

Predators select against high growth rates and risk-taking behaviour in domestic trout populations

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Domesticated (farm) salmonid fishes display an increased willingness to accept risk while foraging, and achieve high growth rates not observed in nature. Theory predicts that elevated growth rates in domestic salmonids will result in greater risk-taking to access abundant food, but low survival in the presence of predators. In replicated whole-lake experiments, we observed that domestic trout (selected for high growth rates) took greater risks while foraging and grew faster than a wild strain. However, survival consequences for greater growth rates depended upon the predation environment. Domestic trout experienced greater survival when risk was low, but lower survival when risk was high. This suggests that animals with high intrinsic growth rates are selected against in populations with abundant predators, explaining the absence of such phenotypes in nature. This is, to our knowledge, the first large-scale field experiment to directly test this theory and simultaneously quantify the initial invasibility of domestic salmonid strains that escape into the wild from aquaculture operations, and the ecological conditions affecting their survival.

Keywords: risk-taking; growth–mortality trade-off; behaviour; predation; domestic; invasion

1. INTRODUCTION

Theoretical studies suggest that the trade-off between growth and mortality rates, mediated by prey foraging behaviour, may be a general mechanism that links individual behaviour to populations. The theory predicts that prey should select habitats that minimize the ratio of predation rate to growth rate (the μ/g hypothesis; Werner & Gilliam 1984). Under a wide variety of fitness functions, this criterion (among others) yields the general prediction that animals should increase their activity and use of risky habitats when food is scarce, thus increasing growth but also predation rates (Houston *et al.* 1993; Werner & Anholt 1993; Mangel & Stamps 2001). In other words, growth and mortality rates must be correlated through differences in foraging behaviour. Studies in the laboratory (e.g. Gilliam & Fraser 1987; Anholt & Werner 1995, 1998) and in the field (Biro *et al.* 2003a,b) support these predictions and show substantial increases in prey activity, use of risky habitats and greater predation mortality with declines in food abundance. Risk-taking behaviour probably results from constraints that force individuals to take risks, such as time constraints to reach a particular body state, or a baseline risk of predation that is independent of behaviour (Rowe & Ludwig 1991; Walters & Juanes 1993; Werner & Anholt 1993).

Artificial selection for maximum growth rates in salmonid fishes (trout and salmon) has demonstrated that domestic salmonids have a much greater capacity for growth than wild strains (Gross 1998; Devlin *et al.* 2001) owing to higher levels of growth-hormone, which stimulates appetite (Johnsson *et al.* 1996; Fleming *et al.* 2002). Given

that such elevated growth rates are physiologically possible, then why are they not observed in nature when so many fitness traits are positively correlated with body size? Given that growth and predation rates are correlated when food is limiting, we would expect predation to select against elevated appetite and the risk-taking required to achieve elevated growth rates. In this study, we quantify the behaviour, growth and survival of domestic versus wild strains of rainbow trout (*Oncorhynchus mykiss*) as a function of predation risk in a replicated whole-lake experiment. This study allows us to rigorously test, for the first time to our knowledge, the hypothesis that predators select against extreme growth rates of fishes in nature. While this sheds light on the evolution of growth rate, it also represents a rare large-scale test of the μ/g hypothesis because it manipulates behaviour directly to test for the predicted mortality effects, and is therefore a direct test of the contribution of behaviour to populations (Anholt 1997). This study also addresses the predation conditions that may affect the survival of domestic (farm) salmonids escaping from aquaculture operations. Each year, tens of thousands of domestic salmonids escape into the Pacific and Atlantic oceans from net-cage aquaculture operations, and potentially threaten wild populations (Gross 1998). Field studies have been undertaken of the reproductive behaviour and success of escapees and their hybrids (Fleming *et al.* 2000; McGinnity *et al.* 2003), and laboratory studies show a greater willingness of domestic fishes to accept risk to access food-rich habitats (e.g. Johnsson & Abrahams 1991; Johnsson *et al.* 1996). However, no large-scale field experiments yet exist that directly quantify the relative survivorship of wild and domestic strains and the ecological conditions affecting their survival. Therefore, the likelihood that escaped fishes will survive after escape and

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potentially compete and interbreed with wild fishes is not known.

