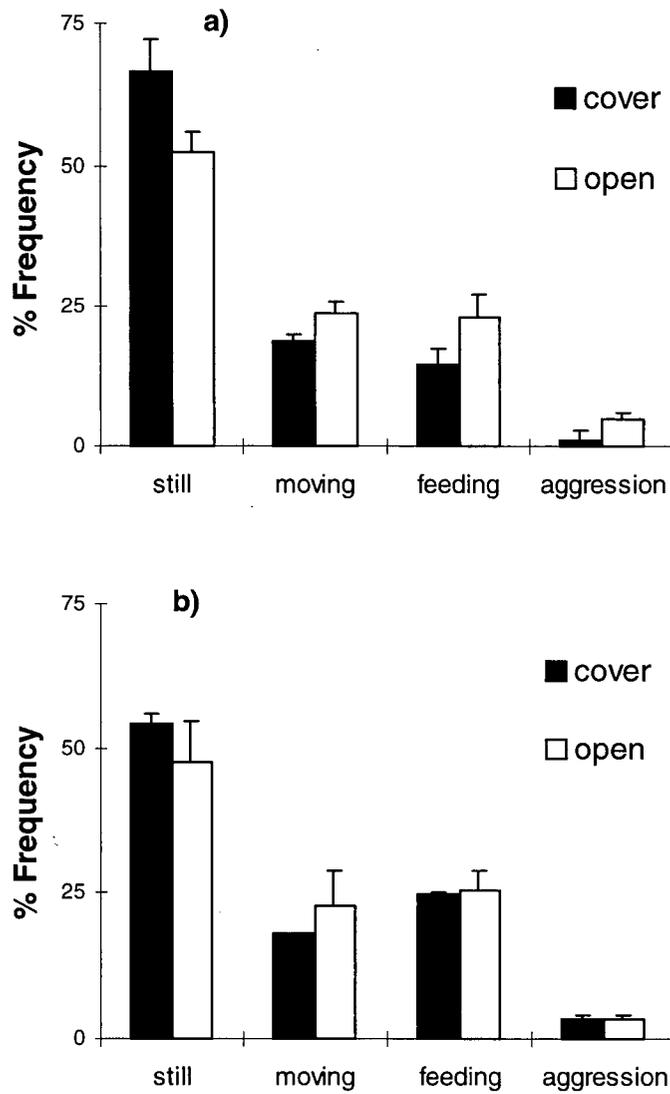


Fig. 2.6 Mean frequency (+ 2 S.E.) of coho behaviour inside ('cover') and outside ('open') of brushy cover in the One-pool Experiment a) before and b) between foraging events by a merganser duck. See text for details on statistical analysis.

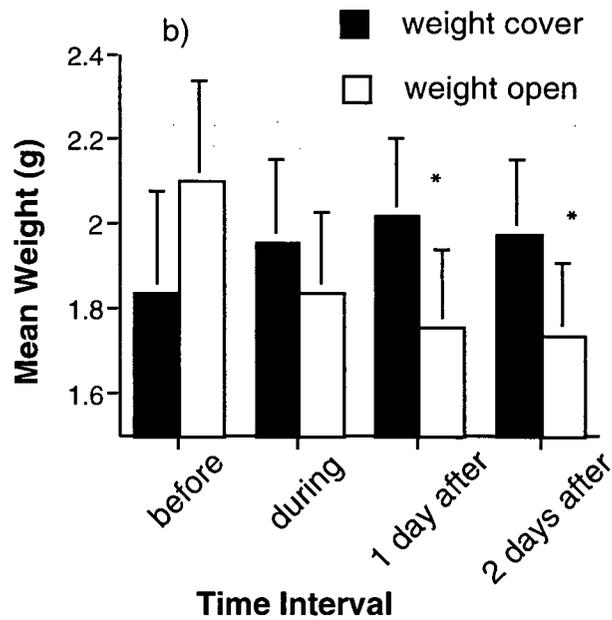
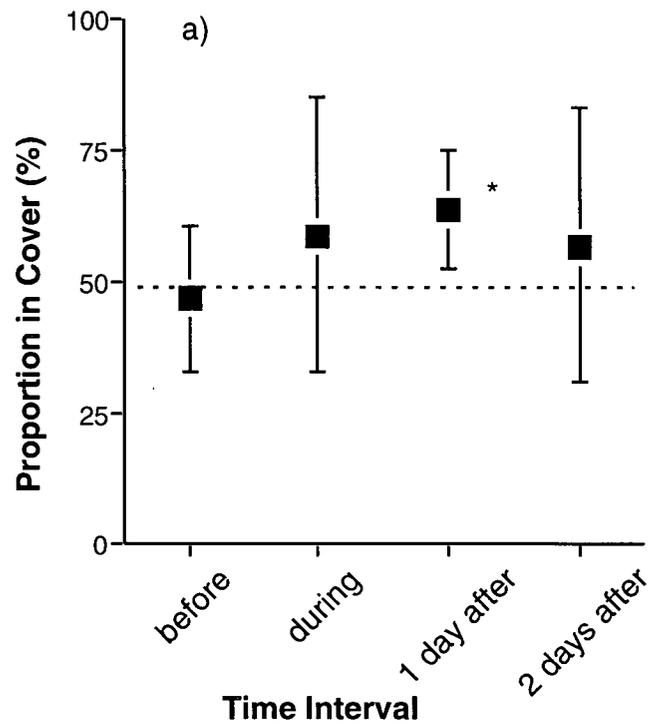


Fig. 2.7 Distribution of a) percent of fish observed in the open pool and b) weights of coho salmon in open and covered pools in the laboratory experiment. Data points represent the mean and 2 S.E. of 12 replicates with 20 fish each. Observations are grouped according to time intervals related to simulated predation events. Asterisks (*) denote statistically significant differences between open and cover.

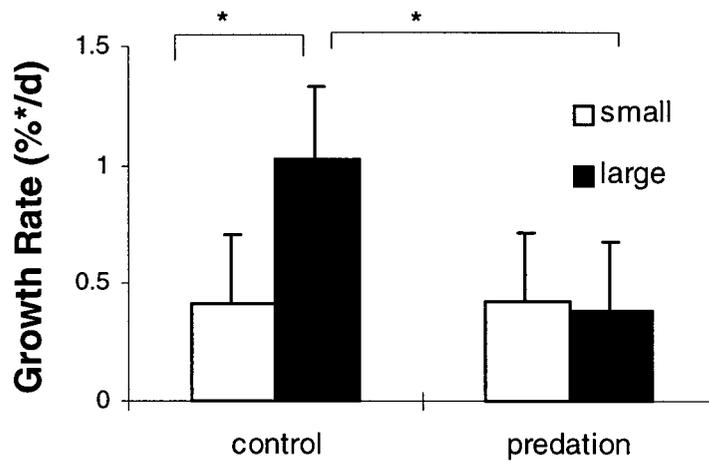


Fig. 2.8 Mean (and 2 S.E.) specific growth rates (% body weight/day) of large (i.e. fish below median weight in each tank) and small fish in the laboratory experiment in presence ('predation', n= 224) and absence ('control', n=112) of simulated predation. Asterisks (*) denote significant post-hoc comparisons among groups.

Chapter 3 **The Influence of Predation Risk on Territorial Behaviour and Growth of Individual Fish of Different Sizes**

Introduction

In Chapter 2, I showed that larger age-0 coho salmon (*Oncorhynchus kisutch*) were more risk averse than smaller fish in accordance with predictions based on the 'Asset Protection Principle' (Clark 1994, see also Chapter 4). Larger individuals avoided exposure to a predation threat and experienced reduced growth rates, whereas smaller individuals apparently were less risk averse and maintained their growth rate in the presence of a threat. Growth depensation which results from size-dependent feeding hierarchies in coho (Sandercock 1991, Ryer & Olla 1996) and other salmonids (e.g. Elliott 1990) did not occur under simulated predation threat.

In this chapter, I analyze behavioural observations of coho fry interacting in groups in the laboratory experiment described in Chapter 2. I examine agonistic interactions among fry of different sizes to show how the social dynamics that cause growth depensation are influenced by predator presence.

Recent studies on juvenile salmonids have raised interest in individual variation in foraging behaviour and the relationship between individual characteristics and indicators of fitness in different environments. For example, studies on Atlantic salmon juveniles (*Salmo salar*) (Metcalf et al. 1989, 1995) showed that variation among individuals in competitive ability and feeding motivation influenced the timing of ontogenetic habitat shifts. It was shown that greater feeding motivation was correlated with higher standard metabolic rates in newly-hatched Atlantic salmon fry, suggesting a genetic

influence on social dominance and timing of smoltification. Experiments on Arctic char (*Salvelinus alpinus*) showed that different individual foraging strategies conferred growth advantages in different rearing environments (Adams & Huntingford, 1996). To further explore the issue of individual variation in foraging tactics under different predation regimes, I also examine in this chapter the relationship between body size, risk taking, and growth success of coho fry in my experiment.

Materials and Methods

The experimental design of this experiment is fully described in Chapter 2. Groups of 20 coho fry were held for one week in re-circulating stream tanks with two pools, one ("exposed" pool) into which an electrified bird model was intermittently introduced in predation experiments, and one ("refuge" pool) which contained cover and where the fish were safe from the simulated predation threat.

For the three days of simulated predation threat ("during predation") and 2 days afterwards ("after predation"), I assessed the position and behaviour of all visible fish several times per day (5 times /day "during predation", 3 times/ day "after predation") For each fish I recorded the pool it was in and whether it occupied the upstream 3/4 of the pool or the downstream 1/4 (farthest away from the feeder, Fig. 3.1). I then observed the behaviour of the fish for three 5 second periods. During each 5 s, I recorded three kinds of agonistic interactions in what I perceived as ascending order of intensity: i) lateral display (showing the side of the body with erected dorsal and pectoral fins), ii) charge (rapid acceleration toward a conspecific to within 1 body length or less, sometimes followed by bumping into the other or nipping), and iii) chase (chasing the other fish for more than 2 body lengths after a charge) (after Swain and Hotlby 1989). I also recorded whether a fish attacked an opponent or received the attack. I recorded one behaviour for each 5 s period, so that a maximum of 15 observations was collected for each fish and each day. If more than one aggressive interaction occurred within the 5 s, I

recorded the highest ranking behaviour. In the control experiment, I followed the same experimental protocol with the exception that no predation threat was simulated and the fish were observed only three times per day over five days, for a total of 15 observation periods, compared to 21 observation periods in the predation experiment. Therefore, not all of the results (e.g. number of switches between pools,) can be compared between control and predation experiments.

On the 7th day of each experiment, all fish were removed, anaesthetized, and weighed to allow calculation of growth rates over the previous week. Four weeks of the experiment with predation treatment (12 replicates) preceded 2 weeks (6 replicates) of control observations. Different fish were used in each replicate.

Data Handling and Statistics

A group of 20 fish, observed for 5 days, was considered one replicate for most statistical analyses, with the exception of one Chi-square test where pooled observations of agonistic acts across replicates were used. For the analysis of social hierarchies and growth rates, fish were divided into two groups, those heavier than the median weight of the 20 fish in each replicate ('large' group) and those smaller than median weight ('small' group). Since in the control observations (no predation), there were no differences in the number of fish and their behaviour between the two pools of the tanks, observations from the two pools in the control experiment were pooled for analysis. Data from the predation treatment were divided by location ("exposed" and "refuge" pool), and time relative to the predation simulation ("during": day 2 and 3 of each trial and "after": day 4 and 5). A dominance index was calculated for each fish for which I had observed a minimum of 2 agonistic interactions. A lateral display, charge or chase performed by the focal fish, was awarded a positive score of 1, 2 and 3 points, respectively, and equivalent negative scores when the focal fish was the receiver of such behaviours

(e.g. a fish observed to have chased others twice while having been charged once would receive a dominance score of $3 + 3 - 2 = 4$). P-values given for all statistical tests are two-tailed; $\alpha = 0.05$ was used as the significance criterion throughout. Frequency data and proportions were arcsine-sqrt-transformed for statistical analyses, weight data were log-transformed.

Results

Social Interactions in Absence of Predation Threat

Of all observed agonistic interactions, charges against an opponent were most frequent (about 70%), followed by lateral displays and chases (Fig 3.2). Lateral displays against a focal fish were more difficult to detect, which probably accounts for their being less frequently recorded than lateral displays by the focal fish (Fig 3.2). Large fish engaged in more agonistic behaviour than small fish (0.15 agonistic acts per 5 s observation period versus 0.11 for small fish; paired t-test: $t=2.94$, d.f. = 5, $p < 0.05$). In all six replicates (sign test, $p < 0.05$), large fish were more often attackers than receivers (Fig 3.2, 3:1 ratio of attacks/ defenses when focal fish large), whereas small fish more often were receivers of aggressive actions (2:3 ratio of attacks/defenses with focal small fish).

The mean size of fish in the downstream quarter of the tank was significantly smaller than in the rest of the pool (paired t-test on mean weights of fish in the two areas of the tank: $t= 7.25$, d.f.= 5, $p < 0.01$), confirming the visual impression that small fish mainly occupied the downstream part of a pool (farthest away from the feeder) where the frequency of agonistic interactions was lower (mean frequency of 0.08 per 5 s observation period in the downstream area versus 0.15 in the upstream part; paired t-test on frequency of aggressive acts, $t= 2.96$, d.f.= 5, $p < 0.05$).

The specific growth rate was correlated with the dominance index of the individual fish (Fig. 3.3, Pearson $r = 0.337$, $p < 0.05$) (see Data Handling section for details on calculation). Division into negative and positive dominance score (Fig. 3.3) reflects the division of fish into a small and large group: only 7 (15%) of the fish with a positive score were small and 10 (25 %) of fish with a negative score were large.

Social Interactions under Simulated Predation

During the days that the predator model was dipped into the exposed pool, mean level of aggression in the exposed pool was reduced by about 50% compared with the control experiment (Fig. 3.4, exposed pool: mean of 0.07 agonistic acts/observation period, range 0 - 0.16) and returned after predation simulation to values comparable with the control observations (Fig. 3.4, control treatment: mean of 0.14, range 0.07 - 0.2). In the refuge, the mean frequency of agonistic interactions during the simulated threat was intermediate between values for the exposed pool and the control experiments (Fig. 3.4). The frequencies of agonistic interactions differed significantly among the four location/time intervals in the predation treatment (rep. measures ANOVA: $F_{3,33} = 5.08$, $p < 0.01$). Compared to the control experiment and to after predation, levels of agonistic behaviours were significantly lower during predation in the exposed pool, but not in the refuge pool (Fig. 3. 4, t-tests: control vs. exposed/during, $t = 2.16$, $p < 0.05$; control vs. refuge/during, $t = 0.85$, n.s.; both d.f. = 16; Tukey's test: exposed pool during vs. after: $q = 4.72$, $p < 0.05$; refuge pool during vs. after: n.s.).

During predation simulation in both the exposed and refuge pools, the relative frequency of lateral displays was reduced while the relative frequency of chases was about twice that of the control observation (Table 4). Patterns in the distribution of the three types of agonistic interactions (display, charge and chase) were analyzed with a series of pair-wise Chi-square tests using pooled counts of

agonistic interactions. In both exposed and refuge pool, the distribution of agonistic interactions during predation differed significantly from control and after-predation distributions (Table 4).

In the predation treatment, as in the control treatment, fish in the downstream end of the tank were smaller on average than those in the upstream part of the tank, closer to the feeder (Fig. 3. 5). However, the size difference was smaller during the days of simulated predation (paired t-test on mean weights of fish in the downstream quarter/ vs. weights in the upstream part, a) exposed pool during predation: $t = 1.54$, d.f. = 11, n.s., b) refuge pool during predation: $t = 1.37$, d.f. = 11, n.s.). After predation simulation was halted, fish in the back were again significantly smaller than those closer to the feeder (paired t-test on mean weights of fish in the downstream quarter/ vs. weights in the upstream part: exposed pool after predation: $t = 3.1$, d.f. = 11, $p < 0.01$; in the refuge pool after predation, $t = 2.75$, d.f. = 11, $p < 0.05$).

Choice of Habitat and Growth Rate

To get an indication of habitat preference of the fish, I divided the number of times an individual was observed in either pool by the number of all observations for that fish. In the control and predation experiment, the majority of fish showed a strong preference for one of the two pools (Fig. 3.6), with a slight tendency in the control experiment for large fish to be more bound to a single pool (Fig. 3.6, paired t-test on mean proportion of observations in the preferred pool by small and large fish: control $t = 5.9$, d.f. = 5, $p < 0.001$; predation: $t = 1.61$, d.f. = 11, n.s.) This preference for one habitat was not due to a general lack of sampling of the available choices by the fish: the mean number of confirmed switches between pools (number of times an individual was observed in different pools in subsequent observations periods as a minimum estimate of switches) was 1.6 (median =1) in the control experiment and 2.7 (median =2) in the predation experiment. Small fish did not switch pools significantly more often than large fish (control: small fish, mean number of switches = 1.4, large = 1.9; paired t-test on sqrt-transformed mean number of switches per replicate, $t = 1.65$, d.f. = 5, n.s. predation: small = 2.8

large = 2.6, $t = 0.86$, d.f.= 11, n.s.). Number of switches in the predation treatment were not comparable with the control treatment because of differences in the number and spacing of observations over time.

To compare growth rates between risk-prone and risk-averse individuals, the fish were separated into two categories of habitat choice: those with $\geq 60\%$ of all observations in the exposed pool ("risk-prone") and those with $\geq 60\%$ in the refuge pool ("risk-averse"). In absence of predation, large fish grew better than small fish (Fig. 3.7, reported in Chapter 3). In the predation experiment large fish also grew better among the risk-averse group and the ratio of growth rates was similar to the control (Fig. 3.7). In the risk-prone group, the ratio of growth rates of large versus small fish was less than one (Fig. 3.7, significant interaction in ANOVA, Table 5). Risk-prone fish on average grew 0.73 % /d versus 0.29% / d for the risk-averse group - a difference which was not quite significant (Table 5). Small risk-prone fish grew significantly faster than small risk-averse fish (Fig. 3.7, Tukey's test $p < 0.05$), whereas risk-prone and risk-averse large fish achieved similar growth rates (Fig. 3.7, Tukey's test n.s.).

Discussion

In the absence of predation risk, coho fry formed dominance hierarchies. Rate of aggression and dominance status increased with body size relative to tank mates. This agrees with earlier studies, which showed that coho juveniles form size-dependent hierarchies when food sources can be monopolized (e.g. Holtby et al. 1993, Ryer & Olla 1996, Grand 1997a). Larger and more dominant fish subsequently grew better so that initial size differences in the group increased. In natural systems, this growth depensation has been shown to lead to mortality and emigration of the smaller members of a cohort (Elliott 1989, Sandercock 1991).

The presence of a predation threat changed the group dynamics and growth patterns considerably. As in previous experiments on coho behaviour in the presence of predation risk (Dill & Fraser 1984, Martel & Dill 1992, Healey & Reinhardt 1995, Martel 1996), activity rates of fish were reduced following exposure to a predator. Small fish, which are more risk-prone and resume feeding earlier after being threatened (Chapter 2, Grant & Noakes 1987), were able to profit from reduced levels of intraspecific aggression and gained access to food sources from which they previously had been excluded. Additionally, as shown in Chapter 2, large fish tended to avoid the exposed pool so that the presence of the disturbance indirectly provided growth opportunities for individuals willing to risk exposure to the (simulated) predator.

