

Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch*

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The effects of food restriction on predation risk-taking behavior were studied in juvenile coho salmon, *Oncorhynchus kisutch*, during the period before seawater migration in the spring. A radiographic technique enabled the study of individual food intake in a safe and risky food patch before and after exposure to a piscivorous predator. The study revealed a significant increase in food intake and specific growth rate in the weeks following deprivation, resulting in compensatory growth and a recovery of the weight loss caused by dietary restriction. The increase in food intake resulted from a change in risk-taking behavior. Following a period of diet restriction, the fish habituated faster after predator exposure, and the proportion of fish in the risky patch was significantly higher than before deprivation. Deprived fish took greater shares of the group meal compared with control fish, and the pattern of the individual share of the group meal after food restriction indicated a change in the social hierarchy. This study indicates that risk-taking behavior is state dependent and changes temporarily to compensate for a period of food restriction. The results are discussed in terms of trade-offs between food and risk in a period leading up to an ontogenetic habitat shift. *Key words:* coho salmon, *Oncorhynchus kisutch*, predation, risk taking, Salmonidae, social hierarchy. [*Behav Ecol* 9:26–32 (1998)]

It has become increasingly clear that individuals are able to make behavioral trade-offs between food intake and risk of predation in a state-dependent fashion. Foraging at an increasing rate may be costly in terms of an increase in the risk of mortality due to predation (Godin and Smith, 1988). A hungry animal is more willing to take risks simply because an increase in the benefit of risk-taking behavior (food) results in an increase in the willingness to pay the potential cost (risk of injury or death). Such a compromise in a conflict situation has been demonstrated for several species, including mammals, birds, fishes, and invertebrates (reviewed by Lima and Dill, 1990). For example, prey attack distance declines with increasing satiation in coho salmon, *Oncorhynchus kisutch* (Dill and Fraser, 1984); parasite-infected three-spined sticklebacks, *Gasterosteus aculeatus*, are more willing to take risks compared with uninfected fish (Godin and Sproul, 1988); hunger level determines the time before Atlantic salmon, *Salmo salar*, resume feeding after exposure to a predator (Gotceitas and Godin, 1991); and hungry crucian carp (*Carassius carassius*) spend more time in an risky patch with food than in a safe patch without food (Pettersson and Brönmark, 1993).

Despite numerous descriptions of risk-taking behavior in the literature (Lima and Dill, 1990), the complex relationships between body size, food intake, and risk taking at an individual level are not completely understood. In nature, bigger prey fish are difficult for a piscivorous predator to catch and handle, confining the vulnerable prey to a size range dependent on the gape of the particular predators. Within this size range, relative vulnerability decreases as a function of prey body size, and beyond a certain size, depending on the size of the predators, the prey attain a prey-size refuge (Damsgård, 1995; Hambright et al., 1991). Growing fish thus face a fun-

damental behavioral dilemma: a high growth rate will on one hand reduce the time a prey is vulnerable to a predator, but on the other hand a high food intake and growth rate can only be obtained through an increase in the risk of predation. The resulting size-dependent prey behavior can lead to complex patterns of habitat use and trophic interactions. For example, small, vulnerable bluegill sunfish, *Lepomis macrochirus*, shift their foraging behavior and reduce their use of open habitats in the presence of predators, while larger, nonvulnerable sunfish have a higher growth rate in the presence of predators than in their absence (Werner et al., 1983).

To examine the relationship between growth, food intake, and risk-taking behavior, we studied individually tagged coho salmon before their downstream spring migration to the sea. Coho salmon in southern British Columbia (Canada) migrate to sea near the end of May (e.g., Fraser et al., 1983), normally after spending one winter in fresh water. However, some coho do not descend to the sea as yearlings, but spend 2, 3, or even 4 years in fresh water before migration (Groot and Margolis, 1991). The frequency of older migrants increases in northern areas, but the size of coho smolts (i.e., seaward migrants) is fairly consistent throughout the species' geographic range (Groot and Margolis, 1991), indicating that age at seawater migration is related to growth in fresh water.