Our research lakes provide distinct spatial and temporal habitats for trout that differ in the abundance of food and exposure to predators, allowing us to test for the predicted behavioural responses in response to variation in food and predation. The only significant predator on age-1+ trout in our lakes are loons (*Gavia immer*; C. Beckmann, P. A. Biro and J. R. Post, unpublished data, this study). Therefore, absence of loons from some lakes effectively constitutes predator-free conditions. Nearshore and bottom habitats may provide physical structure as a refuge from predation by loons but little plankton food (the main food source for the trout), whereas deep openwater habitats provide abundant food but lack physical structure and are risky (Post *et al.* 1999; Biro *et al.* 2003a). However, loons are visual predators, making the risk of predation lower during low-light periods at dusk. Therefore, we predicted that the elevated appetite of domestic relative to wild trout would result in an increased willingness to accept risk by foraging more in food-rich, but risky pelagic (open-water) habitats during the day. Consequently, domestic trout should grow more quickly than wild trout, but experience greater predation mortality as a cost when in the presence of predators.

2. METHODS

Trout were stocked on 6 June 2003 into five small experimental lakes (1.5 to 4 ha) located in British Columbia, Canada. Characteristics of the lakes used (K1, K2, B2, B3 and CP1) are described in detail in Biro *et al.* (2003a). The lakes contain no natural fish populations and are closed to fishing. Domestic and wild strains of rainbow trout were obtained from the Fraser Valley Trout Hatchery (Abbotsford, British Columbia), raised to a common average length (mean length of 15 cm) and sorted into two non-overlapping size-classes by evenly splitting the length-frequency distribution. Fins were clipped to identify strain (adipose fin, a vestigial fin or no clip) and size-class (left or right ventral fin). Each strain was stocked at a density of 165 trout ha⁻¹ into each lake. The domestic strain of trout has a higher intrinsic growth rate than the wild strain when reared under identical conditions, achieving greater growth via greater appetite (K. Scheer, Fraser Valley Trout Hatchery, unpublished data). Because the two strains are reared identically, variation in growth and survival rates should be driven primarily by genetic variation between these strains (Johnsson & Abrahams 1991). By examining differences in performance between the two phenotypes within a single lake, we were able to control for biotic and abiotic variation among lakes and obtain a more powerful experiment. If the wild strain is in some way 'domesticated' slightly during rearing, then this would make our comparisons of the two strains conservative.

We assessed use of the food-rich but risky pelagic habitat by trout with floating experimental gillnets with graded mesh sizes (see Biro *et al.* 2003a) within two weeks of stocking. We conducted only a single netting trial for habitat use to minimize killing fishes that had survived, because vulnerability to gillnets (and therefore mortality) increases with body size (Biro *et al.* 2003a). Rainbow trout of the size used in this experiment primarily eat zooplankton, which is most abundant in the open-water, or pelagic, habitat (Post *et al.* 1999). We assumed that the pelagic habitat was the most risky based on previous work showing avoidance of this habitat by trout (Post *et al.* 1999), the absence

of any physical structure into which they could escape, and focal animal observations of loons which indicated that loons initiate their foraging dives in the pelagic habitat (C. Beckmann, unpublished data). We surveyed the loon lakes over 6 days immediately after stocking, 5 days during the netting trial in the latter half of June, and 4 days in mid-July. In total, 58 survey visits were conducted whereby 15 min were spent surveying each lake with binoculars for the presence of loons to assess variation in loon presence among lakes. Lakes B2 and B3 never had loons present (Biro *et al.* 2003c), and so represent our control zero-risk treatment. Lakes K1 (14 out of 16 survey visits) and K2 (10 out of 19 surveys) frequently had one, but never two loons on each lake. Lake CP1 had frequent loon visitation, whereby on 10 out of 23 survey visits two loons were present and on 21 out of 23 surveys one or more loons were present. Thus, because of the relatively limited data, lakes K1 and K2 were classified as intermediate risk, lying between the zero-risk lakes and lake CP1, which frequently had two loons on the lake. Therefore, to be conservative, we treated loon presence as a categorical variable rather than continuous.

We estimated autumn population size and mean mass from 22 to 27 September by lethal gillnet sampling in all habitats for five consecutive nights with a standardized effort (Post *et al.* 1999; Biro *et al.* 2003a). One week before autumn netting, we stocked two size-classes each of domestic and wild trout into all lakes to estimate the proportion of each group recaptured over the five nights of netting, and size dependence in recapture probability (maxillary and ventral fin clips were used). We used these values (domestic = 0.36 and wild = 0.45, $p < 0.05$, no size effect, $p > 0.05$) to correct our total catch and obtain an estimate of the number of survivors (accounting for netting mortality during the summer). It is possible to obtain survivorship values of greater than unity when applying such correction factors to the total catch (Post *et al.* 1999), but this bias will not affect conclusions drawn from estimates among experimental treatments. Instantaneous growth rate was calculated according to Post *et al.* (1999) using the vulnerability-corrected mean mass for each cohort in September.