The greater relative frequency of chases versus aggressive displays during the days of simulated predation is somewhat surprising since previous studies have indicated that predators detect moving prey more easily (Martel & Dill 1995) and I expected that the coho fry under threat would not only reduce frequency of agonistic interactions but also use less overt types of behaviour. However, since this increase in severity of agonistic acts was also observed in the refuge, where no direct contact with the threat was present, it may have been caused by the need to re-establish dominance hierarchies in both pools following the redistribution of the animals after the start of the predation simulation. The level of agonistic interactions and spatial segregation by size within the pools in the two days after predation simulation were similar to the undisturbed pattern, which indicates that the social hierarchies within pools were quickly re-established. In Chapter 2, I showed that it takes a week or more for numerical and size distributions among pools to return to undisturbed levels after predation, and in this analysis I showed that individuals tend to spend most of their time in one pool. This relative stability in the distribution of fish is likely due to costs individuals have to pay for switching habitats, such as the cost of contesting a feeding spot against a prior territory holder (e.g. Cutts 1997).

Considering the distance between exposed and refuge pools and their visual isolation from one another, it is surprising to find indications of similar behavioural patterns in response to the predation threat in the refuge and exposed pools. It appears that some transfer of information between pools on the threat was responsible for the apparent behavioural spill-over effect. As has been shown in recent years, coho salmon show risk avoidance behaviour in response to chemical stimuli associated with predator presence (Martel and Dill 1992) and injury of conspecifics (Brown & Smith in press). However, since my model predator (made from wood and fiberglass) was unlikely to smell like a natural predator and did not injure any fish, it is unlikely that chemical cues such as the ones described by Brown & Smith (in press) traveled around the re-circulating tank to alert the fish in the refuge. Salmonids and other fish react to visual cues from conspecifics that were conditioned to a frightening stimulus (Suboski and Tempelton 1989) so that a mixed group of stimulus-naive and experienced fish reacts like an experienced group (Bams 1967, Olla & Davies 1989). Therefore, it is possible that in this experiment fish that came in contact with the model predator moved into the refuge pool, where some aspect of their behaviour (e.g. rapid opercular beats as a sign of stress, Metcalfe et al. 1987) influenced the other fish. I observed a fairly strong variation in fright responses among groups of fry, ranging from apparent ignoring of the model to complete abandonment of the exposed pool by the whole group. I suggest that this was due to those groups consisting of a few particularly bold (or timid, respectively) individuals which influenced the response of the whole group.

Among small fish, the choice by individuals to occupy the exposed or refuge pool strongly affected their growth. Small fish in the predation experiment could be classified as those that avoided risk and grew slowly and those that were risk prone and grew fast. The latter pattern is similar to the one observed in juvenile Atlantic salmon, where smaller members of the cohort show markedly reduced feeding motivation by July of their first feeding season and delay seaward migration for one year,

whereas larger and/or more dominant fry continue to compete for food vigorously through the fall and initiate seaward migration the following spring (Thorpe et al. 1992). Juvenile coho salmon have been less well studied in this regard, but it is known that the proportion of fish that smoltifies at age 1 + or age 2+ varies with growth conditions among geographical regions and years (Holtby & Hartman 1982, Randall et al. 1986). It is, therefore, possible that the two risk-taking and growth strategies of small coho in my experiment reflect the outcome of a division into prospective one and two-year old smolts. More experimentation is needed to decide whether coho and Atlantic salmon follow similar behavioural patterns with respect to their decision to smolt as one or two-year-olds.

Why a number of the relatively large fish chose the risky pool without being rewarded with greater growth rates than their risk-averse counterparts is not obvious from this analysis. It is possible that these fish were relatively weak competitors who would have fared poorly in direct competition with the fish in the refuge pool.

It is important to note that in this experiment a high-risk, high-growth strategy for smaller, competitively inferior, individuals was only possible in the presence of the predation threat. As shown in Chapter 2, the disturbance caused by the predator model caused larger fish to show risk-avoidance behaviour. This opened the opportunity for some small fish to grow at a relatively high rate while paying the cost of greater exposure to a predator. If these results have significance for natural systems, then predation should not only be seen as an agent of mortality, but also as a creator of a behavioural niche, by breaking up size-dependent dominance hierarchies. Environments with frequent predator presence may, thus, allow for a wider variety of foraging strategies than environments with low predation pressure, where growth success is predominantly determined by an individual's ability to compete for a feeding territory.

Table 4. Relative frequency (%) and number (in parentheses) of 3 types of agonistic behaviours in control and predation experiments (using pooled observations across replicates), divided into four combinations of location and time relative to the predation simulation. Chi-square values are given for significant pair-wise comparisons among groups.

Treatment	Display	Charge	Chase	Comparison	X ² -value	P(α)
Control	18 (112)	68 (420)	13 (80)			
I Exposed/During	11 (23)	63 (132)	27 (56)	Contr vs. I	28.2	<.001
II Refuge/During	10 (43)	68 (304)	23 (101)	Control vs. II	26.9	<.001
III Exposed/After	18 (48)	67 (176)	15 (38)	III vs. I	13.7	<.01
IV Refuge/After	13 (46)	73 (258)	13 (49)	IV vs. II	10.72	<.05

Table 5. Results of 2-way ANOVA on log- transformed specific growth rates with relative body size ('small' and 'large') and risk taking category ('risk-prone' and 'risk-averse') in the predation treatment.

Source	d.f.	Mean Square	F-Ratio	P(α)
Size Group	1	0.01	0.06	0.8
Risk Group	1	0.56	3.3	0.077
Interaction	1	0.76	4.5	0.041
Error	39	0.17		

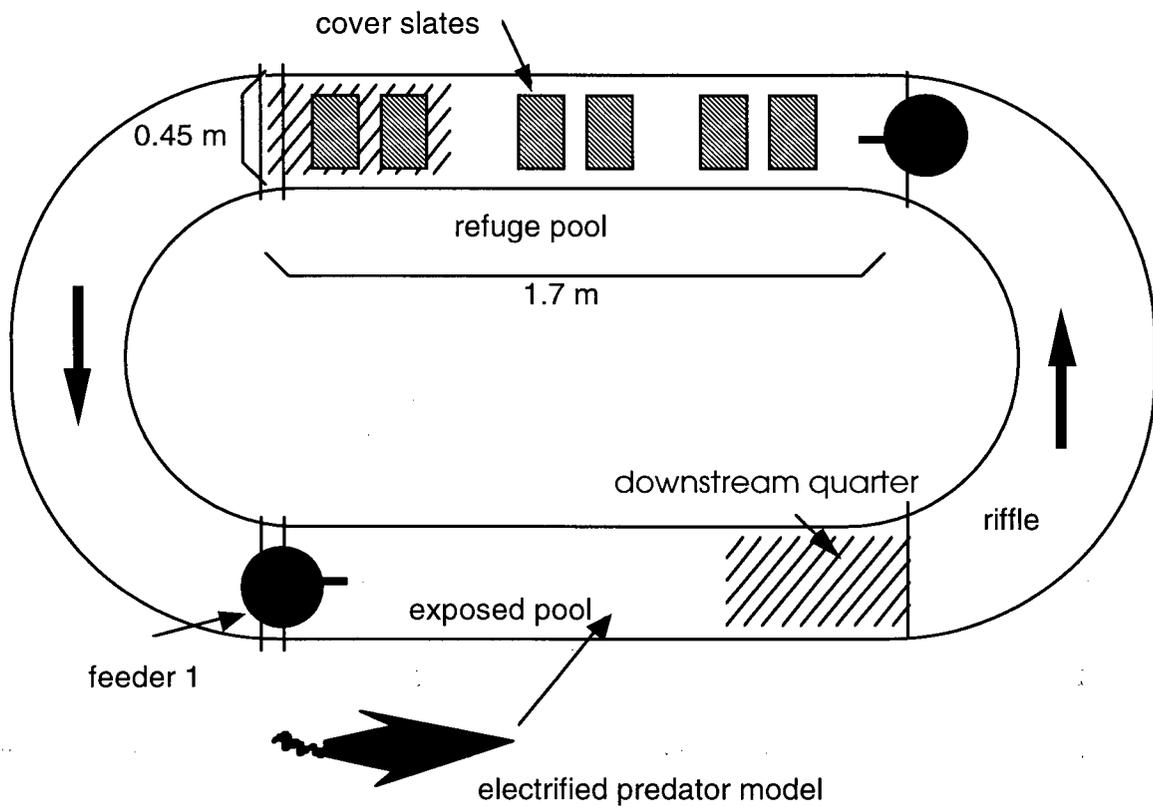


Fig. 3. 1 Experimental set-up. Fish in the exposed pool were subjected to simulated predation risk by dipping an electrified bird model during the first 3 days out of a total of 5 days that behavioural observations were made. See text for details.

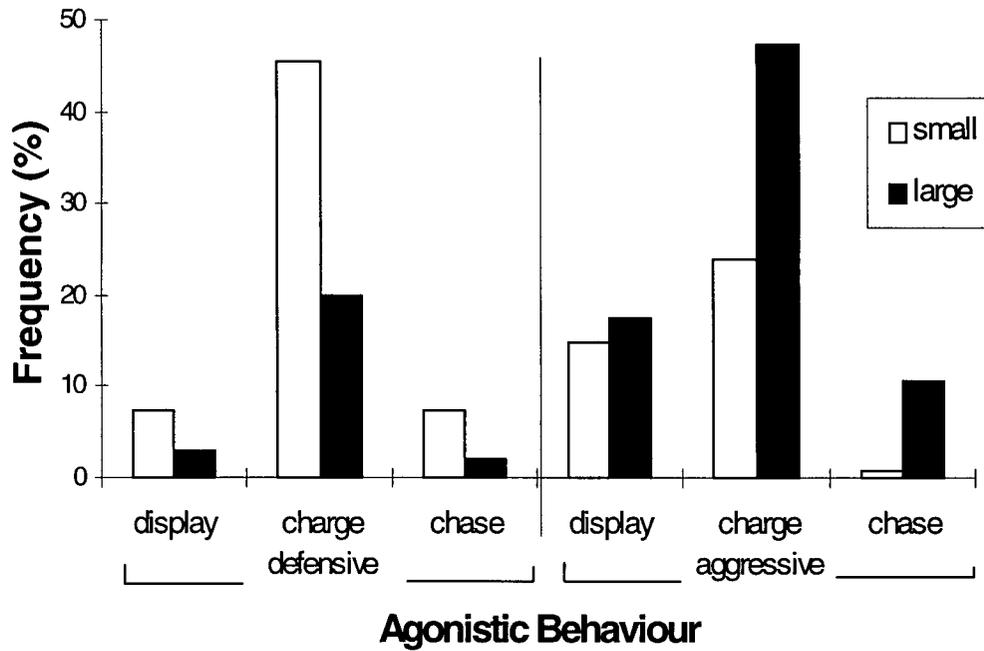
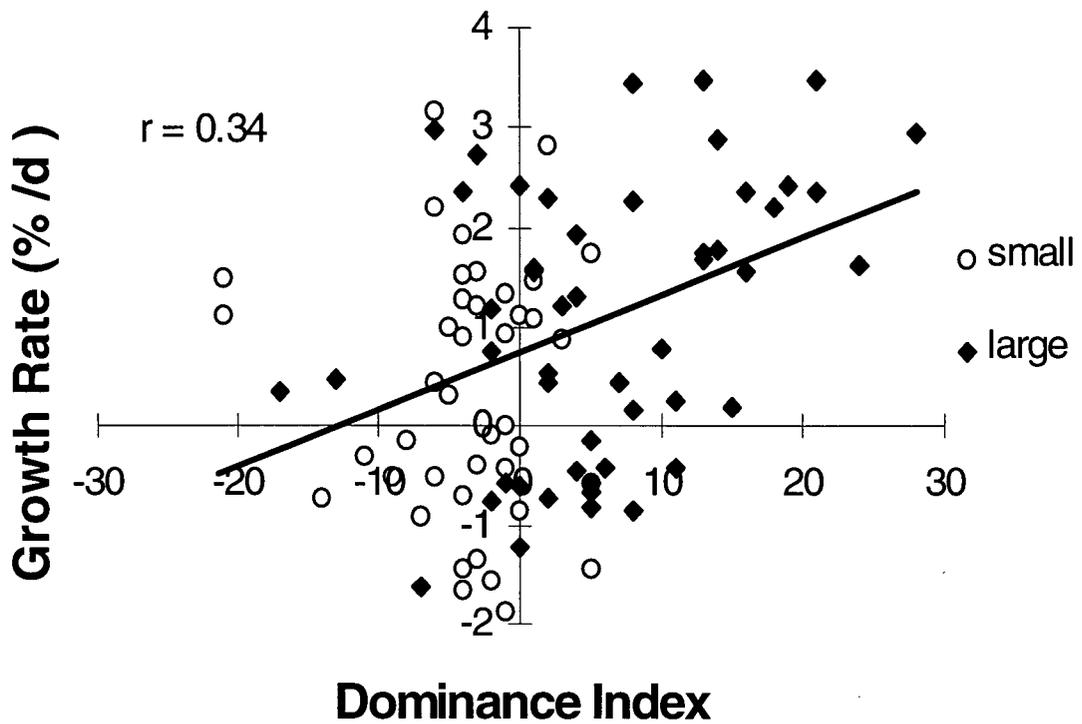


Fig. 3. 2 Distribution of agonistic activities (pooled observations across replicates) for coho fry above ("large") and below ("small") median body weight in the control experiment. "Defensive" refers to a focal fish being the receiver of an agonistic action; "Aggressive" refers to an attack by a focal fish.



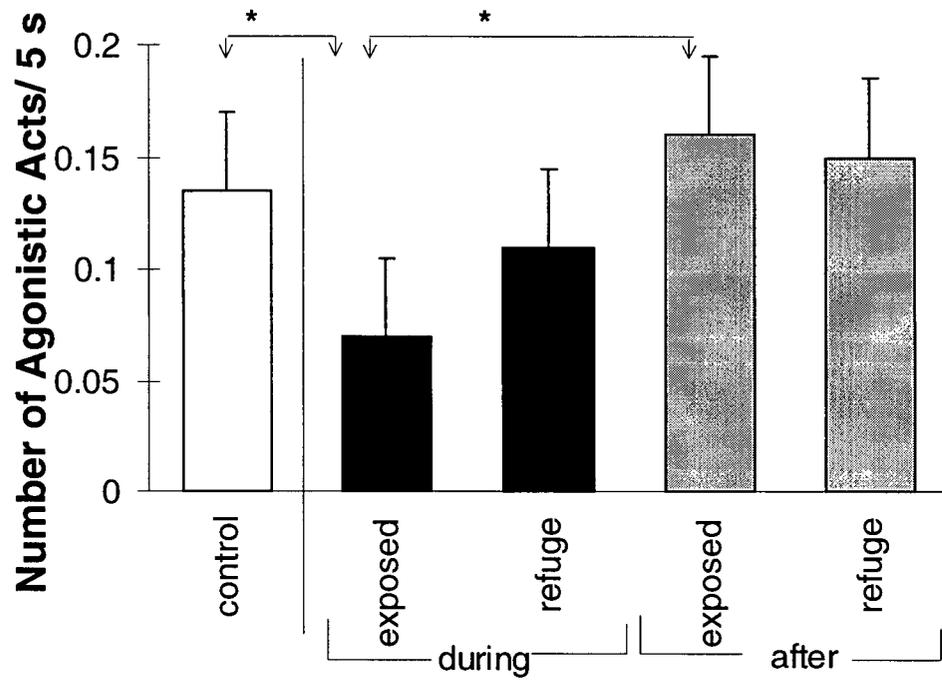


Fig. 3. 4 Mean frequency (+ 2 S.E.) of agonistic interactions in the control (n=6) and predation treatment experiment (n=12). Data for the predation treatment are divided by location (exposed/refuge pool) and time relative to the predation simulation (during/after). Asterisks (*) denote significant single d.f. tests with arrows indicating the groups between which the difference was significant.

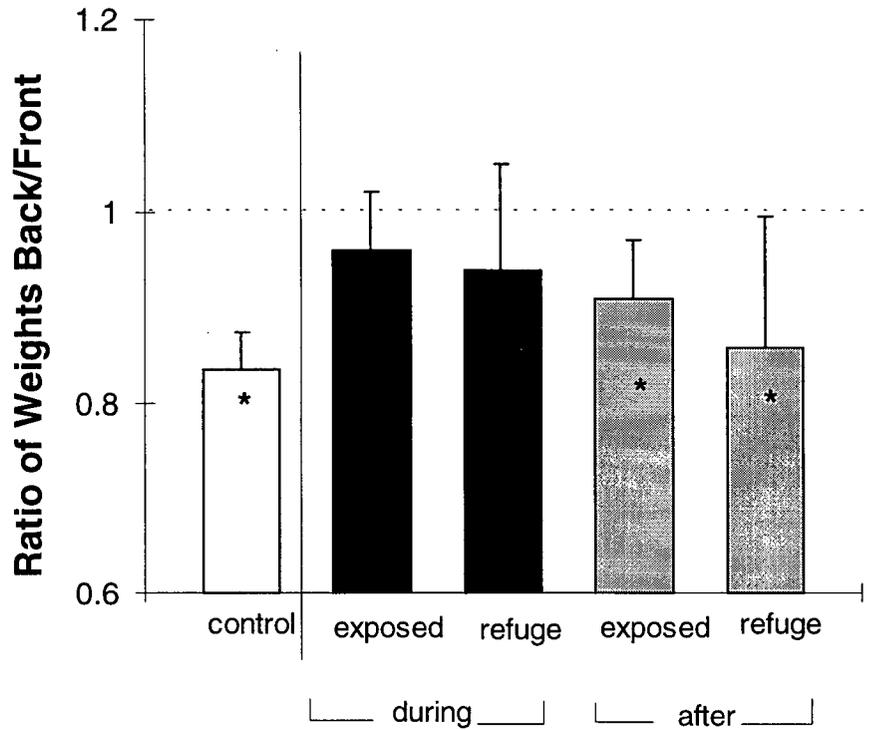


Fig. 3. 5 Ratio of mean body weights (+ 2 S.E.) of fry in the downstream 1/4 versus the upstream 3/4 of a pool in the control (n=6) and predation experiment (n=12), separated by location (exposed/refuge pool) and time relative to the predation simulation (during/after). Asterisks (*) denote that the ratio was significantly smaller than one.