Smoltification involves a series of physiological, morphological, and behavioral changes that preadapt salmonids to a marine life (reviewed by Hoar, 1988). Many salmonid populations segregate into two subpopulations, displaying a bimodal growth pattern before smoltification (e.g., Thorpe, 1977). Individuals within Atlantic salmon populations that do not smolt enter a state of metabolic arrest and overwinter anorexia (sensu Mrosovsky and Sherry, 1980) and spend most of their time hiding in stony substrata (Metcalf and Thorpe, 1992). A high growth rate may thus be regarded as one result of the decision to become a smolt, and individual risk-taking behavior will depend on fish size, food availability, and the time remaining until migration. The high size-dependent mortality during seaward migration and the early seawater period in anadromous salmonids (Holtby et al., 1990) indicate

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that body size at the time of migration, together with the occurrence of predators, will strongly affect fitness and thus select for animals reaching a minimum size before departure from the stream. In the present study, we tested the prediction that smolting coho salmon, deprived of food for a period of time, will be more willing to take risks in the presence of a predator, to compensate for the weight lost and increase their likelihood of reaching the threshold size by the time of migration.

MATERIALS AND METHODS

Coho salmon (age 1+) from Inch Creek Hatchery, Fraser Valley, British Columbia, Canada, were acclimated to laboratory facilities at Simon Fraser University in December 1993. The fish were individually tagged (Fingerling Floy Tags), randomly divided into two groups of initially 100 fish each, and reared in 170-l holding tanks (10°C and a 12 h:12 h light:dark regime). The fish were handfed dry pellets (2.4 mm; Moore-Clark, Vancouver). Based on recommendations from Moore-Clark, the daily ration was calculated as 2.2 and 1.6% of total biomass, for the period when mean fish weight were smaller and larger than 12 g, respectively.

We conducted the study between week 5 (1 February) and week 16 (21 April) in 1994. During weeks 11–13 (11 March–1 April), one of the groups was deprived of food by giving only 25% of the normal ration, while the other served as a control, receiving its full ration. Twice before dietary restriction (weeks 7 and 10) and twice after restriction (weeks 13 and 16), four replicate experiments were conducted in an observation tank. Each experiment included 22–25 fish from each group (depending upon the number of fish still alive), and thus totally approximately 50 fish. We randomly sampled the fish so each fish was tested once at every occasion, and groups were randomly reassembled for each testing period. In both weeks 7 and 10, one experiment was excluded due to aeration problems. The observation tank (270 × 98 cm) was divided with Plexiglas walls into three chambers. The central chamber (132 × 98 cm) served as the experimental arena for the prey fish. A mesh screen was located 5 cm above the bottom of the tank, and the water depth over the mesh was 25 cm, giving a total water volume of 320 l. One of the end chambers served as a predator compartment and had a clear Plexiglas window (30 × 25 cm) with an opaque sliding door behind it (operated with monofilament lines from outside the tank). The predator (a 35 cm, 0.5 kg, rainbow trout, *Oncorhynchus mykiss*) was kept in a separate aquarium behind the door. To reduce the possibility that prey fish learned the position of the predator, the second end chamber was identical to the predator chamber.

We placed prey fish in the observation tank 1 day before the experiment and did not feed them; this ensured that all fish had equally empty stomachs at the time of testing. Throughout the experimental period, prey fish were fed with a belt feeder, providing the calculated amount of food at irregular intervals. The food was delivered at equal rates through Plexiglas tubes to two separate areas in the tank. The feeding stations were located 15–20 cm and 110–115 cm from the predator window, thus dividing the tank into a risky and a safe feeding patch of equal size. The bottom mesh prevented the fish from bottom feeding; thus, the fish had to stay at the feeding stations to be able to feed.

The experiment started at approximately 0900 h. We monitored the positions of the fish using a video camera mounted above the tank. After 1 h, the fish were visually exposed to the predator by removing the opaque partition between the chambers. The number of fish in the risky patch was recorded every 5 min from 45 min before to 90 min after exposure to

the predator (the predator remained visible throughout this 90-min period). To control for the effects of partition movement, three identical experiments were conducted without the predator behind the Plexiglas window.

We examined food intake by individual coho using radiography (Jørgensen and Jobling, 1989; Talbot and Higgins, 1983). During the experiment, the normal food was replaced with pellets of identical composition but formulated to contain X-ray dense glass beads (Ballotini, Jencons Ltd., Leighton Buzzard, Bedfordshire, UK; size 7, 8.5, and 10). Three types of food with different sizes of glass beads were fed during the experiment; one before exposure and one in each patch after exposure to the predator.