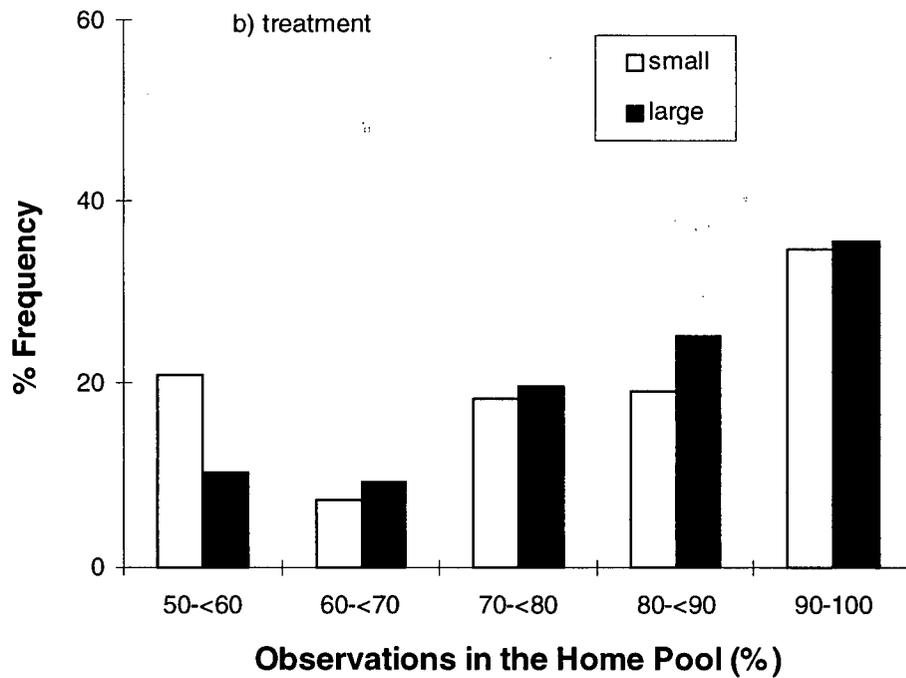
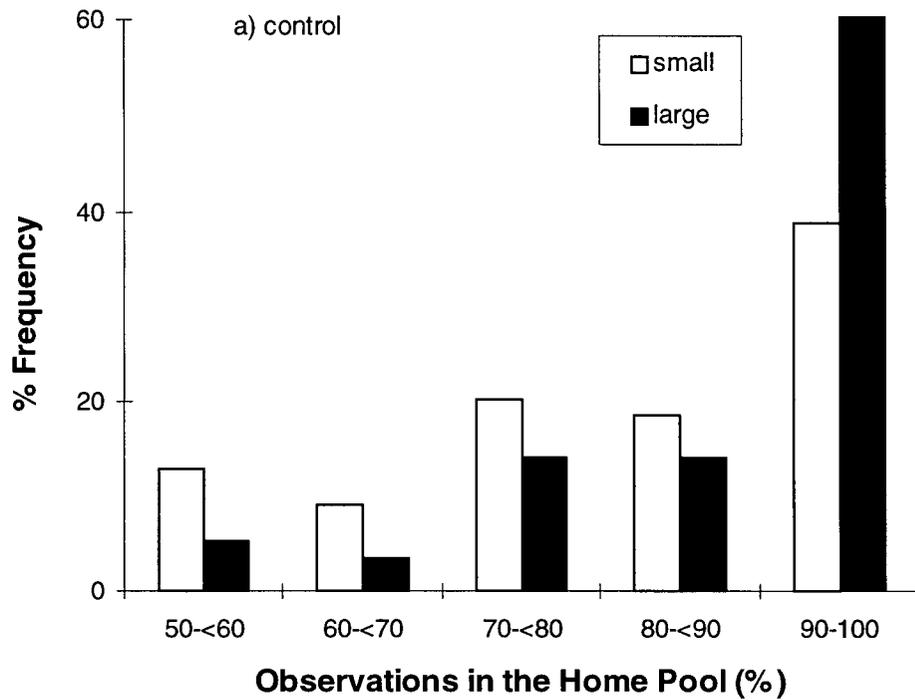


Fig. 3. 6 Location fidelity of small and large coho fry in the control and predation experiment during 5 days of observations (observations pooled across replicates). The x-axis represents frequency of observations in the pool that an individual was more often observed in ("home pool").

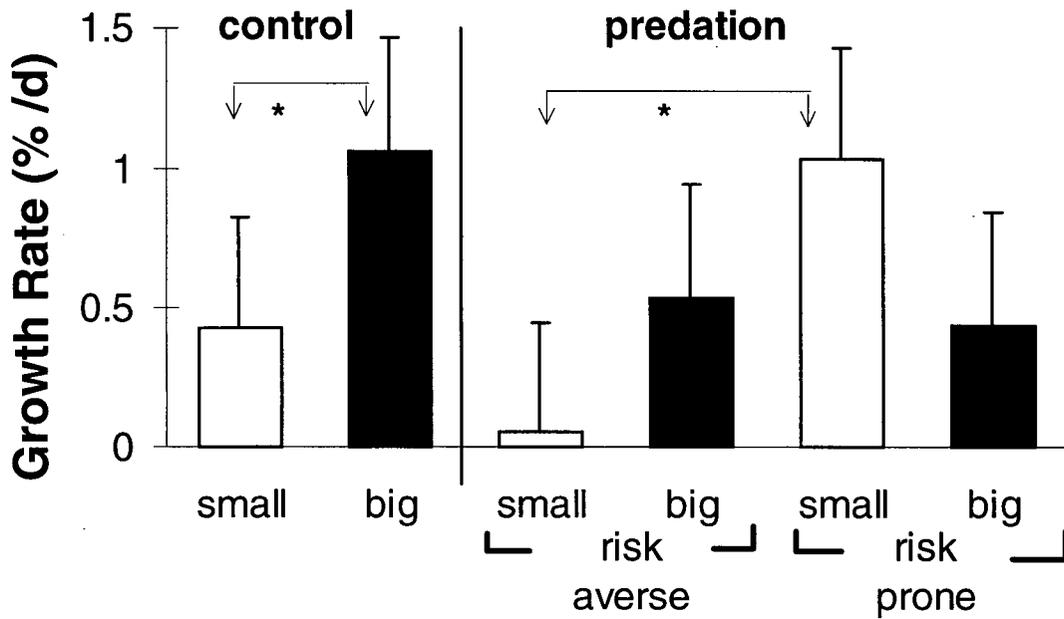


Fig. 3. 7 Mean (+ 2 S.E.) specific growth rate (% body weight/ day) of large and small fish in the control and predation experiment. Data for the predation experiment are divided into categories of risk taking, according to the preference of individual fish for the exposed ('risk-prone') or refuge pools ('risk-averse'). Asterisks (*) denote a statistically significant post-hoc comparison with arrows indicating the groups between which significant differences occurred. Data for the control experiment previously presented in Chapter 2.

Chapter 4 **A Dynamic Model of Juvenile Coho Foraging under Seasonally-changing Constraints on Feeding**

Introduction

Mathematical models of optimal behaviour often use arbitrary units of fitness and dynamics of fitness value accumulation. In that way, the models become quite general and applicable to a variety of organisms and life history conditions. If predictions from these general models are applied to a specific organism or life history stage, one should determine whether major limiting factors in the biology of the organism in question change the predictions of the general model. In this study, I explore whether the predictions of a general dynamic model of optimal foraging under predation risk are applicable to juvenile salmon in their foraging season in freshwater.

The dynamic programming model by Clark (1994, see also McNamara and Houston 1986) predicts that if fitness pay-off at the end of a time period of foraging increases linearly with accumulated assets (e.g. body size or fat reserves), individuals with larger assets should be more risk averse than individuals with small assets if foraging gains are traded off against risk of predation. This effect, which has been named the Asset Protection Principle by Clark (1994), arises because for a given increase in assets, the individual which has more assets also has more to lose if caught by a predator. The second prediction from the general model is that, if time to accumulate assets is limited (e.g. one season to feed) the optimal level of risk taking should increase over time for any level of assets. This is because fitness gains accumulated early in the season are discounted by the multiplicative effects of mortality risk over the remainder of the season.

I use the example of juvenile coho salmon foraging through their first summer in the stream as a real life model to explore these general predictions. I incorporate bio-energetic growth parameters and seasonal cycles of food availability and temperature typical for juvenile salmonids to examine whether Asset Protection is expected under those constraints. Furthermore, I explore the effect of fitness functions derived from field experiments on the expected seasonal patterns of risk taking.

Methods

The Model

The model simulates in daily time steps the foraging behaviour of individual age-0 coho salmon from the time of emergence from the gravel until the fall of the same year. It is a dynamic computer model in which the model output, the behaviour that maximizes expected fitness at any time t , is derived by back-calculating from a terminal reward function $F(x, t)$ that links expected fitness F to the value of a state variable x . The state variable in my case is body mass (in g) of the juvenile fish at the end of the first summer (t_{end}) of foraging (day 180), and the proxy for fitness is the probability of survival over the winter. Winter survival in juvenile salmonids is generally positively correlated with size (Holtby & Hartman 1982, Burrows 1993, Quinn & Peterson 1996). In the simulation, there is a choice among 11 foraging rates, $e_0 - e_{10}$ (e_{10} subsequently called e_{max}) that vary in their profitability in terms of foraging gains, g , and risk of predation, p , in a way that creates a trade-off situation between growth and survival probability. Growth is negative and p is zero at e_0 (equivalent to staying in a refuge and drawing on energy reserves for maintenance). Both g and p increase linearly with e to g_{max} and p_{mx} at e_{max} . The optimal behaviour e^* at time t , is the one that yields the maximum expected fitness for a given x . It is derived by calculating for all levels of e , growth, $g_{(e)}$, and survival probability, $1 - p_{(e)}$, and choosing the one that maximizes $F(x, t+1)$ (formula 4.1)

$$e^* = \max_{(e)} (1 - p_{(e)}) E\{F(x + g_{(e)}, t + 1)\} \quad (4.1)$$

F, which at the start of the simulation represents the relationship between size and winter survival, is then updated for the next time step (backwards from t_{end}) in the simulation using growth and survival probabilities associated with e^* in the previous time step (see Fig 4.1). This is done until t_0 , the beginning of the season, is reached.

To achieve realistic foraging parameters for juvenile salmonids, I incorporated equations from a bio-energetic growth model for fish as a sub-model in the DPM, with specific parameter values for coho salmon (Hewett & Johnson 1992). The bio-energetic equations calculate metabolic rates, maximum rate of food consumption, and loss of energy as wastes, which in fish are all strongly dependent on the size of the animal and the ambient water temperature. For example, the maximum growth rate is a decreasing power function of body size and an increasing function of temperature (Fig. 4. 2). The relationship between foraging effort and consumption of food was modeled as a linear relationship between effort and consumption with zero consumption at e_0 and maximum possible daily consumption for a given body weight at e_{max} . By scaling maximum available food to body weight, I incorporated an assumption that bigger fish can gather more food in absolute terms. Moreover, since maximum consumption is temperature-dependent, this method of modeling food consumption simulates the fact that stream productivity generally is positively correlated with water temperature because stream invertebrate life cycles are shorter if water temperature is higher (Horne & Goldman 1994). In some versions of the model, I modified this relationship between food availability and temperature. Maintenance and activity costs are incorporated into the model by subtracting energy equivalent to basal metabolic rate at e_0 and linearly increasing in cost to a maximum of three times the basal metabolic rate at e_{max} . Growth is calculated in the model by further subtracting the energy equivalent of waste losses from the consumed energy. If the energy expended in maintenance and activity surpass assimilated energy from food intake, growth is negative. I compared maximum growth of simulated fish from my

model to growth predictions by another growth model for salmonids (Cho 1990) to verify choice of realistic model parameters.

A further cost is paid by the fish in the form of predation risk, p , which is zero at e_0 and increases linearly with e to reach p_{\max} at e_{\max} . I chose p_{\max} to be constant over time and independent of body size of the simulated fish. I, thus, assume that predation risk is dependent only on the activity of the forager and not its body size, as shown by Martel & Dill (1995) for merganser ducks preying on coho fry. Table 6 lists the major assumptions underlying the growth and survival dynamics in my model.

To show the effect of the various input parameters on e^* of the simulated forager, I use two model outputs: a) e^* for various sizes over time (“optimal effort”); and b) the seasonal trajectory of e^* and body weight that a fish of 1 g body weight early in the season would have, if it followed the e^* trajectory through to t_{end} (“forward simulation”). The first output is the optimal choice, determined in backward simulations, by fish of different sizes. The second output shows the growth pattern and total survival probability over the summer that derive from applying the optimal choice in a forward simulation starting with fish of 1 g at time 30. In the various simulations, I explore the effect of different terminal fitness functions, levels of predation risk, seasonal temperature regimes, and seasonal changes in stream productivity on the optimal foraging effort and size at the end of the season.

Results

The Influence of the Fitness Function

I examined the effect of three different relationships between size at t_{end} and over winter survival probability on optimal foraging effort (Fig. 4. 3). The first was a linear relationship with an arbitrary slope, the other two were derived from studies on the relationship between size in the fall and over

winter survival in age-0 coho salmon by Holtby & Hartman (1982) and Quinn & Peterson (1996). Quinn and Peterson's (1996) data represent one season of assessment of size-related winter survival of individually marked fish in Big Beef Creek, Washington, whereas Holtby & Hartman's (1982) data represent mean survival of a whole coho cohort in Carnation Creek, B.C. in relation to mean body size of the cohort in the fall assessed over several years.

With the linear fitness function, e^* of smaller individuals is greater (i.e. the foraging rate is higher) than that of larger individuals (Fig. 4. 4a). Over the season, e^* increases for all sizes, so that it converges over time to e_{\max} . This result is very similar to that of Clark (1994), and shows that the prediction of Asset Protection made by Clark's (1994) model holds for coho salmon when bio-energetic constraints on feeding and growth are incorporated into the model. As the animal grows, it becomes progressively more risk averse which cancels out the seasonal increase in risk taking so that e^* is nearly constant over time (Fig. 4. 4b).

When using the fitness functions derived from field data, larger fish face a diminishing increase in fitness for each increment of weight increase. The result is that the difference in e^* between body weight classes becomes more pronounced over time (Figs. 4. 5 and 4. 6). Optimal effort increases over the season but compared to the linear fitness function, the increase is small in larger fish. Early in the season, the Asset Protection effect is weaker, which can lead to e^* of larger individuals being greater than that of small fish (Figs. 4.5a and 4.6a) because larger animals pay relatively lower metabolic costs for active foraging. Because of the decelerating relationship between fitness and size, e^* is lower than in the model with the linear fitness function, so that the fish are much smaller at the end of the season (Fig. 4. 5b and 4. 6b), but have suffered lower summer mortality. Simulations using the two fitness functions derived from field data (Fig. 4. 5 and 4. 6) show qualitatively similar patterns of optimal behaviour. However, since the Big Beef Creek fitness function (Quinn & Peterson 1996) increases less steeply with

size than does the Carnation Creek fitness function (Holtby & Hartman 1982), the optimal level of effort is lower when the Big Beef Creek function is used, so that at t_{end} the body weight of fish is lower, but summer survival probability is greater in the former case.

The Effect of a Seasonal Temperature Regime

I simulated different temperature regimes because water temperature has a strong impact on metabolic costs and growth potential of fish and varying the temperature parameter of the model is a means of simulating seasonal variation in stream productivity. I used stream temperature records from Carnation Creek, B.C. (Brown & McMahon, 1987) from May to October, the time during which juvenile coho salmon typically forage, to model temperature parameters. The temperatures increased from 9 °C in May to 14 °C in August and then dropped to 8 °C by the end of October (Fig. 4.7).

When terminal F is a linear function of weight, the trajectory of e^* under the seasonal temperature regime increases sharply for all sizes of fish as temperatures (and thus food availability) increase (Fig 4. 8a). The e^* curve flattens out toward the end of the season as falling temperatures make foraging less profitable and cancel out the increase in e^* expected toward the end of the season when temperature is constant (cf. Fig 4. 4). In the forward iteration (Fig. 4. 8b), e^* is high early in the year and decreases as size increases and temperature decreases.

When seasonal changes in temperature are combined with a fitness curve derived from field data (Holtby & Hartman 1982) the optimal effort increases strongly with increasing productivity early in the season and then, toward the end of the season, decreases for all but the smallest body weights (Fig 4.9a). In the forward iteration (Fig 4.9b), we observe a rapid increase of e^* as temperature increases, and fast growth in the first half of the season, then a rapid decline of e^* as decreasing growth potential

(due to seasonally dropping temperatures) and the Asset Protection effect combine to make foraging progressively less profitable, resulting in a dramatic cessation of growth late in the season.

The Effect of Predation Risk

To explore the impact of variation in predation risk, I changed p_{\max} , the parameter that determines the mortality risk at maximum foraging effort. In Figs. 4.10 and 4.11, two levels of p_{\max} , 1 % per day and 2 % per day, are combined with a seasonal temperature regime and a fitness curve derived from field survival data (Holtby & Hartman 1982). Increasing p_{\max} lowers the survival probability, and therefore fitness, at a given foraging effort. As a result, e^* is generally lower at greater p_{\max} . In the forward iteration (Fig. 11b), this manifests itself in a later onset of early season foraging and earlier cessation of foraging in the fall. The result is that at high risk levels, foraging is concentrated around the times of highest growth potential in the summer. Because the simulated animal can avoid predation mortality only at the cost of reduced growth, increasing risk leads to lower summer survival and smaller fish in the fall. In that way, summer predation risk indirectly influences the winter survival of the animal. In the examples shown in Figs. 4.10 and 4.11, at $p_{\max} = 1$ %/day, fish end the season at 7g with a summer survival probability of 0.5, yielding a total survival probability to the next spring of 0.44, whereas at $p_{\max} = 2$ %/day fish weigh 4.8 g in the fall with a summer survival probability of 0.32, and a total survival probability of 0.23.

Impact of Seasonal Changes in Stream Productivity

Studies on the seasonal production of invertebrates in streams suggest that food availability to juvenile salmonids does not perfectly follow stream temperature regimes. Food availability is probably greatest in early summer (May/June), low in mid-summer when temperatures are highest, and shows a small peak in early fall (September/October) (O'Hop & Wallace 1983, Bachman 1984, Allan 1987). To

explore the effects of those seasonal trends in food availability on optimal foraging behaviour, I modified the relationship between temperature and maximum food consumption by reducing maximum temperature-dependent consumption in mid-summer and fall as shown in Fig. 4.7. This way, the available food was the same as in the preceding simulations (that included a seasonal temperature pattern) in spring, but reduced in mid-summer and fall compared with the earlier simulations.

Fig. 4.12 shows the results of a simulation with the Carnation Creek fitness function, seasonal changes in temperature, and seasonal trends in food availability. The lower relative food availability at the time of greatest metabolic cost in mid-summer produces a decline of e^* during that time. After the summer low in food availability, there is another smaller peak in e^* , after which e^* declines with temperature for all but the smallest sizes (Fig. 4.12a). In the forward simulation, the decline in effort in the summer is quite pronounced with the parameter values chosen, so that metabolic costs outweigh foraging gains and the animal loses weight for some time.

Compared with the situation without seasonal adjustment of food availability (and otherwise the same parameter values), there is a markedly higher e^* early in the season (compare Fig. 4.12 with Fig. 4.9). The reason for this difference in early season foraging ($t= 1-50$, under the same conditions of temperature and maximum consumption) is that the simulation proceeds backward in time so that the size-fitness relationship (the basis for calculating e^*) in the spring has been influenced by feeding conditions in the summer period.

Discussion

The optimal foraging behaviour is a long term average selected to provide the individual with the maximum fitness in a predictable environment. This model shows how the incorporation of

biological information for a specific organism can profoundly influence the predictions of a dynamic programming model of behaviour. Choosing model dynamics that reflect temperature- and size-dependent foraging constraints on coho salmon changed the prediction of optimal effort from a gradual seasonal increase under the assumptions of the simplest model to a spring and fall peak in foraging effort in anticipation of poor feeding conditions when the model simulated seasonal trends in stream productivity and growth potential of the organism.

Using coho-specific model dynamics, however, did not change the general prediction that animals with greater fitness assets should take less risks to forage than animals with small asset values. In fact, if the foraging behaviour of coho fry is governed by a decelerating relationship between fall size and winter survival, the impact of the Asset-Protection Principle (Clark 1994) is likely stronger than predicted by models which assume a linear fitness function. Several workers observed an apparent negative correlation between body size and risk taking in experiments with juvenile salmonids (Grant & Noakes 1987, Mikheev et al. 1994, Grand 1997). My simulation results support the notion that Asset Protection is a contributing factor to this observation.

In addition to the prediction of lower risk taking in bigger fish, the model makes a series of testable predictions regarding coho foraging behaviour under predation risk in relation to body size and season:

1. Increasing predation risk should result in lower growth rates of the fish. In Chapter 2 I showed in laboratory experiments that the mean growth rate of groups of coho fry was reduced in the presence of a simulated predation threat. Abrams & Matsuda (1993) and Clark (1994) use mathematical models to explore further possible effects of varying predation risk on the size of the prey and on population-level predation rate if prey can respond to risk with avoidance behaviour.

2. In the fall, large fish should cease foraging earlier than small fish. Coho fry stop foraging in the fall in October-November (Sandercock 1991) at about the time predicted by my model when seasonal temperatures are considered, but to my knowledge, no data exist on size-related foraging effort in the fall, or the order in which fall migration of coho fry out of the feeding areas proceeds.

3. Foraging activity should anticipate seasonal trends in growth potential. It is well established that salmonids follow seasonal trends in food availability, for example by stopping foraging activity when growth potential is low (Sandercock 1991). However, my model also predicts changes in foraging in anticipation of changes in growth conditions (see also Clark 1994). For example, the prediction from my model is that in spring, juvenile coho salmon from a stream which regularly shows a seasonal decline in food availability in mid-summer should be more likely to forage under risk than juveniles from a stream without pronounced seasonal changes. Also, juveniles from streams with seasonal cycles in food abundance should show seasonal changes in risk taking. Fish should be more willing in spring than in summer to forage under predation risk under otherwise equal conditions (temperature, body size, food reward offered). Such anticipatory changes in appetite could be effected through hormonal changes and synchronized to the time of year by photoperiod cues. Bull et al. (1996) developed a dynamic optimal foraging model for Atlantic salmon fry in the winter and showed experimentally that motivation to feed depended on the period in the winter when the experiment was carried out. As predicted by the model, the animals' feeding motivation was matched to anticipated energy requirements in the spring. Swift (1955) showed a period of lower feeding motivation in subadult brown trout in May/June, independent of temperature. Simpson et al. (1996) observed a decline in feeding motivation in juvenile Atlantic salmon in June/July under a constant feeding regime and argued that this pattern represented an adaptation to seasonal cycles in food production in the wild.

Some limitations of my model need also to be considered. First, the model does not account for competitive interactions among juveniles or density-dependent survival rates which can be present in

juvenile coho salmon and other salmonids (e.g. Sandercock 1991, Elliott 1990). Designing a DPM that simulates territorial conflict was beyond the scope of this study. However, one can guess that the inclusion of direct competitive interactions into my model would have increased optimal foraging effort early in the spring if animals determine territorial dominance after their entry into the feeding grounds. Prior studies have suggested that territorial conflicts in age-0 coho (Nielsen 1992) and density-dependent mortality in brown trout (Elliott 1990) are more intense in the spring.

Second, I assumed that susceptibility to predation was independent of body size of the fish. If probability of capture by a predator increases with size of the prey (positive size dependence), we would expect the motivation to feed to decrease more strongly with size than in my model. Conversely, if capture risk decreases with body size, foragers gain an extra advantage of growing, which should lead to a diminished effect of Asset Protection. Both, positive and negative prey size-dependence of capture have been reported in the literature (for juvenile coho e.g. Wood & Hand 1985, Healey & Reinhardt 1993), the sign of size-dependence apparently depending on the type of predator (Sogard 1997). Juvenile coho salmon are hunted by a wide variety of bird and fish predators (Sandercock 1991) and, as they outgrow the prey size range of one predator, they probably enter the size range of another. This makes it difficult to suggest a general relationship between size and susceptibility to predation over the whole season and range of coho body sizes.

Third, I did not incorporate into my model an option of delaying smolting. Coho salmon are known to stay in their natal streams a further year if growth conditions are poor (Holtby & Hartman 1982, Randall et al. 1987), and studies on Atlantic salmon suggest that the animal's smolting age is determined in the summer of their first year after which the motivation to feed under risk markedly declines in those fish that delay smolting (Thorpe et al. 1992). My model is only applicable to those fish that do not delay smolting. Grand (1997b) developed a DPM for juvenile coho foraging that showed

likely behavioural effects of the decision to delay smolting. Her model suggests that, as the feeding season progresses, it becomes more advantageous for small fish to reduce foraging effort and delay smolting for a year than to continue to increase foraging under risk.

Apart from the result of lower optimal risk taking of fish that delay smolting, Grand's (1997b) model differs from mine in the predictions of seasonal patterns in foraging effort. Since her model assumes no changes in growth conditions, her predictions resemble those of Clark's (1994) model, whereas my model predicts that optimal foraging effort will be highest early in the summer.

Table 6 Major assumptions incorporated into the growth and survival dynamics of my DPM.

Assumption	Comments
Survival probability in winter is the decision rule governing summer feeding behaviour	Winter survival probability chosen as proxy for fitness; assumes that size-dependent survival in later life history stages has little impact on summer feeding behaviour
Predation risk is zero at e_0	Equivalent to using a refuge. Salmon have been shown to shelter for extended times under rocks (Fraser et al. 1995).
Food intake is a positive function of body size	Larger salmonids can gather more food in absolute terms due to better swimming ability (Bams 1967) and larger gape width
Maximum (size-dependent) food intake can be achieved at highest foraging effort	Assumes that foraging success is only influenced by behaviour of the individual (and water temperature), not by other factors such as dominance relationships or limited food. See Discussion for evaluation
Food availability is positively related to water temperature	Based on observation of shorter life cycles of stream invertebrates in warmer water (Horne & Goldman 1994). Assumption altered in some simulations.
Predation risk is independent of body size of the fish	See Discussion.

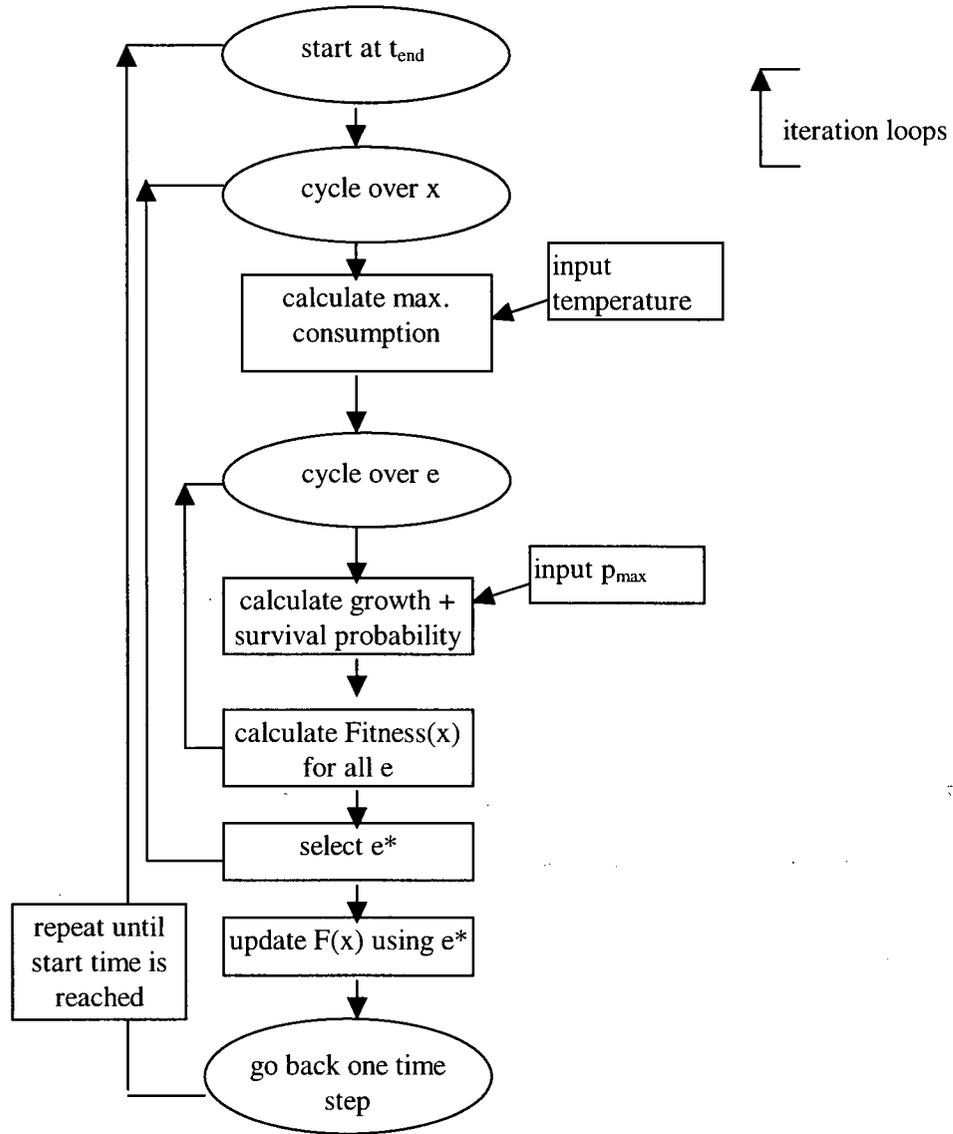


Fig. 4.1 Schematic drawing of the dynamic programming model.

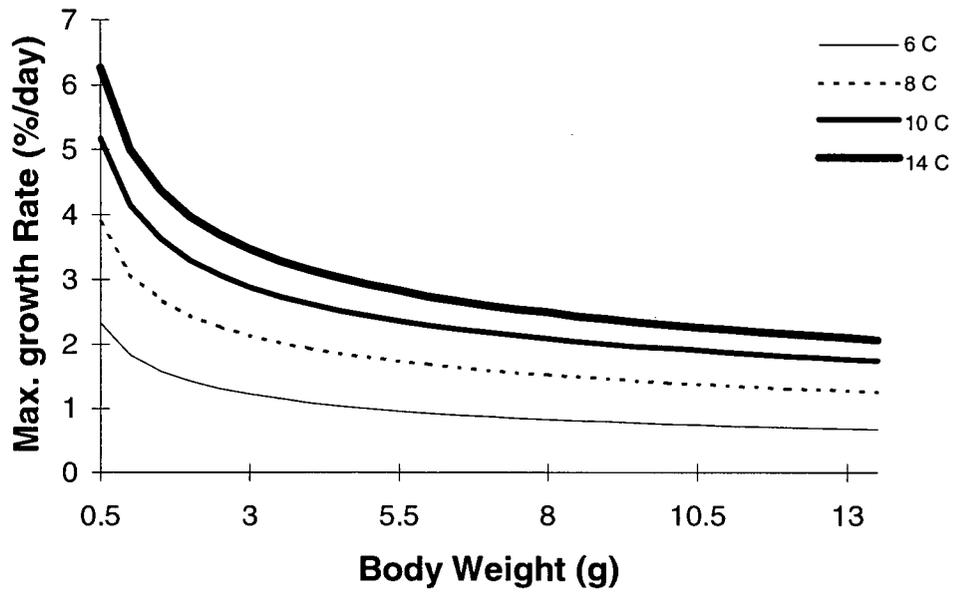


Fig. 4.2 Relationship between body weight of coho salmon and maximum specific growth rate (% per day) for various temperatures as calculated by the bioenergetic submodel.

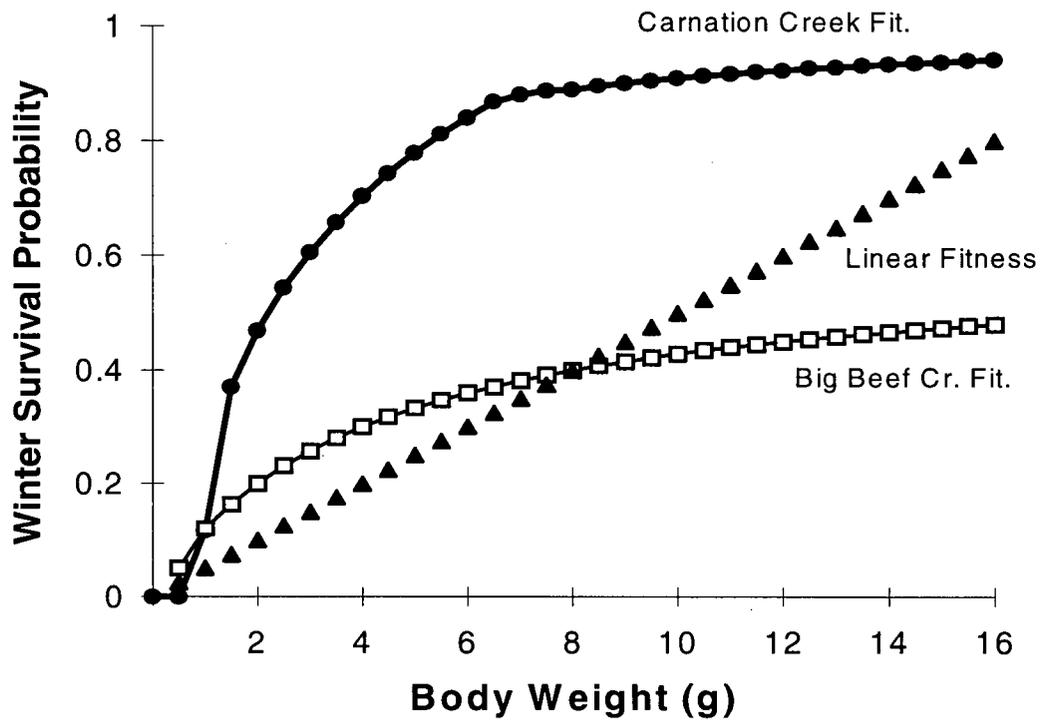


Fig. 4.3 Terminal fitness functions used in the dynamic programming model. The lines marked as Carnation Creek Fitness and Big Beef Creek Fitness were derived from data on the relationship between body weight of juvenile coho salmon in the fall and over winter survival probability.

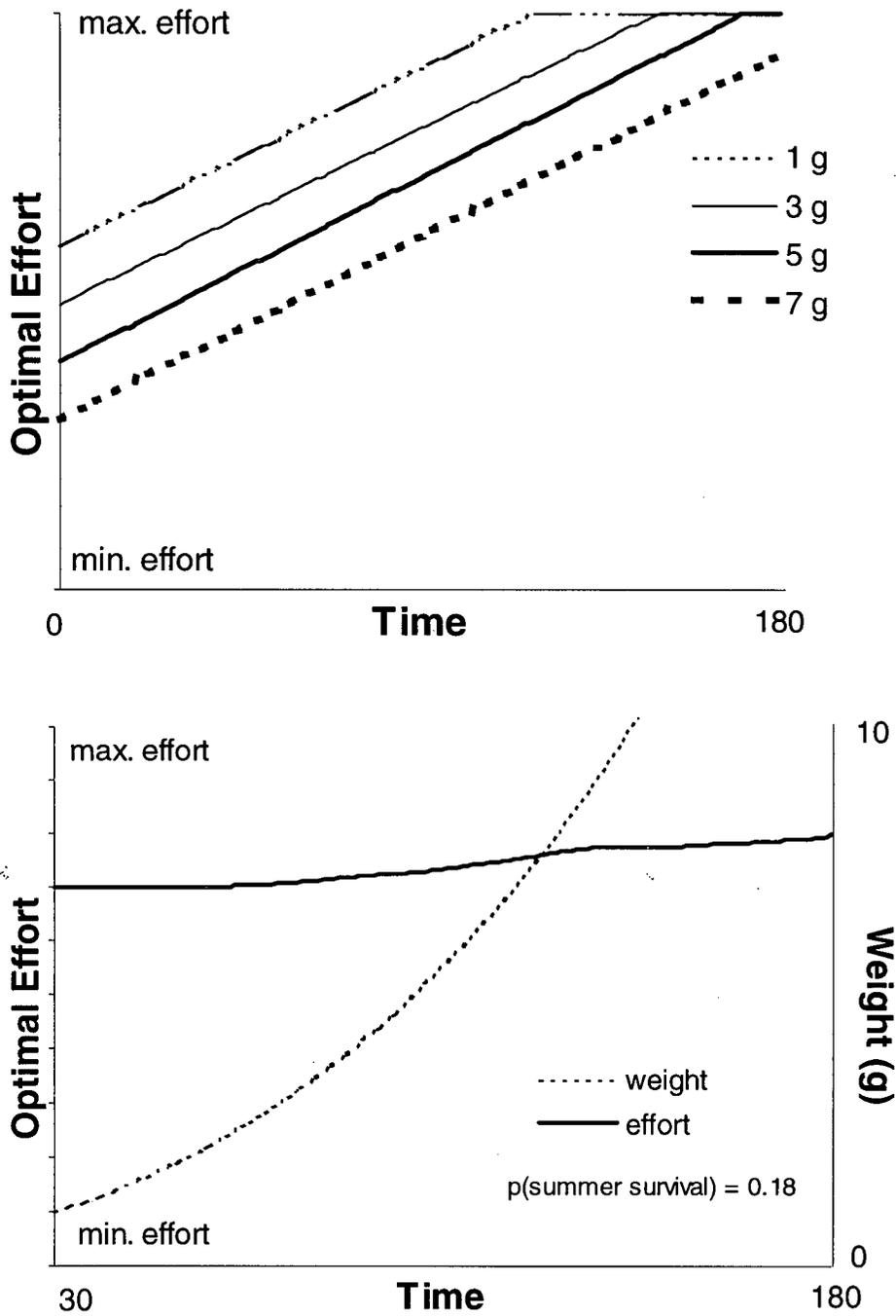


Fig. 4.4 Optimal effort, e^* , based on a linear fitness function for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b). Other parameters: $p_{\max} = 1.5\%$, temperature = 10°C constant. Note: curves in this and subsequent figures were smoothed using a sliding ten-time-step average.

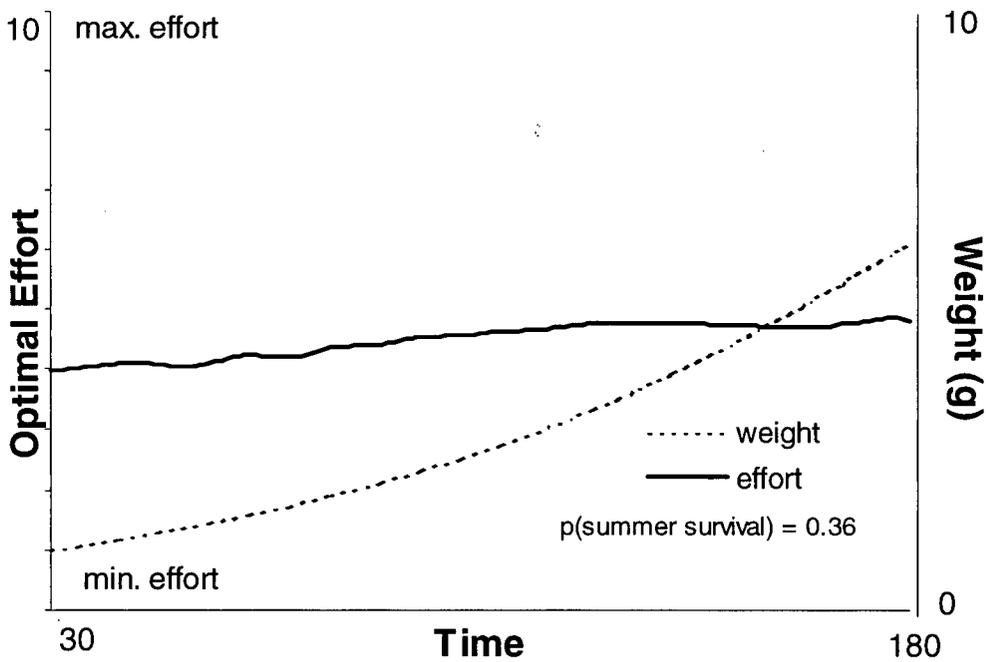
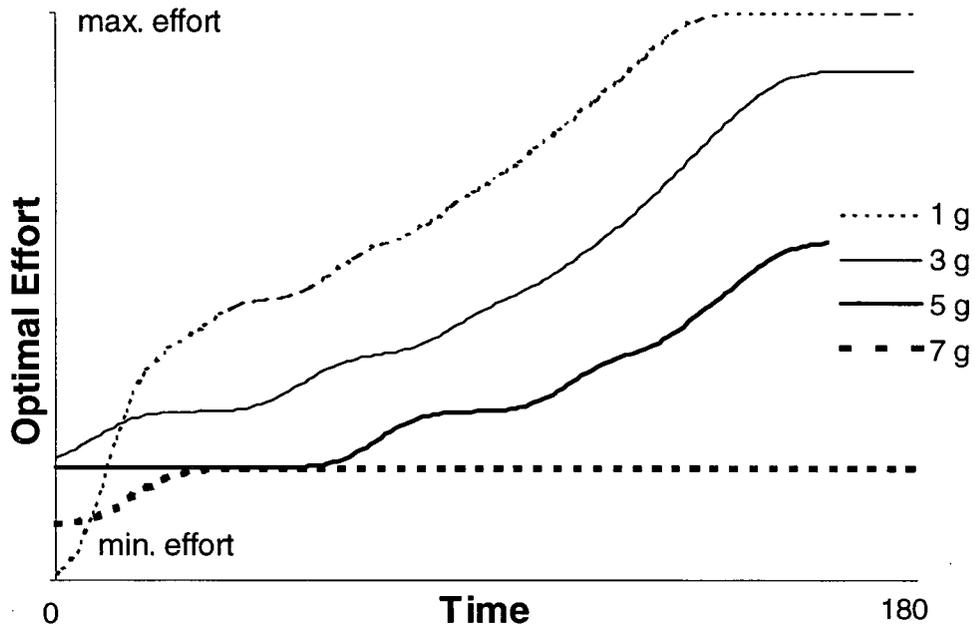


Fig. 4.5 Optimal effort, e^* , based on the Carnation Creek fitness function for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b). Other parameters: $p_{\max} = 1.5 \%$; temperature = 10°C , constant.