After each experiment we anesthetized the coho using phenoxyethanol, weighed them to the nearest 0.1 g, and X-ray photographed them (MicroVet MV 200 machine, 3.5-s exposure, 63 kV, 42 mAs, AGFA Structurix D7 film). Counts of the three different sizes of bead found in the stomachs enabled us to determine where, when, and how much each individual fish had eaten during the experiments. We calculated food intake of individual fish using the known relationship between numbers of glass beads and weight of food pellets. Weight-specific food intake was expressed as milligram dry weight of food per gram fresh weight of fish per hour ($\text{mg dw} \times \text{g fw}^{-1} \times \text{h}^{-1}$) after exposure to the predator. We classified individual fish as either nonfeeding fish, safe feeders (fish with more than 50% of their food from the safe patch), or risky feeders (fish with more than 50% from the risky patch) after the exposure to the predator. The individual share of a group meal (McCarthy et al., 1992) was calculated as food intake by single fish as a percentage of the total amount of food eaten in each experiment. The specific growth rates (SGR; % body weight $\times \text{day}^{-1}$) between two successive experiments were calculated as $\text{SGR} = 100 \times (\ln W_2 - \ln W_1) / t$, where W_1 is the weight at time 1, W_2 is the weight at time 2, and t is the time in days between the experiments (Jobling, 1994).

The state of the smoltification process during the experimental period was measured as the frequency of fish showing externally visible smolt characters, according to Gorbman et al. (1982). Before the experiment, 78.3% of the fish were classified as parr (with parr marks and without silvery), 21.7% as silvery parr (with partial parr marks and silvery), and none of the fish as smolts (without parr marks and with full silvery). During the course of the experiment, the frequency of parr decreased, and the frequency of smolts increased, and by week 16 only 1.1% of the fish were classified as parr, 65.1% were silvery parr, and 33.7% were smolts.

RESULTS

There was no significant difference in weight, food intake or specific growth rates between the deprived group and the control group (Figure 1; week 10, t tests, $p > .05$) before the food restriction that followed the experiment in week 10. During the deprivation period between weeks 10 and 13, the mean weight of fish in the deprived group leveled off (Figure 1a). The specific growth rate was significantly lower (t test, $p < .001$) in the deprived group (mean \pm SE, $0.33 \pm 0.04\% \times \text{day}^{-1}$, $n = 89$) than in the control group ($1.15 \pm 0.05\% \times \text{day}^{-1}$, $n = 88$; Figure 1c). After the restriction period ended, food intake was significantly greater (t test, $p < .001$) in the deprived group ($3.2 \pm 0.2 \text{ mg dw} \times \text{g fw}^{-1} \times \text{h}^{-1}$, $n = 90$) than in the control group ($0.6 \pm 0.1 \text{ mg dw} \times \text{g fw}^{-1} \times \text{h}^{-1}$, $n = 88$; Figure 1b). Accordingly, between weeks 13 and 16 the deprived group had a significantly higher (t test, $p < .001$) specific growth rate ($1.64 \pm 0.04\% \times \text{day}^{-1}$, $n = 88$) than the control group ($1.25 \pm 0.03\% \times \text{day}^{-1}$, $n = 86$, Figure 1c). As