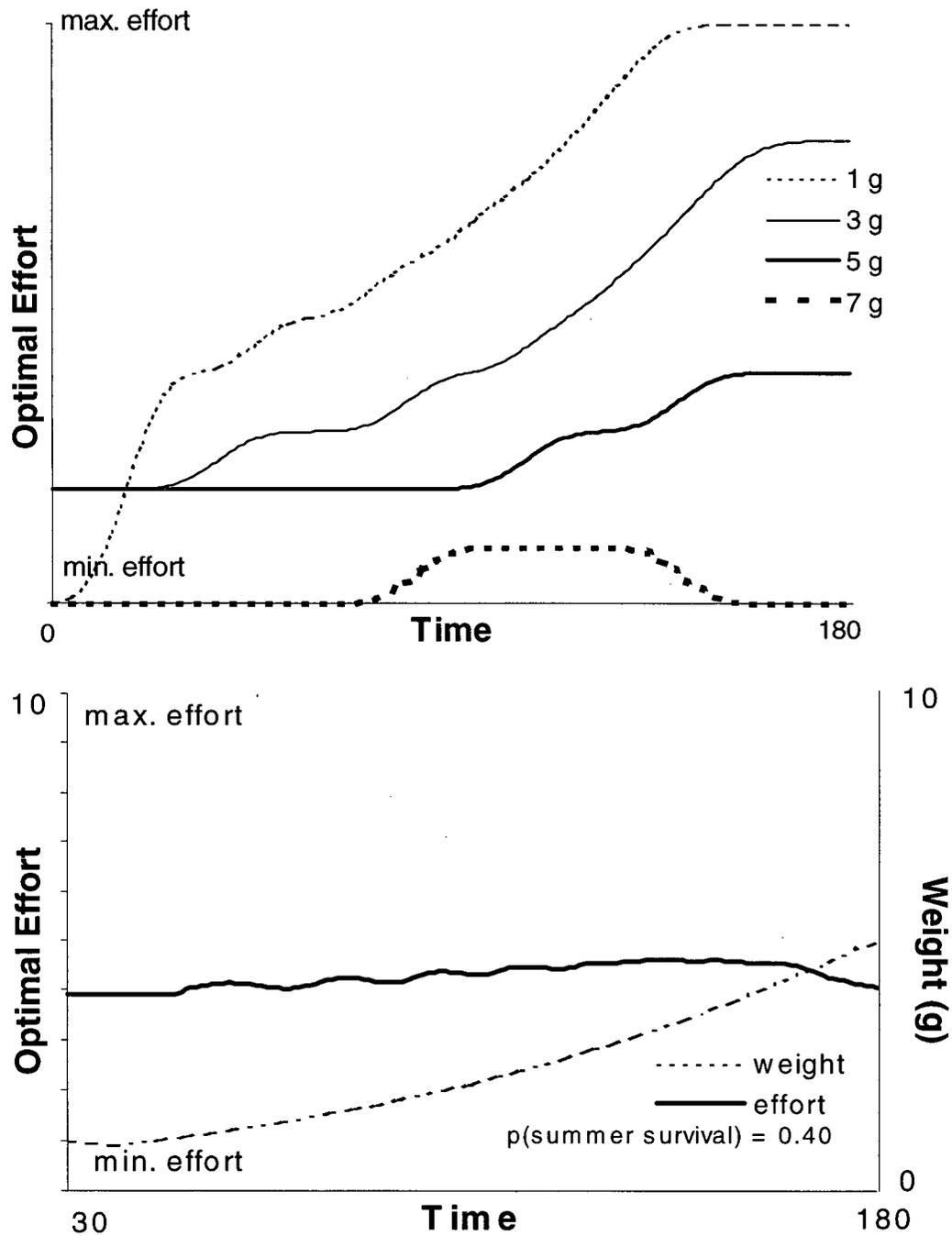


Fig. 4.6 Optimal effort, e^* , based on the Big Beef Creek fitness function for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b). Other parameters: $p_{\max} = 1.5 \%$, temperature = 10°C constant.

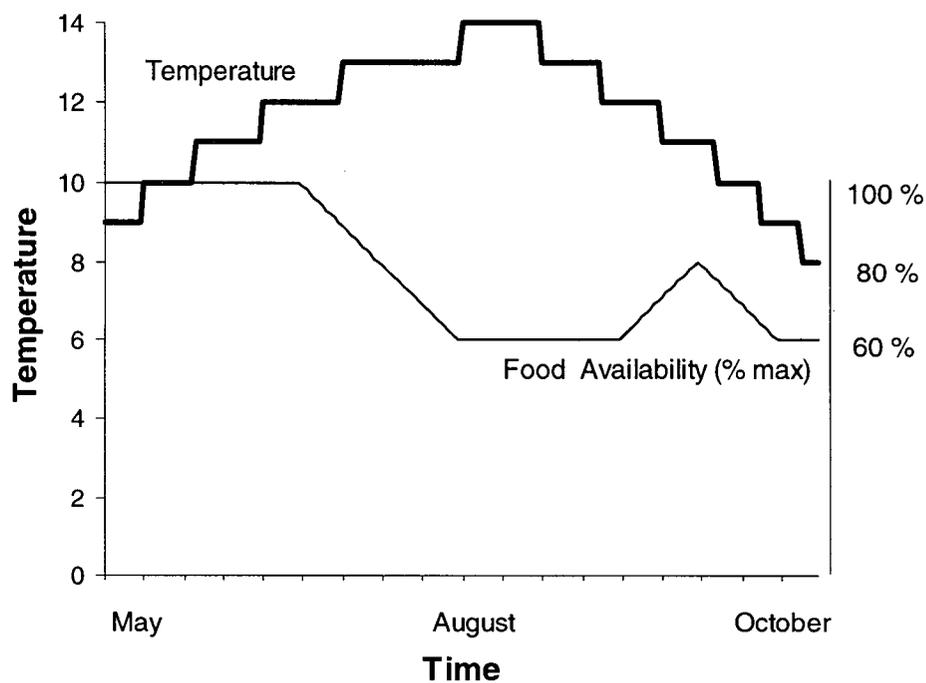


Fig. 4.7 Values used in the simulation of seasonally varying stream temperatures (heavy line, left-hand scale) and food availability modification values used in the simulation of seasonal trends in stream productivity (light line, right-hand scale). For example, food availability of 60% means that the maximum daily ration of the simulated animal was reduced to 60 % of its physiologically allowable maximum daily ration for that temperature.

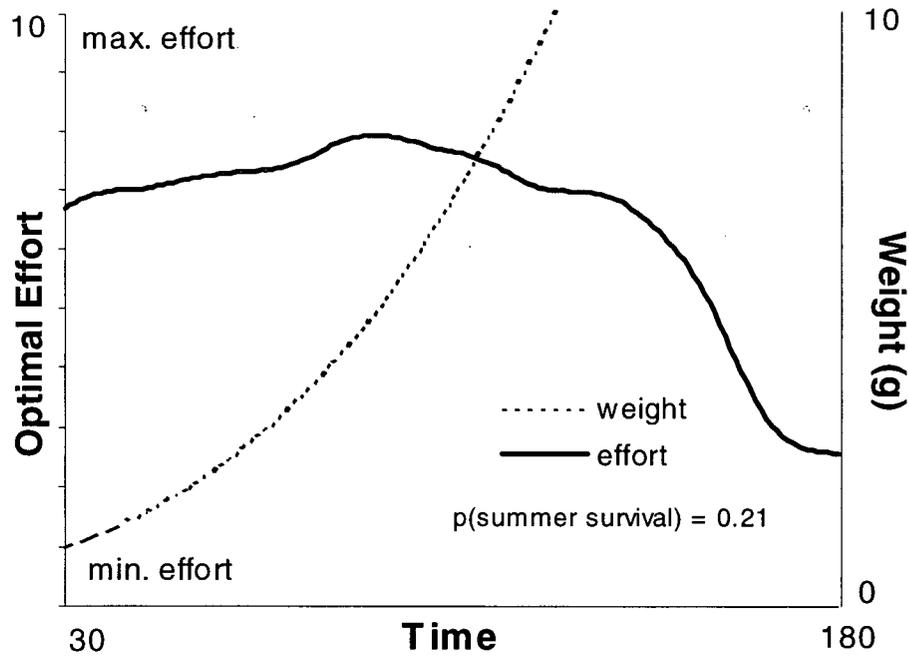
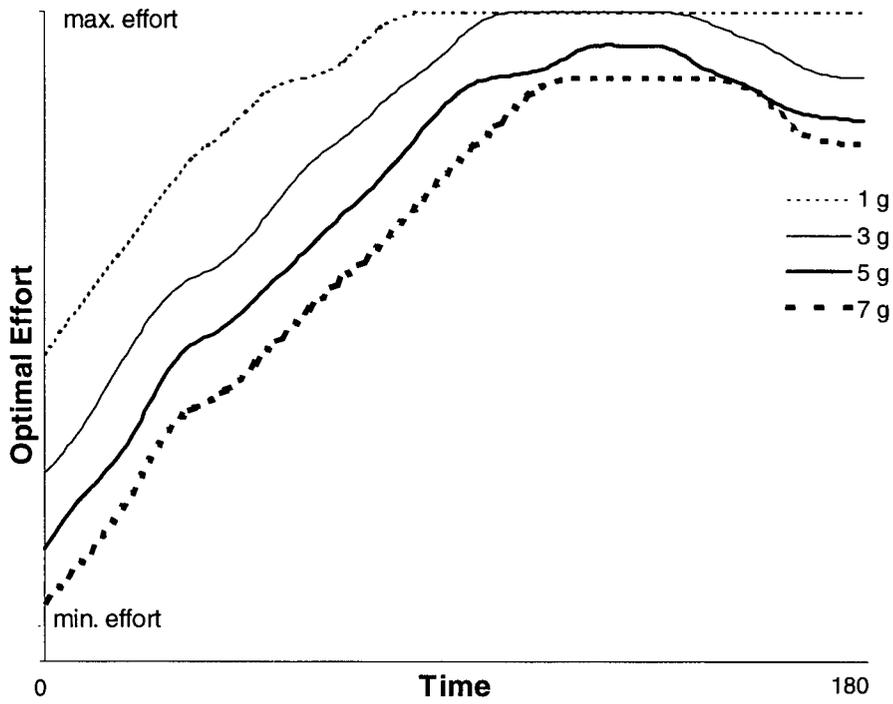


Fig. 4.8 Optimal effort, e^* , based on a linear fitness function and seasonally varying temperatures for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b). Other parameters: $p_{\max} = 1.5\%$.

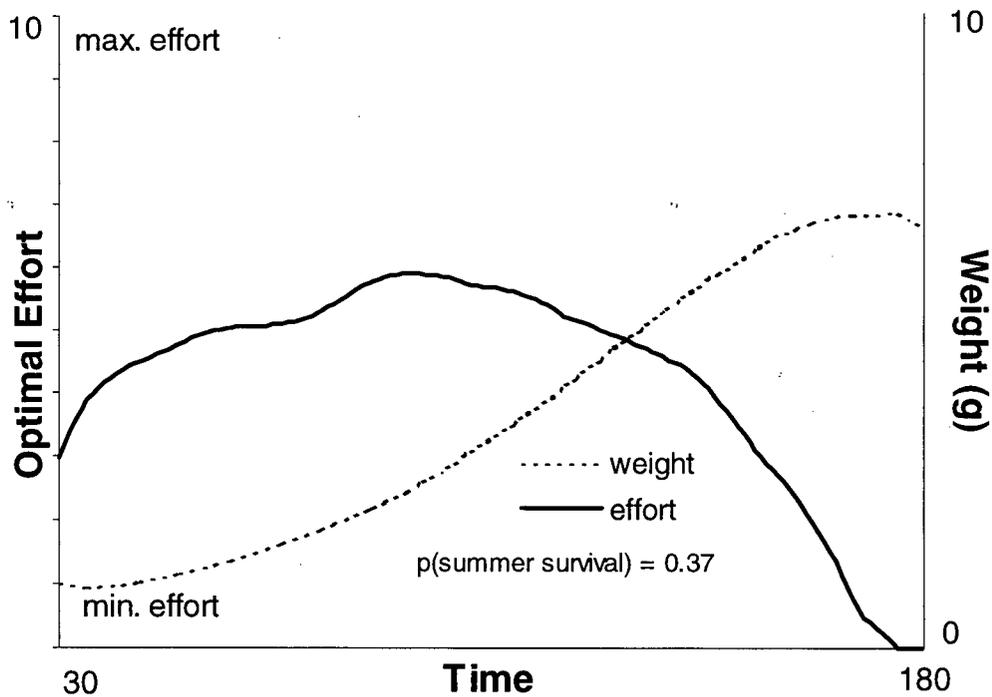
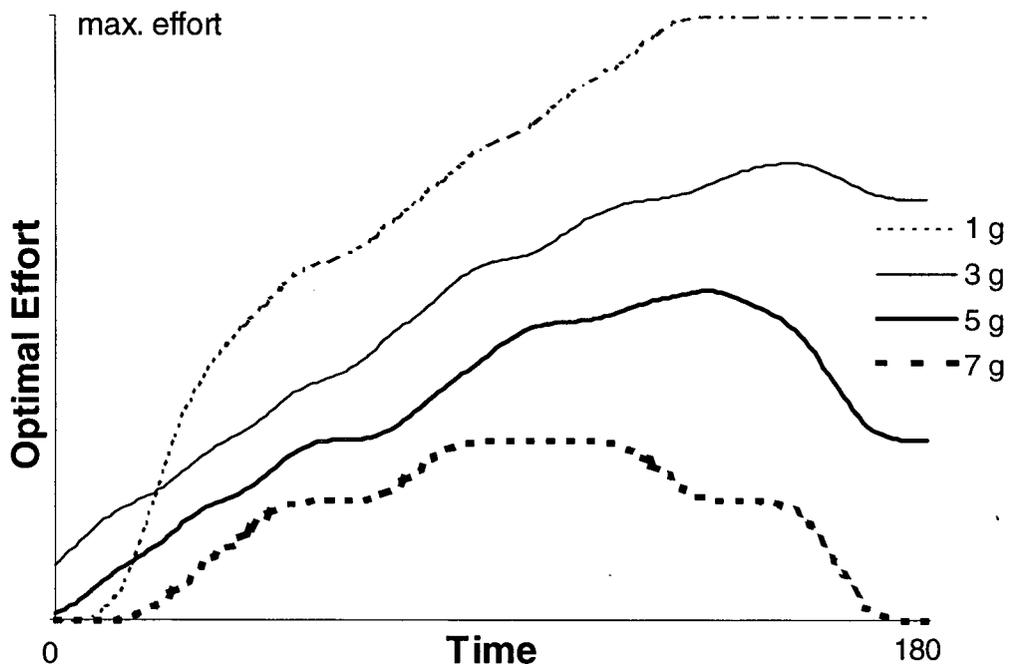


Fig. 4.9 Optimal effort, e^* , based on the Carnation Creek fitness function and seasonally varying temperatures for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b). Other parameters: $p_{\max} = 1.5 \%$.

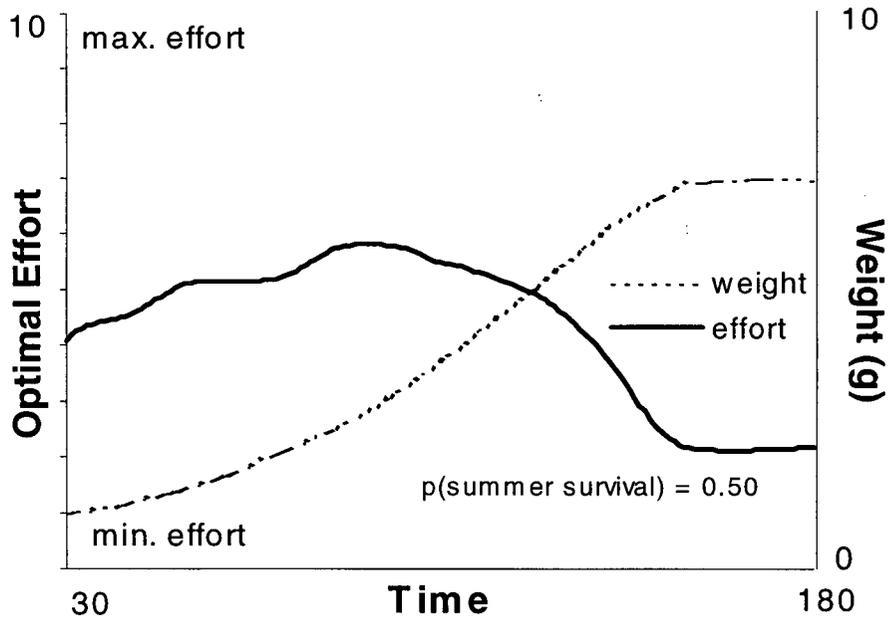
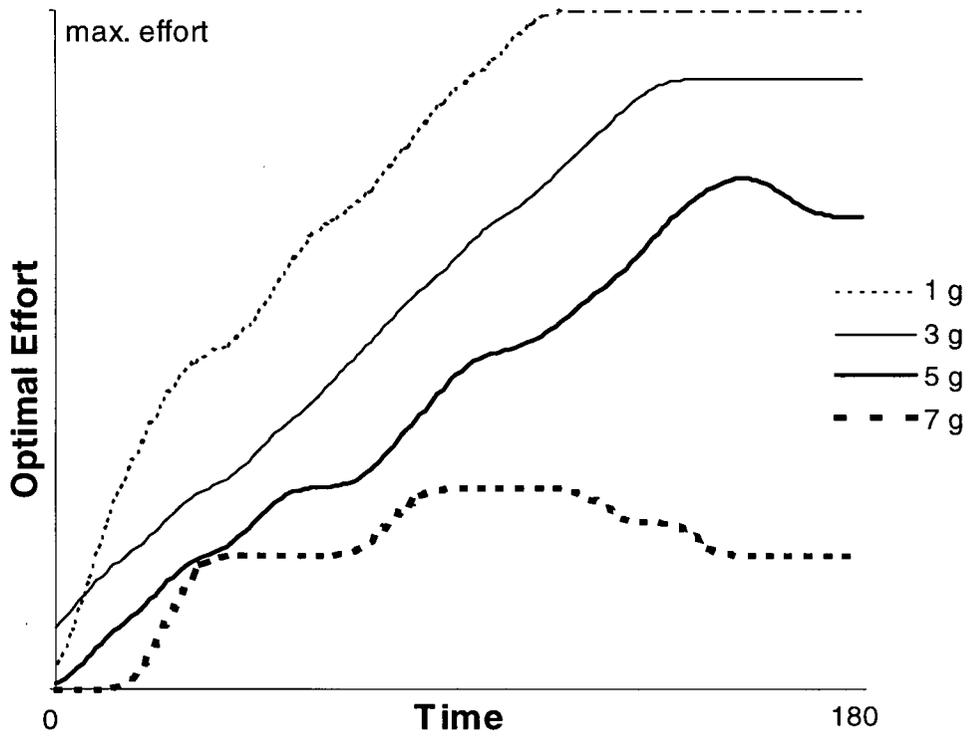


Fig. 4.10 Optimal effort, e^* , based on maximum daily predation risk = 1 %, the Carnation Creek fitness function, and seasonally varying temperatures for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b).