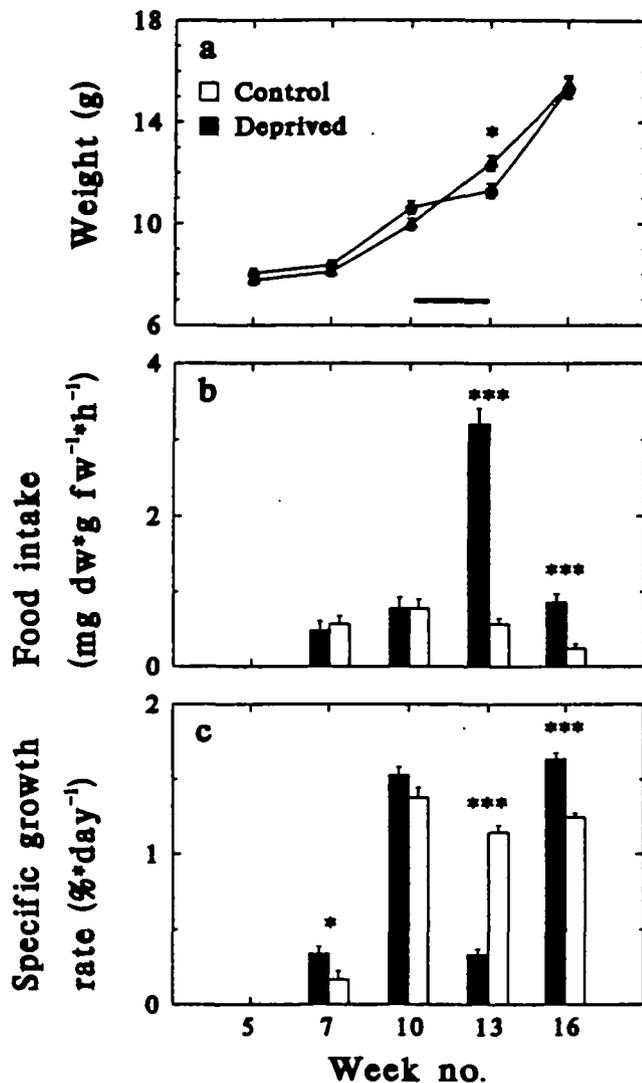


Figure 1
Differences between experimentally food-deprived coho salmon and the control group without deprivation: (a) weight (g; $n = 85-100$), (b) food intake ($\text{mg dw} \times \text{g fw}^{-1} \times \text{h}^{-1}$; $n = 64-90$), and (c) specific growth rate ($\% \times \text{day}^{-1}$; $n = 84-91$). Weights and food intakes represent means and SE at the sampling day; growth rates represent means and SE for the period prior to the sampling day. The deprivation period is indicated with a horizontal bar in panel a. * $p < .05$, *** $p < .001$.

Table 1

Percentage of fish in risky patch before (weeks 7 and 10) and after (weeks 13 and 16) a period of food deprivation, compared with an experiment without a predator

	Mean \pm SE percentage of fish in risky patch			
	Before predator exposure	After predator exposure (min)		
		0-30	35-60	65-90
Week 7	64.8 \pm 3.3	11.3 \pm 3.1	34.2 \pm 5.2	29.9 \pm 3.5
Week 10	57.1 \pm 3.5	9.2 \pm 2.1	18.4 \pm 4.8	37.7 \pm 7.0
Week 13	62.1 \pm 2.3	28.7 \pm 4.6	56.5 \pm 3.3	64.1 \pm 2.7
Week 16	48.4 \pm 4.0	15.7 \pm 4.3	21.5 \pm 4.6	31.6 \pm 4.9
Without predator	63.4 \pm 2.7	18.8 \pm 4.4	58.0 \pm 4.6	53.1 \pm 4.6

Data represent means \pm SE every 5 min from 45 min before predator exposure and during three 30-min intervals after predator exposure.

a result of this compensatory growth, the deprived group caught up with the control group, and there was no difference in mean fish weight by the end of the experiment (15.3 ± 0.4 g, $n = 88$ and 15.4 ± 0.4 g, $n = 87$ in the deprived and control groups, respectively, Figure 1a).

Before predator exposure, the mean proportion of fish in the risky patch ranged from 48.4 to 64.8% (Table 1). In all experiments, the number of fish in the risky patch sharply decreased after the predator became visible and thereafter increased slowly. During this time, both solitary and group predator inspection was frequently observed. A typical inspection involved successive movements toward the predator, often ending with lateral displays in front of the Plexiglas window, followed by rapid movement away from the predator. Before food restriction (week 10), the mean proportion of fish in the risky patch decreased from 57.1 to 9.2% after predator exposure and increased to 37.7% 65-90 min after exposure to the predator (Table 1, Figure 2a). After the period of food restriction (week 13), the proportion of fish in the risky patch did not decrease to zero as it had in week 10 and increased to 56.5% 35-60 min after predator exposure (Table 1, Figure 2a). Four weeks before restriction (week 7), and 3 weeks after the restriction (week 16), the numbers of fish in the risky patch were similar to the results in week 10 (Table 1). There was no significant difference between the numbers of fish in the risky patch before predator exposure in weeks 10 and 13, whereas the differences 0-30 min, 35-60 min, and 65-90 min after exposure were highly significant (Mann-Whitney, $p < .001$, $p < .001$, and $p < .01$, respectively).

The result was not due to disturbance caused by opening the partition between the prey and the predator. The fish did move away from the risky patch after the removal of the Plexiglas window in the experiments without a predator, and the proportion of fish there decreased from 63.4% before to 18.8% after. However, the fish habituated sooner than in the predator experiments, and 35-60 min after removal of the partition 58.0% of fish were in the risky patch (Table 1, Figure 2b).

Most of the feeding fish in both the deprived and the control groups in all experiments ate in only one of the patches ($72.3 \pm 3.0\%$, $n = 8$); the rest of the fish had food from both patches in their stomachs. The distribution of fish among the three feeding types did not differ between the deprived group and the control group before restriction (week 10; Figure 3a). More than 50% of the fish did not feed, while 15-25% fed in each of the safe and risky patches. From week 10 to week 13, the frequency of nonfeeding fish in the deprived group decreased significantly (Mann-Whitney, $p < .05$) from 54.3% ($n = 3$) to 19.3% ($n = 4$), whereas significantly more fish (Mann-Whitney, $p < .05$) fed in the risky patch after deprivation (49.1%, $n = 4$, versus 21.7%, $n = 3$). After the period of food

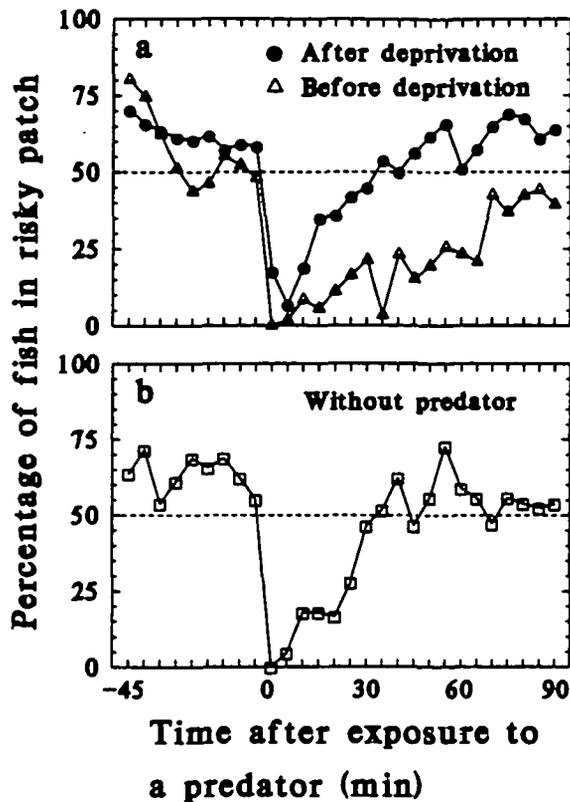


Figure 2
 Mean percentage of coho salmon in the risky patch (a) before (week 10, $n = 3$) and after (week 13, $n = 4$) a period of food deprivation. (b) Experiments without a predator present ($n = 3$).

restriction (week 13), the distribution of fish among patches changed dramatically in the deprived group, whereas only small changes occurred in the control group, and the frequency of nonfeeding fish, fish in the safe patch, the deprived group and the control group (Table 2, Figure 3b). Four weeks before restriction (week 7) and 3 weeks after restriction (week 16), the frequency of nonfeeding fish and the proportions of fish feeding in the safe and risky patches in both the deprived and the control groups were similar to the results in week 10 (Table 2).

Food restriction changed the social hierarchy, and a relatively greater number of deprived fish fed after the period of food restriction. Before restriction (week 10), a small number of fish monopolized the feeding patches and took a large share of the meals (Figure 4a). There was no difference between the number of fish that ate more than the mean share in the deprived group and the control group [6 (24%) and 7 (28%) of 25 fish, respectively]. After the food restriction