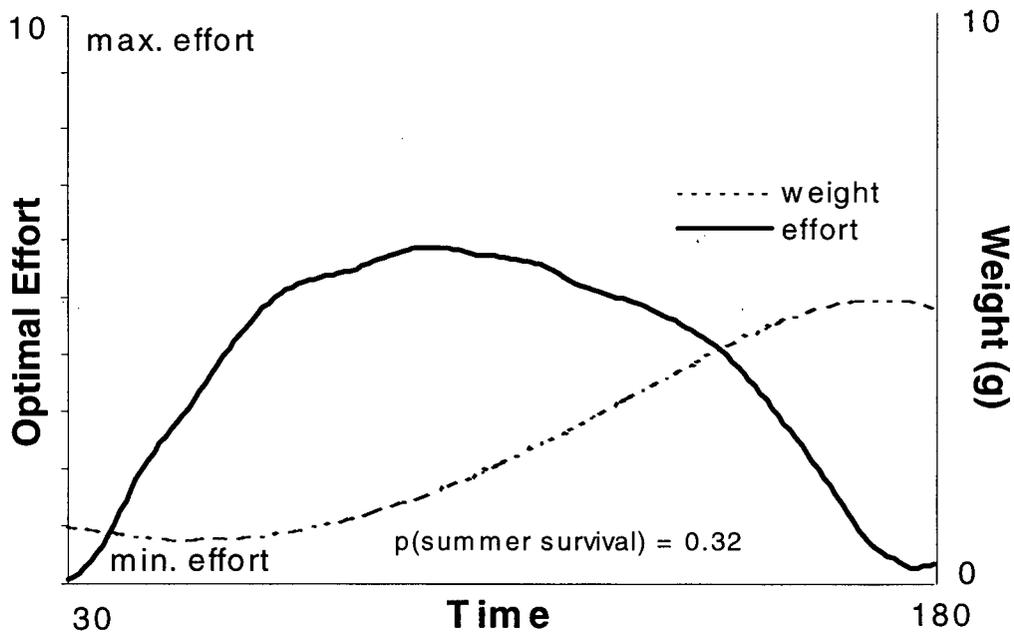
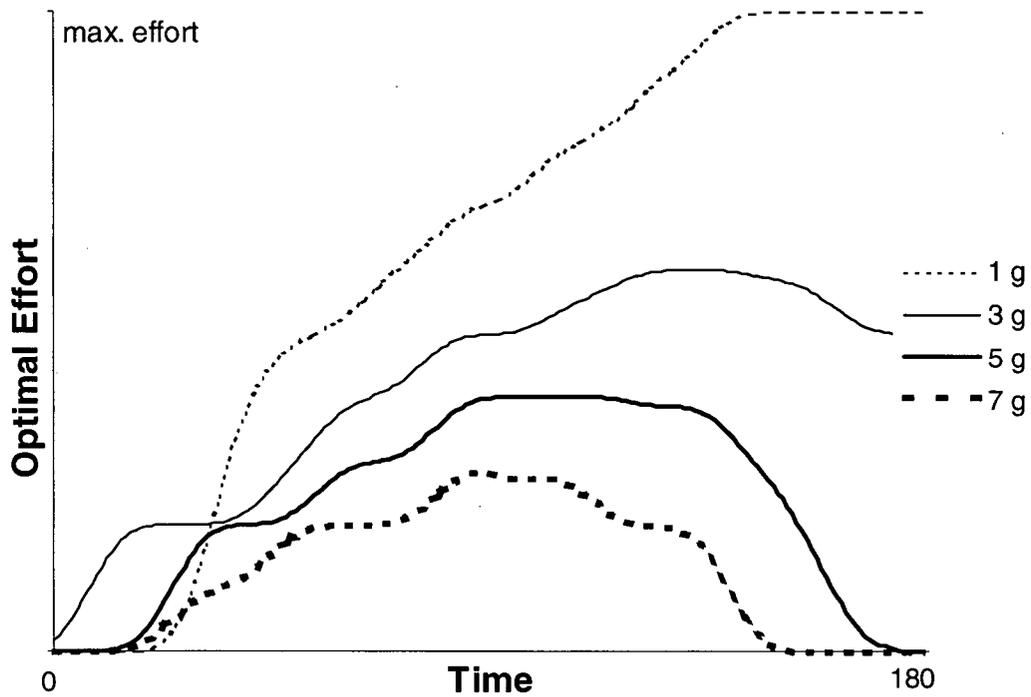


Fig. 4.11 Optimal effort, e^* , based on maximum daily predation risk = 2 %, the Carnation Creek fitness function, and seasonally varying temperatures for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b).

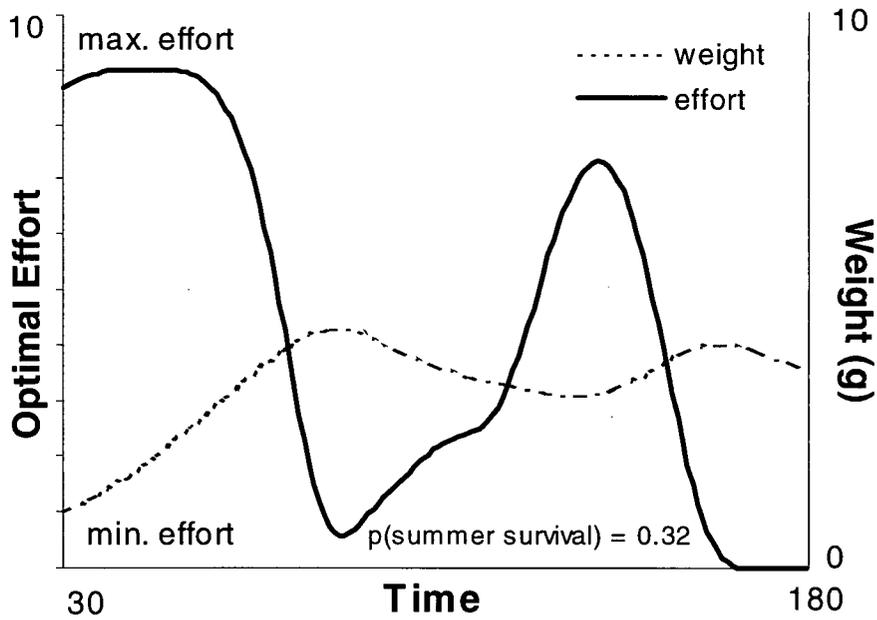
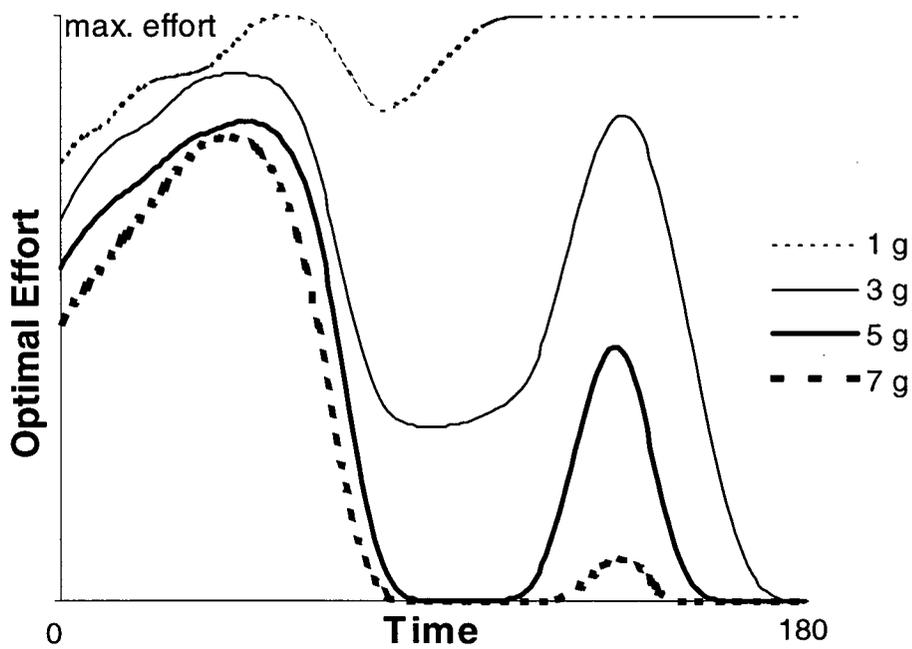


Fig. 4.12 Optimal effort, e^* , based on seasonally varying temperatures, seasonal adjustments to food availability, and the Carnation Creek fitness function for various sizes of simulated fish over the feeding season (a) and results of forward simulation of a fish starting with 1 g body weight at $t = 30$ and using e^* through the season (b). Other parameters: $p_{\max} = 1.5\%$.

Chapter 5 **Season- and size-dependent risk taking in juvenile coho salmon: experimental evidence for dynamic optimization**

Introduction

Dynamic programming models (DPM's) of optimal behaviour have often been used for the *post hoc* explanation of observed patterns of behaviour or life history decisions (e.g. Mangel & Clark 1988). Experimental tests of DPM's usually involve manipulation of a short-term variable such as satiation level and, therefore, say little about long-term dynamic optimal strategies. Observational studies may suggest that an animal is following a strategy of long-term state-dependent optimization, whereas the animal in fact is responding to proximate cues that are correlated with the state variables that change over the long term. For example, Gotceitas & Godin (1991) showed for juvenile Atlantic salmon (*Salmo salar*), and Koivula et al. (1995) showed for willow tits (*Parus caerulus*), that satiation level governed motivation to feed under predation risk - not dominance ability as Hegner (1985) and Hogstad (1988) had suggested.

In this chapter, I test the predictions arising from a simple seasonal DPM with size-dependent over-winter survival as the terminal pay-off function (Clark 1994). Clark's (1994) model predicts that, if the terminal pay-off is a monotonically increasing function of a state variable, here size, a larger animal should be less willing to risk predation for a given increase in size compared with a smaller animal. This is because the larger animal is protecting a greater accumulated fitness asset. A second prediction from this general model is that, for a fixed size of animal, willingness to take risks should increase over the season because the fitness benefits of foraging are more immediate and time constraints more pressing late in the season than early, when many time steps remain to make up for

missed opportunities. The seasonal dynamics of growth and survival in juvenile coho salmon provide an opportunity to test these predictions. The model I presented in Chapter 4 also predicted that larger fish should be more risk averse, but the change in risk taking over the season depended on the seasonal patterns of temperature and food availability.

In Chapter 2, I showed that larger animals behaved in a more risk-averse manner than smaller animals and in Chapter 3 I showed that in the absence of predation risk large coho fry dominate access to food when the fish interact in groups. Since previous studies have shown that coho trade off the risk of predation against feeding reward and decrease risk-taking with satiation (Dill & Fraser 1984, Martel 1996), it is possible that greater satiation of larger fish contributed to their greater apparent risk aversion in my first laboratory experiment. In this laboratory experiment, therefore, I used solitary coho fry to test the willingness of isolated coho of different sizes to risk predation at various satiation levels and seasons. I expected that, at the same satiation level, larger fish would be more risk-averse than small fish and that both size classes would increase their risk-taking with the progression of the season.

Mechanisms of Asset-Assessment in Coho Salmon

DPM's assume that fitness consequences are the ultimate cause of behaviour. However, in order to respond optimally to its environment, an animal needs proximate mechanisms that allow it to assess its state. For example, for an animal to protect its fitness assets, it has to determine its assets and, by comparison of its current state to some genetically determined set-point, adjust its motivation to gather further assets. Experimental studies on appetite and risk taking in juvenile salmonids suggest several internal clues by which fish might determine their current assets. Among these are: recent feeding history (i.e. stomach fullness) (e.g. Dill & Fraser 1984), recent growth rate (Damsgård & Dill 1998), and fat reserves (Bull & Metcalfe 1997). As a further possible mechanism, I suggest that fish

scale their risk aversion by comparing recent growth with their growth potential. The growth potential of salmon declines with size so that, for example, a 1 g coho salmon has a maximum growth rate of about 4.5 % of its body weight per day (at 15° C) whereas a 4 g coho salmon has a maximum growth rate of only about 3 % (Brett 1979, Iwama & Tautz 1981). At a growth rate of, say, 2.5 % body weight per day, therefore, the 1 g coho will have achieved 55% of its potential whereas the 4 g coho will have achieved 83%. If risk aversion scales in proportion to growth potential realized then, in the example above, the 4 gram fish should be 1.5 times (83/55) more risk averse than the 1 g fish. At maintenance ration (zero growth), and assuming equal predation risk for all sizes of fish, juvenile coho of all sizes should be equally risk averse. Above zero growth, larger coho should become progressively more risk averse than smaller fish as growth rate increases, with the greatest difference at the maximum growth rate of the larger fish (Fig 5.1a). Conversely, large fish should be less risk averse than small fish when individuals fail to acquire their maintenance ration because they are losing accumulated assets more rapidly (Fig. 5.1a). When recent growth is expressed in terms of potential growth realized, however, the curves of risk aversion for fish of different sizes collapse into a single curve for all sizes of fish (Fig. 5.1b). In addition to a general test of risk taking in relation to size, satiation and season, my experiments permitted a specific test of this hypothesis. Since two recent studies have shown an inverse relationship between body fat levels in juvenile Atlantic and Chinook salmon and feeding motivation (Bull & Metcalfe 1997, Shearer et al. in press), I also tested whether estimated body fat levels in juvenile coho influence their risk taking.

Methods

General Design of the Experiment

I designed the experiment to test the hypothesis that larger juvenile coho salmon accept less risk in exchange for food than smaller conspecifics. The experiment consisted of first feeding individual coho salmon from two size groups (which I label "small" and "large") three different prescribed rations so that they had different recent feeding and growth histories, second conditioning them to a visual stimulus of a predation threat using a mild electric shock (the electrified kingfisher model described earlier), and finally measuring the latency to resume foraging when exposed to the visual stimulus alone as a measure of risk aversion. I followed the suggestion by Houtman (1995) that, with increasing time after presentation of a threatening stimulus, the probability of continued presence of a predator decreases exponentially. The log-transformed latency time to resume foraging after a threatening stimulus should then translate into a threshold probability of predator presence that is accepted by the experimental subject (i.e. represent its willingness to take risks). I repeated the experiment twice, once in the summer and once in the fall under constant water temperature, so that I tested a total of 12 treatment combinations of small/large size, early/late season, and three feeding levels.

Source of Animals and Holding Conditions

Fish came from the Federal Department of Fisheries and Oceans Inch Creek Hatchery, near Mission, British Columbia. In mid-June of 1996, I transferred fish at the fry stage to the laboratory at the University of British Columbia and held them in groups of about 100 fish in 800 l oval tanks under a 16 L: 8 D photoperiod. In the laboratory, they received a continuous supply of city water which was de-chlorinated by adding 10 mg/l sodium thiosulfate. A similar group was transferred from the hatchery

in late August and the new fish plus any unused fry from the summer experiment were transferred to a 12 L :12 D photoperiod. I produced experimental groups of different sizes by manipulating feeding regimes and/or water temperature. Small and large fish in the summer experiment I obtained by randomly dividing fish into two groups and feeding the prospective "large" fish a high ration, while delaying growth of the prospective "small" group by feeding at a low rate and keeping them in cooler water. Large fish in the fall experiment came from a second transfer of fish from the hatchery. I obtained the small fish group in the fall experiment from a group of fry that had been incubated at lowered temperatures at the hatchery. In the university laboratory, I fed the fry non-floating commercial pellet food (Nutra Starter # 2 with 19 KJ/g Digestible energy, Moore-Clark Co., Vancouver, B.C). Once the fry had reached the desired sizes (1.5 g live body weight for the designated "small" group and 3.5 g for the "large" group), I adjusted the water temperature gradually to the experimental temperature of 15° C (+/- 0.5°) and fed the fish maintenance ration, calculated using a formula by Cho (1990), delivered once a day by broadcast feeding, for a minimum of two weeks before the experiment began. This was done to achieve a similar level of nutrition among all fish prior to the experiment. For holding conditions and experimental procedures, I followed the guidelines of the University of British Columbia animal care policy.

Preparations and Experimental Set Up

Each experimental run lasted two weeks: one week of pre-conditioning to a specific food regime, three days of acclimation to the experimental tanks, two days of conditioning to the threat stimulus, and two days of measuring latency to feed in presence of a model predator. At the start of week 1, I netted 24 fish (12 of each size group) from the holding tanks, anaesthetized them with 10 mg/l Methomidate Hydrochloride (Marinil™ Syndel Laboratories, Vancouver B.C.), blotted them slightly to remove excess water and weighed them to the nearest 0.01 g. I held these fish for one week in small (15

x 10 x 10 cm length, depth, width) individual net pens arranged in batteries of 8 in a larger tank where they received a continuous supply of 15° C water. I fed each fish one of three rations, based on the maintenance ration formula by Cho (1990) and assuming a moisture content of 75% in the fish. The feeding rations for small fish were maintenance ration, 3x, and 6x that amount, and for larger fish maintenance, 2.5x and 5x. Larger fish were fed slightly smaller rations relative to body weight to account for the lower maximum feeding rates of larger salmonids (Brett 1979). The maintenance ration was equivalent to 2- 2.5 % of dry weight of food per dry weight of fish. Small fish received food particles that averaged 1 mg and large fish received particles that averaged 2.2 mg, so that food particle size was roughly scaled to body size. In the net pens, and later in the experimental tanks, feeding was done by rotating disc feeders that were loaded daily with the exact amount of food for each fish and delivered individual pieces of food spread over a 12 hour period. On day 7, I removed the fish from the net pens, anaesthetized them, re-weighed them and transferred them to randomly assigned compartments in the experimental tanks. I adjusted each fish's food ration for the second week to account for body weight changes.

Experimental tanks consisted of four Plexiglas troughs (180 x 70 x 35 cm length, width, depth) painted a light blue and subdivided into 6 compartments (50 x 35 x 35 cm) by plywood panels (Fig. 5.2). Water entered at one end and the plywood dividers had a series of 0.5 cm diameter holes that allowed water to flow through at a low rate and exit at the other end of the trough. Water depth was 22 cm. Black plastic sheets with viewing slits were draped around each trough to minimize disturbance of the fish and plywood blinds visually isolated each compartment. The food from the disc feeders fell into each compartment about 8 cm from a small (5 x 10 cm) overhead shelter. A layer of gravel under each feeder discouraged the fish from picking up food particles that had sunk to the bottom (because they fell into the spaces between the gravel).

Conditioning Procedure

I allowed the fish about 60 hours (days 8 - 10) to settle into the experimental compartments and checked to ensure that they were accepting food. On the 4th and 5th day in the experimental compartment (days 11 and 12 of the experiment), I conditioned the fish to a predator model by association with a mild electric shock. I choose this procedure because prior trials with the model revealed that neither a visual stimulus alone nor dipping the model into the water near the fish caused any measurable delay in the subsequent feeding response of the fish.

The predator model was a kingfisher made from wood and Plexiglas and painted in realistic colours. The model was 35 cm long and had wings that extended 5 cm from either side of the body. The model had a metal core with a metal protrusion in place of the beak. The core was connected to a backpack-type electrofishing device delivering a 250 V, 75 Hz, square wave. I dipped the model briefly (ca. 0.5 s) into the middle of the compartment and retracted it immediately. I repeated this procedure twice, a minimum of two hours apart, on days 10 and 11. The fish reacted to the first dipping of the electrified model by a twitching of the body and accelerated swimming for about 5 s. After the first exposure, the fish hid under the shelter and did not normally leave it during subsequent exposure. No fish were narcotized by the shock and I saw no obvious differences in immediate reaction between the two size groups of fish. The shock did not seem to influence fish in neighbouring compartments.