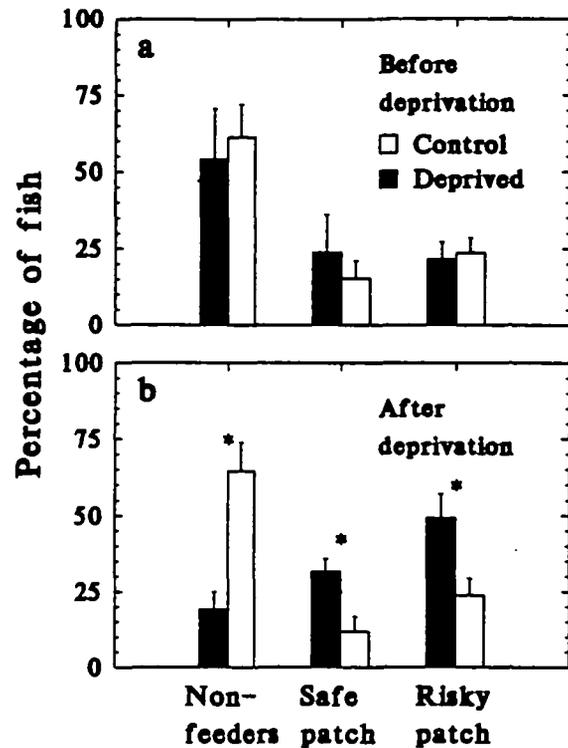


Figure 3
 Feeding in food-deprived coho salmon and in a control group. Frequency of nonfeeding fish and fish feeding in safe and risky patches (a) Before deprivation (week 10, $n = 3$) and (b) after deprivation (week 13, $n = 4$). The data represent means and SE. * $p < .05$

(week 13), the deprived group increased, while the control group decreased, their share of the food eaten (Figure 4b). In the deprived group, 15 of 25 fish (60%) ate more than the mean share, compared with only 2 fish (8%) in the control group.

DISCUSSION

We have demonstrated experimentally that coho salmon are able to compensate for a period of low food availability with an increase in food intake after the deprivation period. In nature, variation in food availability causes many organisms to experience periods of low growth. As an adaptation to this variation, many species grow faster than normal after a period of undernutrition or famine. Such "compensatory growth" or "recovery growth" has been observed in invertebrates (Bradley et al., 1991), several species of mammals and birds (Ashworth, 1986; Thornton et al., 1979; Wilson and Osbourne,

Table 2

Mean \pm SE frequency of nonfeeding fish and fish feeding in safe and risky patches after exposure to a predator before (weeks 7 and 10, $n = 3$) and after (weeks 13 and 16, $n = 4$) a period of food deprivation, compared with fish from the control group without deprivation

	Deprived fish			Control fish		
	Nonfeeding	Safe patch	Risky patch	Nonfeeding	Safe patch	Risky patch
Week 7	77.4 \pm 7.1	14.4 \pm 3.6	8.2 \pm 4.2	75.8 \pm 5.2	12.5 \pm 4.0	11.7 \pm 2.4
Week 10	54.3 \pm 16.4	24.0 \pm 12.2	21.7 \pm 5.5	61.2 \pm 10.7	15.2 \pm 5.9	23.6 \pm 5.0
Week 13	19.3 \pm 5.8	31.7 \pm 4.2	49.1 \pm 7.8	64.5 \pm 9.2	11.7 \pm 5.0	23.8 \pm 5.5
Week 16	44.9 \pm 8.4	33.4 \pm 10.4	21.7 \pm 4.1	79.5 \pm 4.3	13.6 \pm 4.6	6.9 \pm 3.1

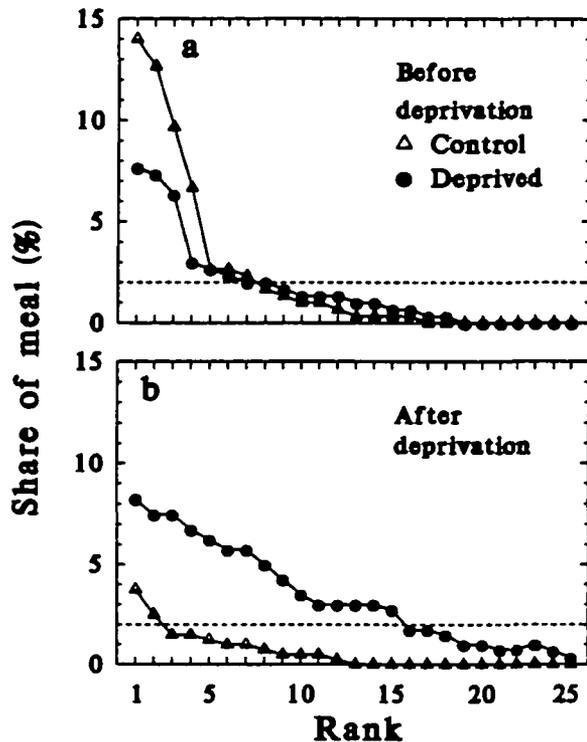


Figure 4
Individual share of meal as percentage of total food eaten by food-deprived coho salmon and by individuals in the control group: (a) Before deprivation (week 10, $n = 3$), and (b) after deprivation (week 13, $n = 4$). The dotted lines represent the mean share of the meal.

1960) and fish species, such as rainbow trout (Dobson and Holmes, 1984; Quinton and Blake, 1990; Weatherley and Gill, 1981), sockeye salmon, *Oncorhynchus nerka* (Bilton and Robins, 1973), Atlantic salmon (Mortensen and Damsgård, 1993), and Arctic charr, *Salvelinus alpinus* (Miglav and Jobling, 1989; Mortensen and Damsgård, 1993). According to these studies, the control of food intake and growth can be explained in terms of an individual "set-point" weight (Le Magnen, 1985; Mrosovsky and Sherry, 1980). Animals "remember" their nutritional history and meet all deviation from a predetermined growth trajectory by compensating as soon as food is available.

Our study demonstrates that compensatory growth involves a change in the trade-off between food intake and risk of mortality due to predation, explaining an individual's increase in food intake in terms of an increase in risk taking. The willingness to risk exposure to a predator varies between species of fish (Abrahams and Healey, 1993; Magnhagen, 1988) and with fish size (Johnsson, 1993), life history, and sex (Abrahams and Dill, 1989; Gilliam and Fraser, 1987; Huntingford et al., 1988). The behavioral flexibility we have demonstrated indicates that individual fish may temporarily alter their behavior to become risk prone. All fish in the current study had the same gastric emptiness at the time of the experiments, and the regulatory mechanism must therefore represent a metabolic hunger rather than a gastric one. These regulatory mechanisms allow fish to optimize their behavior during long-term shifts in food availability. In nature, such flexibility is selectively favored as compared with having a constant risk-prone or risk-averse behavior (Lima and Dill, 1990).

The existence of a "shy-bold" continuum as a fundamental behavioral axis has been demonstrated in several species in-

cluding humans, fish, and invertebrates, having been measured, for example, as the response to novel objects (reviewed by Wilson et al., 1994). The evolutionary implications of boldness are still poorly understood, and the existence of "high risk-high gain" phenotypes probably involves complex physiological and hormonal regulation mechanisms in addition to a genetic component. Our findings suggest that an individual's position along the shy-bold continuum is state dependent. A norm of reaction to a predator must be related to environmental conditions and factors such as hunger, sex, maturation state, and other life-history characters.

The theory of ideal free distribution (IFD) describes the spatial distribution of competitors between patches with varying suitability (Abrahams, 1989; Fretwell, 1972; Fretwell and Lucas, 1970; Parker and Sutherland, 1986). Despite the fact that assumptions in IFD models may be violated, the theory has been useful in understanding the mechanisms underlying patch choice. In the current study, we provided an identical amount of food in each patch and, accordingly, the fish distributed approximately evenly in the two patches. We observed that most of the feeding fish only fed in one of the two patches, possibly due to travel costs between patches (Godin and Keenleyside, 1984), perceptual constraints (Abrahams, 1986), or the establishment of a feeding hierarchy in each patch. In many of our experiments, however, more fish preferred the risky patch before the exposure to the predator, indicating a possible side bias.

The effects of predation risk were measured as deviations from the fish distribution before predator introduction. These deviations resulted both from an initial decrease in numbers of fish in the risky patch and a time lag before the fish habituated to the predator and began using the patch again. Before food deprivation, the recovery time in our study was approximately 60–90 min. In comparison, juvenile Atlantic salmon recovered during 2 h after a brief exposure of a predatory fish (Metcalf et al., 1987). The increasing numbers of fish in the risky patch after the period of food restriction may be explained in terms of a decrease in the time lag caused by predator inspections. The observed predator inspections were similar to those reported in other studies (e.g., Godin and Crossmann, 1994; Pitcher et al., 1986), but we were not able to evaluate whether inspecting coho had a higher food intake or spent more time in the risky patch.

Coho clearly are unequal competitors, and a small number of fish monopolized each feeding patch. Feeding hierarchies have been demonstrated in a wide range of fish species (Damsgård et al., 1997; Li and Brocksen, 1977; McCarthy et al., 1992; Metcalfe, 1986). Social hierarchies are size dependent (e.g. McCarthy et al., 1992) and dominant fish grow faster than subordinates (Abbott and Dill, 1989), but food acquisition will also be strongly affected by factors such as hunger and, according to our study, long-term energetic need. After food restriction, food-deprived fish took a greater share of meal, whereas nondeprived fish fed little or nothing. Both food-deprived and non-deprived fish were tested simultaneously. Food intake in the two groups was thus not independent of each other, and the decrease in the nondeprived group may be explained as a change in the social interactions. The aggressive behavior required to assure success in intraspecific competition may increase risk of predation (Martel and Dill, 1993); so the interaction between deprivation level, predation risk and food share is likely to be complex.