Testing Procedure

On days 13 and 14 (days 6 and 7 of the second week), I first checked to determine that the fish were taking food. I then measured the willingness of the fish to leave the shelter and accept food in presence of the kingfisher model over the tank. Fish that did not take food in the absence of the predator

model during days 13 and 14, I recorded as “not feeding”. If a fish was accepting food, I stopped the feeders and inserted the model through a slit in the drapes so that it was suspended motionless at a height of about 20 cm above the water in the centre of the compartment. I then began dropping single pieces of food for the fish at the usual feeding location until it left the shelter and took the food. The first piece of food was dropped 15 s after insertion of the model, then at 30, 45, and 60s and at lengthening intervals thereafter, each time roughly 1.58 x the previous (equal to $\text{Log}(\text{time } 2) = \text{Log}(\text{time } 1) + 0.2$). Thus I assumed that the habituation response to the continuously visible predator model fitted the same negative exponential scenario as the reaction to a brief occurrence of a threatening stimulus (Houtman 1995). Once a fish had accepted food, I removed the predator model, restarted the disc feeders and allowed a minimum of two hours before the next trial. If the fish did not resume feeding within 2 h, I retracted the model and continued dropping food in the absence of the stimulus. In only two cases did the fish not resume feeding within 24 h after the visual model presentation. I terminated the trial and recorded the time to resume feeding for these fish as 24 h. If latency to resume feeding was short, I carried out two trials per day for a maximum of four trials over the two days.

My measure of willingness to feed under simulated predation risk consisted of either the behaviour “not feeding” (as described above) or the latency time to resume feeding in presence of a visual stimulus. If more than one presentation of the model was done for a fish, I averaged the latency times to provide a single measure of risk taking per fish. After the last trial, I removed the fish, weighed them and determined dry matter content after desiccating the carcasses at 65° C. The ratio of dry / wet weight was used as an estimate of fat stores because of the inverse relationship between moisture and fat content in salmonid fishes (Brett et al. 1969, Ludwig 1982).

I assumed for my experiment that size-related differences in the risk of capture by an avian stalking predator, such as the kingfisher, are negligible in the range of sizes I used, so that differences in

latency time to resume feeding are not biased by a fish's perception of size-biased susceptibility. Martel & Dill (1995) found that in coho fry of a similar size range, the susceptibility to detection by live merganser ducks (*Mergus merganser*) was related only to movement, and not to body size of the fish.

Because it is known that the effect of electrical currents is positively related to length of a fish (Bohlin et al. 1989, Vibert 1966), I did a separate experiment to assess the stress reaction of fish of different sizes conditioned by electroshock. Using individual fish (1 to 5 g live weight) in 50 l aquaria, I observed the increase and decline of opercular movement rate as an indication of stress levels (Metcalf et al. 1987) after an electric (conditioning) stimulus and after exposure to a visual (conditioned) stimulus alone. The conditioning protocol and voltage settings were similar to those in the main experiment. Results showed a weak but significant positive correlation between fish weight and opercular beat rate increase after a conditioning electric shock (linear correlation, $r^2 = 0.14$, $n = 31$, $P < 0.05$), but not after subsequent visual exposure to the predator model without electric reinforcement. ($r^2 = 0.006$, $n = 39$, n.s.). I concluded that even though the electric shock may have induced greater stress in larger fish in my main experiment, its use as a conditioning stimulus did not introduce a size bias in the conditioned response to a visual stimulus.

The two sets of experiments under summer and fall conditions were carried out in exactly the same way with fish of similar size range (see Fig. 5.5), the only difference being the dates during which the experiments were conducted (summer experiment during August 1996; fall experiment during October 1996) and photoperiod. I switched the photoperiod at the holding tanks to 12 L : 12 D four weeks prior to the fall experiment. A four week adjustment time to a new photoperiod has previously been used to induce changes in feeding behaviour of coho salmon (Clarke & Shelbourne 1986).

Data Handling and Statistical Analysis

Each successfully tested fish was considered one replicate of the experiment. All tests used two-tailed P-values and $P = 0.05$ was used as a significance criterion throughout. For non-parametric tests, I followed procedures outlined in Sokal & Rohlf (1981) and Zar (1996). Parametric tests were done using the SYSTAT computer package (SYSTAT Inc., Evanston, Illinois). For tests of contingency, I divided the data set into 3 categories, fish which did not resume feeding after conditioning and 2 categories of latency to resume feeding after conditioning (< 1 min. and > 1 min.). One min. was selected as the dividing point between categories to give approximately equal numbers of fish (49 to 51) in each category over the whole data set.

The model relating risk aversion to growth potential realized was tested with a stepwise multiple regression procedure. I regressed the latency to resume feeding on the weight of the fish (factor 1) and the percentage of their maximum growth rate achieved during the first week of the experiment (factor 2). If the model is correct, then the regression coefficient for weight should not differ significantly from zero, while a positive regression coefficient for weight would signify that larger fish had a longer latency to resume feeding after correcting for realized growth potential.

Results

Forty-two % of the fish (15% to 65% by group, Table 7) did not resume feeding at all during the two days after conditioning with the electric shock. The other fish showed mean latency times ranging from 15 s to 24 h. Since the frequency of the "not-feeding" response was significantly influenced by feeding level in the expected way (Low ration fish were more likely to continue feeding; Chi-square test on observed number of responses versus expected even distribution among feeding

levels, $X^2 = 11.33$ d.f. = 2, $P < 0.05$, Table 7), I included these data in some of my analyses and ranked them as cases of highest risk-aversion for non-parametric tests.

Influence of Feeding Level and Prior Growth Rate on Response to the Threat

Feeding ration and growth rate in the week prior to predator model presentation influenced latency to resume feeding in the expected way: fish that were well fed generally delayed feeding longer (Table 7). For a statistical test of the influence of feeding level and prior growth rate on latency response to the predator model, I used 3 x 3 contingency tables with either feeding level or prior growth rates as rows and three categories of latency to resume feeding as columns. The influence of feeding ration and prior growth rate on latency to resume feeding was only significant for small fish (Table 8), suggesting a degree of interaction between feeding rate and fish size categories.

Differences between Size Groups and between Seasons

As predicted, small fish tended to resume feeding earlier after presentation of the conditioned stimulus than larger fish (Fig. 5.3). The difference, however was only significant under the simulated summer conditions (Mann-Whitney-U test between small and large groups: a) summer: $z = 3.25$, $P < 0.001$; b) fall: $z = 1.52$, n.s.). When the 'not-feeding' observations were excluded from the this analysis, there was still a strong trend in the summer experiment for small fish to have shorter latency times than large fish, but the difference was not quite significant at the 95% level (Mann-Whitney-U test as above; a) summer: $z = 1.94$, $p = 0.051$, b) fall: $U = 137$, n.s.). Latency time differences between the size groups were more pronounced at low and medium feeding rates (Table 7).

Differences between summer and fall for fish of the same size were opposite to expectation: both large and small fry showed a trend toward lower risk-taking in the fall. The decline in risk taking

was significant for the small size groups, but not for the large size groups (Tukey-like non-parametric test adjusting for unequal sample size and tied ranks (Zar 1996): a) small: $q = 3.11$, $P < 0.05$, b) large: $q = 1.96$, n.s.).

Test of the Realized Growth Potential Model

In addition to the separate analyses of the influence of feeding level and size on latency time, I explored whether the size effect may have been caused by the realization of growth potential prior to the predation threat simulation. Mean latency time to resume feeding under summer conditions was positively correlated with the percent of growth potential realized, however, large fish had much longer latencies than small fish (Fig. 5.4). Small fish had to have about 80 % more of their growth potential realized to show the same latency time as large fish. I calculated the multiple regression of log-transformed latency times to resume feeding on weight of the fish and percentage of growth potential realized in the first week of the experiment. Fish that reacted to the conditioning by "not feeding" were excluded from this analysis. Realized growth potential was calculated as actual growth rate (calculated from growth changes during the week prior to the experiment) divided by growth potential (calculated using a formula by Iwama & Tautz 1981). The regression was significant for the summer but not for the fall experiment (ANOVA, summer: $F_{2,59} = 10.6$, $P < 0.001$; fall: $F_{2,34} = 2.55$, $P = 0.1$). The regression coefficient for realized growth was significant, as expected (Table 9). Contrary to prediction from the model, however, the coefficient for weight for the summer data was also significantly greater than zero (Table 9).

The Influence of Estimated Body Fat levels on Latency to Feed

There was a good correlation between fish live weight and percent dry matter content (Fig. 5.5), suggesting greater lipid stores in larger fish. Using a relationship of moisture to fat content established

for juvenile sockeye salmon (Brett et al. 1969), I estimated the lipid content in my fish to range from about 2 to 9 % of live body weight (Fig. 5.5). The two regressions had significantly different slopes (Fig 5.5, ANOVA interaction term: $F_{1, 164} = 65.2$, $P < 0.0001$), indicating different relationships between body size and lipid content in the summer and fall experiments. Estimated lipid levels, however, could not explain further variation in latency to resume foraging after the effect of body size was factored out (multiple linear regression including estimated lipid residuals, live weight and realized growth potential; standardized partial regression coefficients for residuals: a) summer, $r_p = 0.09$, $t = 0.74$, $d.f. = 62$, n.s.; b) fall experiment, $r_p = 0.15$, $t = 0.78$, $d.f. = 35$, n.s.).

Discussion

The combination of dynamic programming with manipulative experimentation is beginning to reveal how complex the decision-making of animals foraging under risk of predation may be. With this study, I add to the list of factors (Table 10) shown to influence risk-taking in salmonids. My experiment showed that juvenile coho salmon integrate cues related to their body size, season, and recent growth history to make decisions regarding their foraging/risk trade off. As predicted by dynamic programming models (Clark 1994, my model in Chapter 4), larger fish on average showed greater risk aversion after a predation threat than small fish at comparable feeding levels, suggesting that they are protecting their larger accumulated fitness assets. Other studies on salmonids and birds have shown apparent greater risk-aversion of larger or more dominant animals (e.g. Grant & Noakes 1987; Hegner 1988; Grand & Dill 1997), but in all cases, the possibility of a confounding effect of greater satiation of the larger animals was present. To my knowledge, this is the first experimental study that shows asset protection without such confounding. I suggest that the Asset Protection Principle, as it was named by Clark (1994), likely accounts for the behaviour of many animal species in pre-reproductive stages. Under dynamic optimality arguments, a larger animal should only accept the same risk of predation as a

smaller conspecific if the marginal increase in expected future fitness associated with a behaviour divided by the already accumulated fitness is equal for both sizes. Juvenile coho salmon have a lower growth potential when larger (Brett 1979) and their over winter survival probability (as a proxy of fitness) seems to increase asymptotically with weight (Holtby 1987; Quinn & Peterson 1996). A larger coho therefore should accept the same level of risk as a smaller fish, only if it is either much hungrier (so that the perceived fitness benefit of a piece of food is greater) or its food reward for taking the risk is much larger (so that the growth benefit is greater).

Other investigators have observed apparent increased risk proneness in larger fish. Johnson (1993) made this argument in an investigation of behaviour of domesticated rainbow trout in the presence of a piscivorous predator and Grand & Dill (1997) suggested the same for larger coho fry. However, Johnson's (1993) study contained problems with sample size (Thomas & Juanes 1996) whereas Grand & Dill (1997) also reported observations that suggested lower risk taking by larger fish. Furthermore, these studies were not designed to filter out effects of genetic factors on feeding motivation and, ultimately, size. Studies on Atlantic salmon juveniles suggest that, under natural conditions, large size may be partly a consequence of innate high feeding motivation (Metcalf et al. 1992, 1995), so that decreasing risk proneness with increasing size may be masked by the higher baseline feeding motivation of the larger fish. In my experiment, size differences among treatment groups were solely a result of prior environmental conditions while genetic differences in feeding motivation may have contributed to the individual variation in risk taking within treatment groups. The effects of inherent differences in feeding motivation should, therefore, be less of a problem in my results.

Two recent studies reported an inverse relationship of appetite and body fat levels in juvenile salmon recovering from a period of starvation (Bull & Metcalfe 1997) or fed food of different fat content (Shearer et al. in press). In addition, Damsgård and Dill (1998) showed that coho fry are more

willing to risk predation for food when compensating for a period of reduced food intake. It is, therefore, tempting to propose that the willingness to risk predation is partially governed by fat stores, perhaps via an appetite-regulating hormonal control system, which is seasonally adjusted using photoperiodic cues (Björnsson et al. 1995, McCormick et al. 1996, Shearer et al. in press). Johnsson et al. (1996 a, b), for example, showed an increase in plasma growth hormone levels in starved rainbow trout (*Oncorhynchus mykiss*) and increased risk-proneness in growth hormone injected trout. Some evidence in support of the idea of fat levels influencing risk taking comes from my observations that for fish in summer there was a strong correlation between size, estimated fat content and risk aversion whereas in the fall experiment, there was a weaker relationship between body size and fat content and no significant relationship between size and apparent risk aversion. However, the (rather small) residual variation in fat levels, after correcting for body size, could not explain any further variation in risk taking.

I tested my proposed model of a functional relationship between risk aversion and realized growth potential and found that the level of risk aversion in large fish relative to small fish was greater than predicted by the model. Thus, realization of growth potential appears not to be the mechanism of asset assessment in coho. Further experimentation is needed to determine the mechanism by which coho assess present size and recent growth history and balance these against risk.

Contrary to predictions from Clark's (1994) dynamic programming model, small and large fish did not increase risk taking under fall conditions. In fact, risk taking declined in both size groups in the fall. Thorpe et al. (1992) also showed a decline of feeding motivation between summer and early fall in Atlantic salmon fry. A possible explanation for the pronounced seasonal decline of risk-taking in the small fish group is a developmental switch by some small fish towards delayed smolting. In coho salmon, the proportion of fish to smolt at age 1+ or 2+ depends on growth conditions in freshwater- if growth is slow, more fish delay smolting (Holtby 1987; Randall et al. 1987). Studies on Atlantic salmon

suggest that the prospective smolting year is set in the early summer of the first year (Thorpe et al. 1992) after which those slated to delay smolting markedly decrease feeding motivation and risk taking (Huntingford et al. 1988). If fish in the small group in my experiment did switch to a different life history trajectory in the fall, comparison of risk-taking between the two size groups based on the Asset Protection Principle would not be meaningful at that time of the year. Large fish showed an insignificant trend toward decreased risk-taking in the fall compared to the summer. Since fish of that size can already be successful 1-year smolts (Holtby et al. 1990), it is unlikely that prospective 2-year smolts were in that group.

Another potential reason why foraging motivation may be higher in spring, independent of seasonal trends in feeding conditions and life history trajectories, has to do with competition for territories. Elliott (1989) argued for a critical period for future fitness early in the season in migratory brown trout (*Salmo trutta*) and estimated it to last for 1-2 months after fry emerge from the gravel. In spring, coho fry, like migratory brown trout fry (Elliott 1990), establish dominance hierarchies which impart a tremendous growth advantage to the dominant fish (Sandercock 1991; Nielsen 1992). Since dominance is closely related to size in coho, it may be that the motivation to feed and establish a strong competitive position is greater in such a critical period early in the year. Thus, in early summer, the fish may have been attempting to maximize a different pay-off function than in the fall.

Table 7 Frequencies of three categories of latency time to resume feeding after the presentation of a predator model in the four treatment groups. The three response categories are: less than 1 min. after visual predator model presentation, between 1 min. and 24 h after visual presentation, and not feeding for two days (NOF) after the electrical stimulus. See Methods section for further details.

Ration	Latency				Latency		
	< 1 min.	> 1 min.	NOF		< 1 min.	> 1 min.	NOF
	small fish summer			large fish summer			
low food	10	1	1	low food	4	7	4
medium	9	5	0	medium	3	6	6
high food	3	7	5	high food	4	5	9
	small fish fall			large fish fall			
low food	6	5	3	low food	1	4	6
medium	4	4	6	medium	1	4	10
high food	2	1	11	high food	2	2	13

Table 8 Summary of Chi-square tests of the influence of feeding level and growth during 1. week of the experiment on the distribution of latency time to resume feeding within four treatment groups. All d.f. = 4. * denotes $P < 0.05$; ** denotes $P < 0.01$ Categories of prior growth rates were obtained by dividing growth rates within each of the four treatment groups into three groups of equal frequencies.

factor	fish group	
	small fish summer	large fish summer
food ration	$X^2_4 = 25.4$ **	$X^2_4 = 3.97$, NS
prior growth	$X^2_4 = 18.8$ **	$X^2_4 = 1.96$, NS
	small fish fall	large fish fall
food	$X^2_4 = 9.52$, *	$X^2_4 = 2.59$, NS
prior growth	$X^2_4 = 3.11$, NS	$X^2_4 = 2.78$, NS

Table 9 Result of multiple linear regression of log-transformed latency time to resume feeding on weight of fish and the percentage of growth potential realized in the first week of the experiment (summer data). $N = 62$, multiple $R^2 = 0.27$. Model: latency = constant + a (weight) + b (realized growth).

Factor	Coefficient	Std. Coefficient	F- value	P α
constant	- 0.91	0.0	2.9	0.005
weight (g)	0.44	0.53	4.43	< 0.001
growth (% max.)	0.011	0.32	2.72	0.009

Table 10 List of factors shown in manipulative experiments to influence the willingness of juvenile salmonids to feed in the presence of a threatening stimulus.

factor	species	authors
size	coho salmon	Johnson (1993), this study
season	coho salmon	this study
prior growth rate	coho salmon	Damsgård & Dill 1998, this study
gastric satiation	various	Magnhagen (1988), Gotceitas & Godin (1991), Dill & Fraser(1984)
growth hormone	rainbow trout	Johnsson et al. (1996 a,b)
experience with predator	coho salmon	Healey & Reinhardt (1993)
handling time of food	coho salmon	Dill & Fraser (1984)
competitor presence	various	Huntingford et al. (1993), Grand (1997)
life history trajectory	Atlantic salmon	Huntingford et al. (1988)
species	various	Abrahams & Healey (1993)

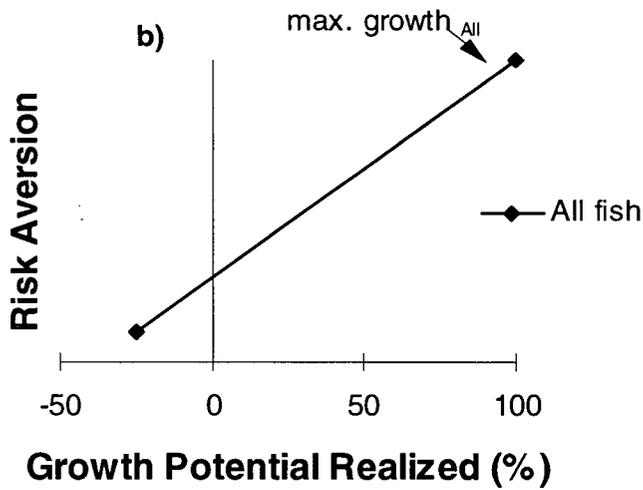
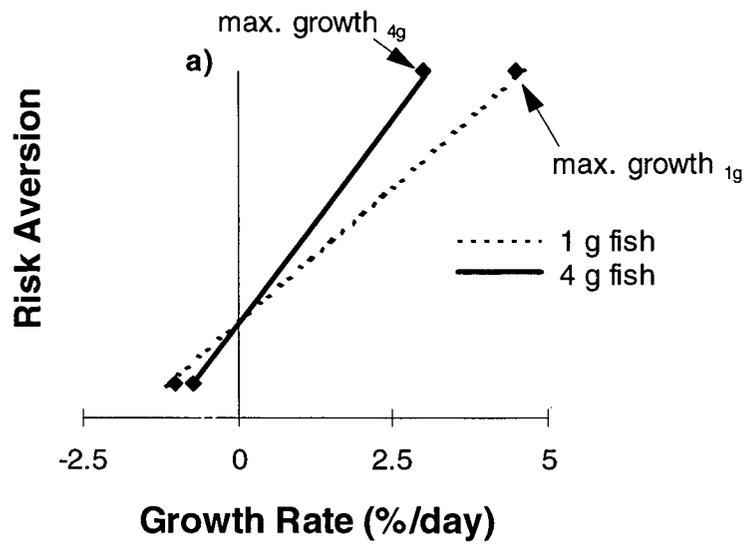


Fig. 5.1 Graphical example of a proposed functional relationship between two measures of growth and the willingness to risk predation in fish of different sizes. a) specific growth rate versus "risk aversion" and b) realized growth potential versus "risk aversion".