The externally visible smolt characters of the fish changed during the course of the study, suggesting that they were likely to smoltify and migrate seaward approximately at the end of the study. Hypothesized risk-taking behavior in a period leading up to an ontogenetic habitat shift, such as migration from rivers to the sea, is illustrated in Figure 5. An individual animal

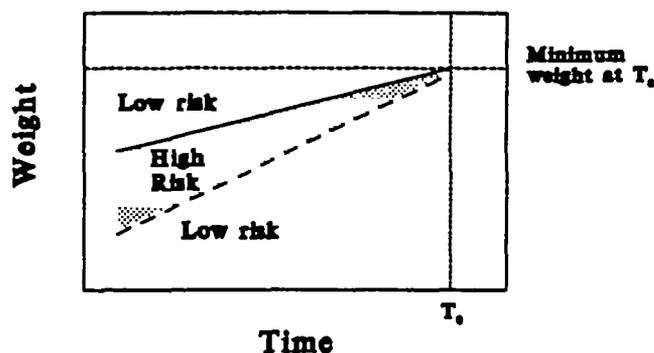


Figure 5
Graphical model of risk-taking behavior before an ontogenetic habitat shift (T_0). The solid line represents a predetermined growth trajectory. A deviation from this trajectory will cause the animal to adopt a low-risk strategy or a high-risk strategy (shaded area), depending on the weight-deviation and the time until T_0 . The dotted line represents the limit below which the animal is no longer able to reach the minimum weight by T_0 , and will adopt a low-risk strategy and exhibit temporary anorexia.

has a predetermined growth trajectory in order to reach a minimum size at the time of the habitat shift (T_0). If its weight is above this trajectory, the individual adopts in a low-risk strategy, taking few risks in the presence of a predator. On the other hand, if the individual's weight is below the set-point weight for that point in time, the animal increases its food intake by adopting a high-risk behavioral strategy until the set-point weight is reached. However, if the weight is forced well below the trajectory, the animal is no longer capable of reaching the minimum weight before T_0 , and will adopt a low-risk strategy and wait for the next opportunity to migrate. This change in the preparation for seaward migration corresponds to the E2 developmental switch proposed by Mangel (1994), and the occurrence of a window of opportunity for this decision (approximately 1 March), indicating the existence of "a point of no return." The change in risk-taking strategy in our study is in agreement with a model of seasonal foraging behavior, developed to study long-term energy requirements and fat storage in anorexic salmon (Bull et al., 1996). According to their model, fish in good condition will forage little or not at all in early winter, whereas fish in poor condition will maintain a high appetite, and the fish will respond differently to food deprivation at different times of the season, anticipating future energy requirements.

It is important to stress that compensatory trade-offs between food and risk may not be a general mechanism in fish. As pointed out by Pettersson and Brönmark (1993), many ectothermic animals are normally not in danger of starvation in a period of low food availability. A low growth rate does thus not necessarily mean that risk-taking must be increased, particularly if conditions are expected to improve in the future. Accordingly, both Atlantic salmon that would become smolts the following spring and fish that would require another year to reach the smolt stage adopted a low-risk strategy in December (Huntingford et al., 1988). Our study concerns how coho respond in the spring before an ontogenetic habitat shift, and we expect that such behavioral decisions may change during the life span of a fish. Although ectothermic animals may be risk prone during the warm growing season and risk averse the rest of the year, it is likely that endotherms will behave in an opposite fashion, taking the greatest risks during the cold season, simply because they, in contrast to fish, face a greater chance of famine and death at that time. However, a study of age-0 largemouth bass, *Micropterus salmoides*, indicated that a

failure to reach a minimum level of energy reserves before winter may be fatal to the fish (Miranda and Hubbard, 1994), suggesting that the annual changes in risk-taking behavior may be complex.

In summary, our study indicates that compensatory growth in coho salmon involves a temporary state-dependent change in the nature of the trade-off between foraging and predation risk. The fish compensated for a period of low food availability with a period of high risk taking, enabling them to return to a predetermined growth trajectory.

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