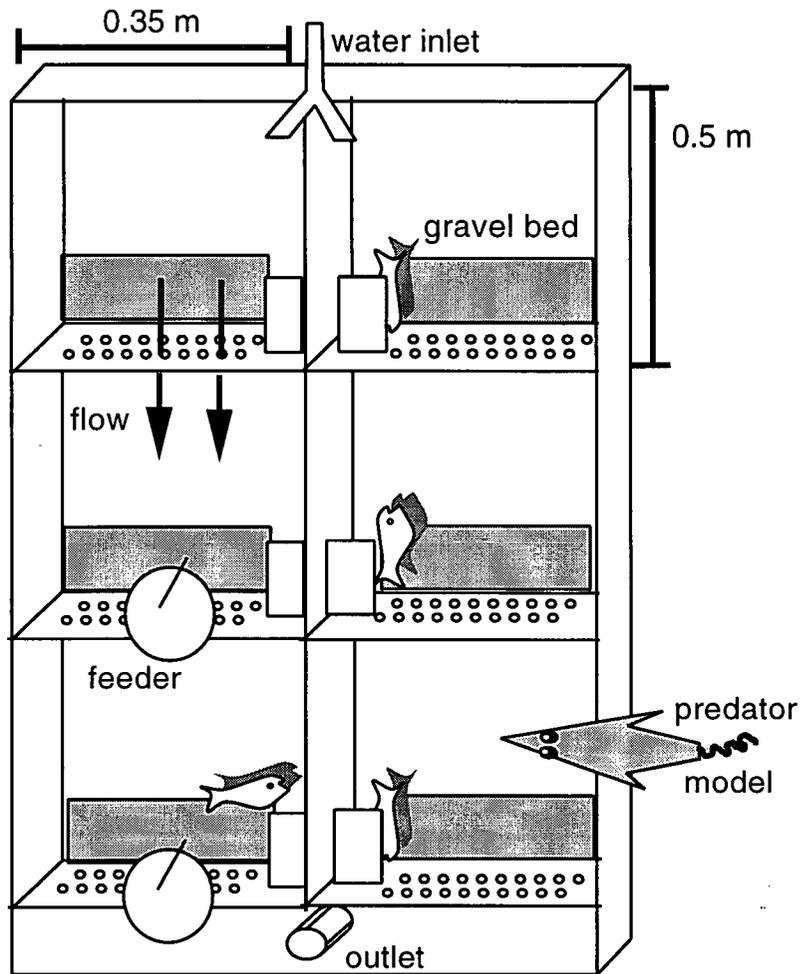


Fig. 5.2 Schematic drawing of the experimental set up. Note: All 6 compartments were identical but for clarity not all details are shown in each.

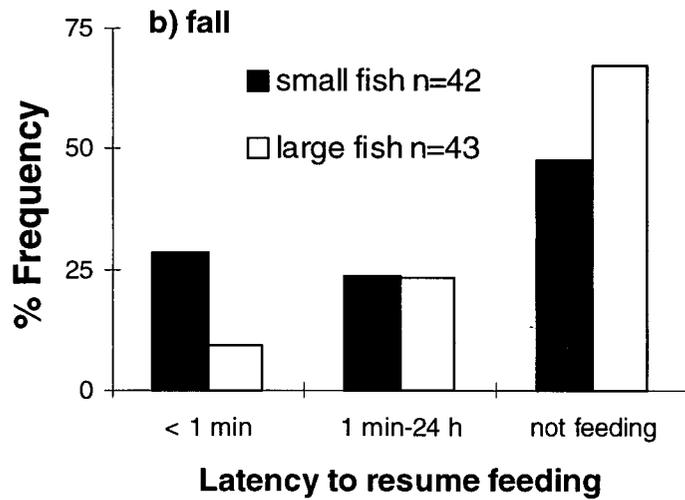
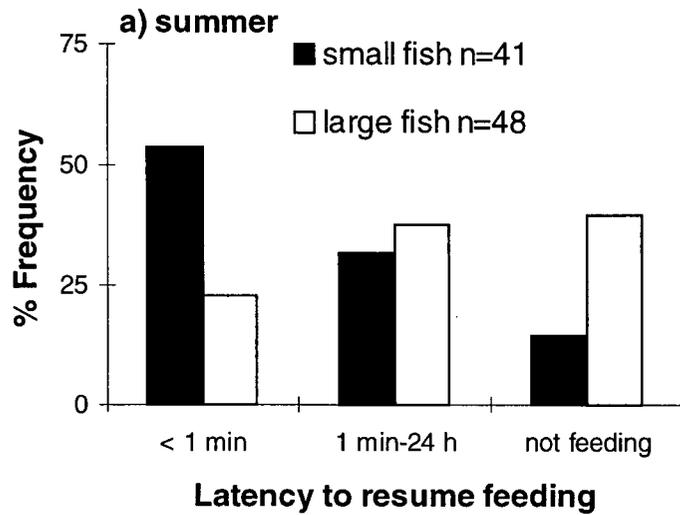


Fig. 5.3 Frequency of three categories of latency time to resume foraging after a predation threat in two size groups of coho fry. a) simulated summer photoperiod, b) simulated fall photoperiod.

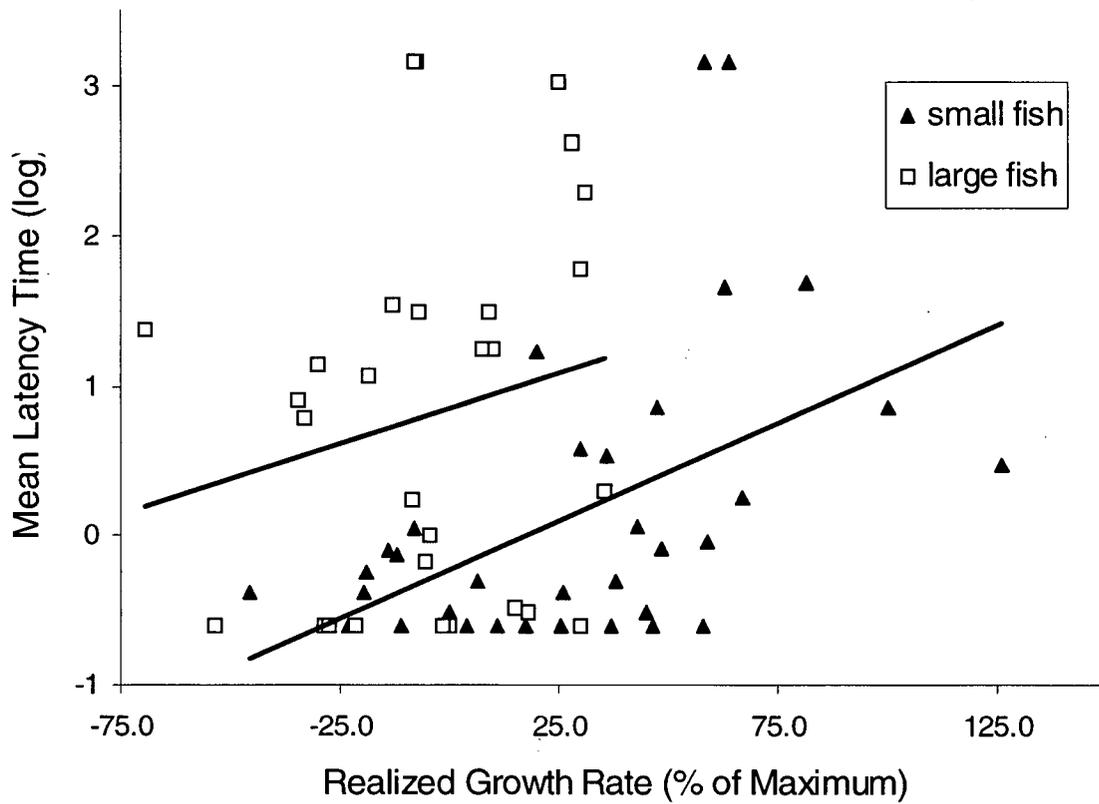


Fig. 5.4 Regression of mean latency to resume feeding after a predation threat in two size groups of coho fry against the percentage of potential growth rate realized in the first week of the experiment. Only data from the summer photoperiod experiment are shown.

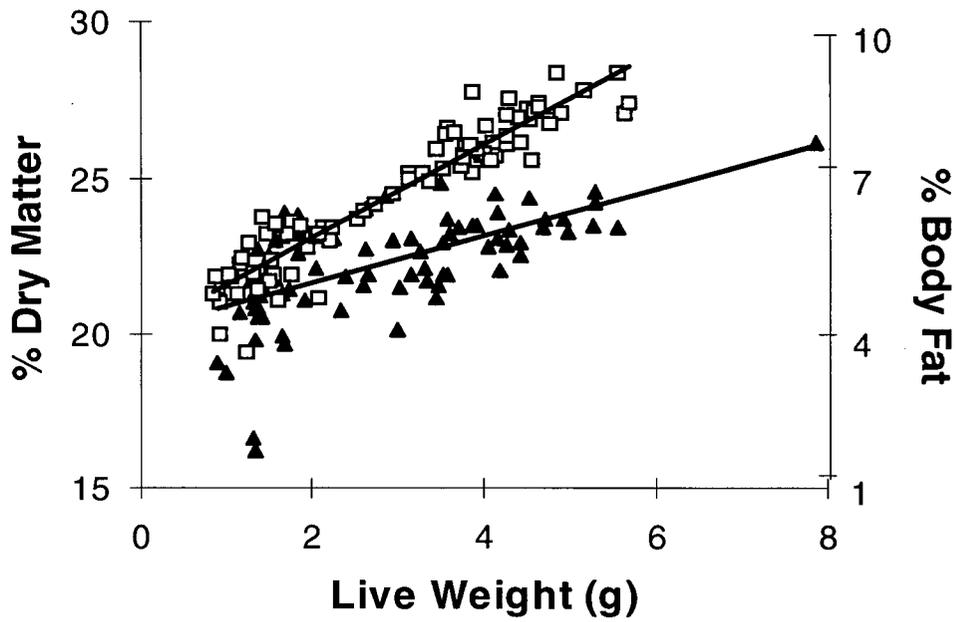


Fig. 5.5 Relationship between live weight of coho salmon fry and percent dry matter for fish used in the summer (open squares) and fall experiment (filled triangles). The right-hand scale gives the corresponding estimated body fat values, calculated from Brett (1969). The slopes of the two regression lines differed significantly from one another.

Chapter 6 **General Discussion**

Dynamic Optimization of Risk Taking Behaviour and Asset Protection

In this thesis, I used the example of juvenile coho salmon during their first year in freshwater to show, with the help of a dynamic model (Chapter 4), that the motivation to risk exposure to predators in exchange for foraging gains should decrease with body size and change with seasonal changes in growth-related environmental conditions. Given that it is based on realistic assumptions, the model shows that Asset Protection likely influences risk taking in juvenile coho salmon. The results of my model are also consistent with more general models of risk taking in relation to size and time constraints (McNamara & Houston 1986, Clark 1994). In laboratory experiments, I showed that the willingness of individual isolated fish to risk exposure to a simulated predation threat is negatively correlated to size and decreases between spring and fall (Chapter 5). My results thus support the prediction of Asset Protection from my dynamic foraging model and add to the growing body of experimental evidence for dynamic optimization of animal behaviour. The seasonal decline in risk taking I observed was different from predictions by the general DPM (Clark 1994) but consistent with predictions from my DPM when it incorporated seasonal changes in food availability (Chapter 4) and with Grand's (1997b) DPM which predicts a decrease in risk taking in small fish in the fall due to a change in life history strategies.

Potential Ecological Consequences of Asset Protection

Other laboratory experiments (Chapter 2 and 3) also provided evidence of lower risk taking in larger fish and showed that individual differences in risk taking can lead to habitat segregation between coho of different sizes. An important consequence of risk avoidance by large fish was that, under predation threat, I observed not only reduced overall growth rates of fish but also reduced growth depensation among fish of different sizes compared to the situation without the predation threat

(Chapter 2 and 3). That in absence of predation risk, larger fish dominate access to food and grow better has previously been shown under field conditions (Nielsen 1992, Martel 1996). The effect of predation threat on growth depensation, however, has not previously been demonstrated. In Chapter 5, I showed that risk taking decreases with recent feeding rate. This relationship has been reported in other studies as well. Thus, risk aversion of larger fish may be a combination of increased satiation and Asset Protection. Both factors make it very likely that, under natural conditions, larger fish will be less willing to expose themselves to predation risk than small fish.

The ecological consequences of lower risk taking of larger fish should be a lower mortality rate from predation, so that mortality becomes biased toward small individuals in a cohort. Furthermore, as the cohort increases in size, overall mortality should decline as long as the environment stays constant. A negative correlation between size and mortality rate in juvenile fish has been shown across many taxa (recent review in Sogard 1997). The mechanisms evoked to explain this pattern usually include enhanced resistance to adverse conditions (starvation, physical extremes) of larger individuals, and decreased vulnerability to predators due to better escape capabilities of the prey or gape limitations of the predators. The environmental conditions and suite of predators to which stream dwelling coho are exposed in summer are not very consistent with these proposed explanations. I suggest that larger fish may experience greater survival rates solely because they avoid risky foraging behaviour. Encounter rates of predators with their fish prey may, thus, decline with increasing size of prey (cf. Juanes 1992, who argued for an increase of encounter rates of piscivorous predators with size of their prey because larger prey supposedly is easier to detect). In coho juveniles, risk avoidance behaviour may include avoiding risky habitats (Chapter 2), enhancing crypsis by reduced movement (Martel & Dill 1995), or daytime sheltering under cover (Fraser et al. 1995). Larger individuals may further decrease their exposure to predators by reducing active feeding time (thus increasing the opportunity for vigilance, Milinski 1993), or by spending more time in sheltered habitats to avoid areas of greater predation risk.

The Costs of Growing vs. the Benefits of Large Body Size

“ Bigger is better” sums up the result of most studies on size versus survival in juvenile fish (Sogard 1997), which has led to the argument that selection should favour individuals with the capability of high growth rates. This argument ignores the likely decreasing benefit/cost ratio of foraging associated with increases in body size. My experimental results add to a growing body of literature showing that individual foraging decisions are based on trade offs between costs and benefits. The trade off between the benefits of *being big* and the costs of *getting bigger* should be one underlying cause for stabilizing selection on the motivation to forage and grow.

Another cause for stabilizing selection on feeding motivation may be decreasing fitness beyond a certain size at later life stages, as was shown for smolt-to-adult survival in sockeye salmon (Koenings & Burkett 1987). Metcalfe et al. (1995) found a positive correlation between standard metabolic rate (SMR) and feeding motivation in Atlantic salmon parr. Fish with high SMR also emerged earlier from the redds and, thus, were bigger than conspecifics with low SMR. Brännas' (1995) observations that early emerging fish suffered high mortality from predation suggests that stabilizing selection on feeding motivation in Atlantic salmon occurs at an early life stage. In those cases mentioned above, the costs of a high feeding motivation were probably linked to mortality from predation. My experiments described in Chapter 3 simulate a situation where predation risk is substantially reduced in the early life stages of salmonids. My observations suggest that under reduced predation risk, competitive ability (i.e. size and aggressiveness) would become a stronger factor for the fitness of the organism. Such a change in the balance between predation and competition, may lead over several generations to a higher innate feeding motivation. The level of aggressiveness is known to be heritable in salmonid fish (Swain & Holtby 1989, Ridell & Swain 1990, Bakker 1986).

Seasonally Varying Environmental Conditions

My DPM suggested that the motivation to forage under risk should change seasonally not only in response to seasonally changing conditions but in anticipation of them. For example, my DPM predicts that foraging effort in the spring should be greater because a period of low food availability follows in the summer. Simpson et al. (1996) showed that the feeding motivation in Atlantic salmon declined during the summer independent of food ration or water temperature. In the fall of the first feeding season, the feeding motivation of Atlantic salmon fry also declines independent of temperature (Thorpe et al. 1992) which is similar to my observation of reduced risk taking of juvenile coho in the fall (Chapter 5).

DPM's make predictions based on evolutionary arguments: a behaviour is optimal because it yields the greatest fitness under the assumed conditions. We can expect the organism in question to have evolved the predicted optimal pattern if it yielded a selective advantage over other behavioural strategies. Such a selective advantage arises if the environmental conditions are predictable (Clark 1994) and if deviations from the optimal behaviour carry a large fitness penalty. Conditions of low growth in temperate streams in winter are very predictable, so that it is not surprising that animals have evolved to forage in anticipation of worsening of conditions. In the summer, however, a juvenile coho salmon is more likely to encounter temporary unpredictable changes to the prevalent feeding conditions. I expect therefore that coho would be selected for high feeding motivation so as to be able to profit from short-term increases in foraging opportunities. Nevertheless, a compromise between adaptation to seasonal cycles and short-term deviations from normal conditions may be achieved. Juvenile coho salmon seem to respond to fluctuations in the level of predation risk (Chapter 2) and take advantage of the reduced competition due to risk avoidance behaviour of some members of the cohort (Chapter 3).

This suggests that they are able to respond in a flexible manner to changing environmental conditions and may, therefore, be able to profit from the unpredictable occurrence of good feeding conditions even when their overall motivation to feed may be low in adaptation to prevalent low seasonal food productivity. Observations of coho behaviour in streams which provide opportunities for growth in winter suggest that coho fry will continue to feed and grow in winter if conditions are favourable (Scott Hinch UBC pers. com.).

Implementation of Optimal Strategies

One has to distinguish between selective pressures as the ultimate causation of the observed behaviour (and the basis of calculations of DPM's) and the proximate mechanism by which the organism may have adapted to them. For example, the selective advantage of feeding below the maximal rate may lie in the decreasing conversion efficiency of food into body tissue with increasing feeding rate (Brett 1979), whereas the mechanism that leads to the observed decrease in foraging and risk taking with increasing stomach fullness (e.g. Dill & Fraser 1984) may have to do with stomach stretch receptors or blood concentration of certain metabolites (Matty & Lowe 1983). Regarding possible seasonal changes in feeding motivation in salmonids, recent work suggests that long-term feeding motivation is influenced by hormonal changes that are governed by changes in the photoperiod (e.g. McCormick et al. 1995, Stefansson et al. 1991). My own experiment (Chapter 5) on seasonal changes in risk taking could not distinguish between the influence of the photoperiod change and endogenous factors, because I could not carry out the summer and fall experiments at the same time. But the number of studies that show changes in feeding motivation due to photoperiod manipulations suggest that the changes in risk taking observed in my experiment were most likely induced by photoperiod changes. The mechanism responsible for the implementation of Asset Protection remains to be found. The general positive correlation between body weight and body fat levels in fish is well established (e.g. Simpson et

al. 1996) and fat levels have been shown to influence growth hormone levels (Shearer et al. in press). Growth hormone levels, in turn, have been shown to influence risk taking (Johnsson et al. 1996a, b). This makes changes in fat levels with increasing body size and associated changes in hormones related to feeding motivation a potential candidate for the mechanism responsible for Asset Protection.

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