All analyses were conducted with general linear models, using type-III likelihood ratio (LR) tests for the significance of effects, which are χ^2 distributed. Least-squares means were also reported to determine which treatment levels differed from one another, or differed from zero, again using LR tests. Analyses of catch rates and proportions of domestic trout caught were done as repeated measures (day and dust samples) on log- (standardized catch rate +1) and arcsine-square root (ASR)-transformed data. Each lake represented a single datum in the analyses of growth and survival, which was expressed as the percentage difference relative to the domestic strain within each lake. Analyses were on the raw data, and normal errors were assumed as they varied both positive and negative. Estimation of the absolute proportion of trout surviving included two size-classes of trout for each strain to yield $n = 20$ and was carried out on ASR-transformed data. Analyses focusing on the differences in growth and survival between strains within each lake and size-class yielded a total sample of $n = 10$. Behavioural data were pooled into only two risk categories because of zero catch rates in one lake (CP1, frequented by two loons), which prevented us from calculating the proportion of domestic trout in the catch.

3. RESULTS

We observed that all trout (domestic and wild) used the food-rich pelagic habitat to a greater extent in lakes without loons than in lakes with loons ($\chi^2_1 = 3.82$, $p = 0.05$; figure

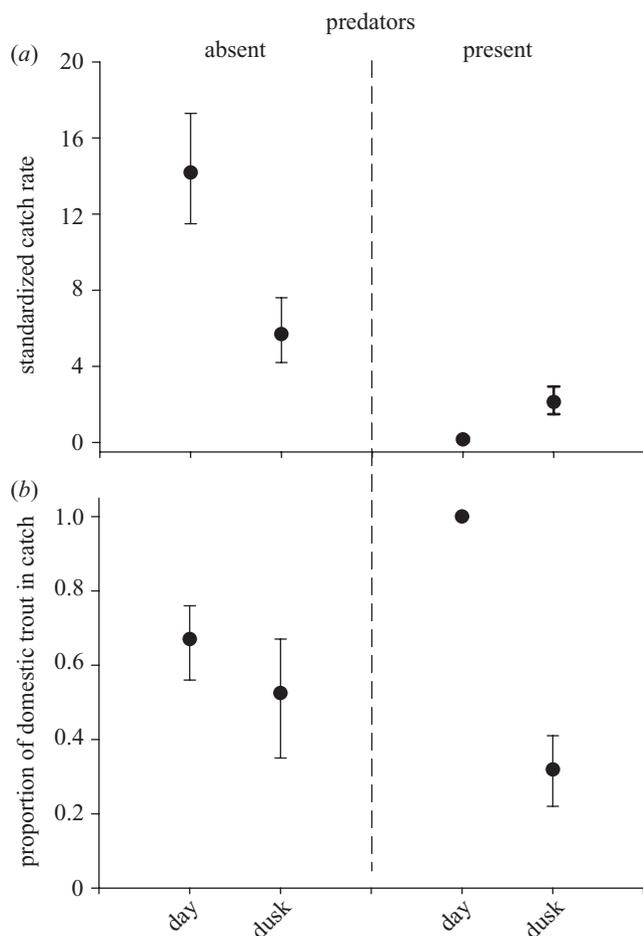


Figure 1. Trout use of the food-rich, but risky open-water (pelagic) habitat in relation to predation risk and time of day. (a) Standardized catch rate (catch net⁻¹ hr⁻¹ ha⁻¹ of lake area) of domestic and wild trout combined and, (b) proportion of domestic trout in the catch in the risky habitat. Back-transformed least-squares means and associated standard errors (s.e.) are shown; *n* = 2 lakes in each treatment.

1a). Catch rates declined from day to dusk in lakes without loons but increased from day to dusk in lakes with loons (predator × time interaction: $\chi^2_1 = 4.19, p < 0.05$; figure 1a). In particular, there was almost no daytime use of the pelagic habitat by trout in lakes with loons, but moderate use at dusk. Differences in mean catch rates between treatments all differed from each other (all $p < 0.03$). With loon predators present, the few trout present in the pelagic habitat by day were all domestic, whereas the proportion of domestic trout declined dramatically at dusk indicating higher crepuscular activity of wild trout (figure 1b). However, the effects of loon presence, time of day and the interaction were not significant (χ^2 *p*'s = 0.2, 0.08 and 0.09, respectively). Nonetheless, contrasts of the least-squares means indicated that exclusive daytime use of the pelagic habitat by domestic trout in lakes with loons differed from low domestic use at dusk, and domestic usage in lakes without loons ($p < 0.05$).

Overall survival of trout in the absence of predators did not differ from 100% (least-squares estimate = 1.07, s.e. = 0.1, $p < 0.05$). However, predator presence reduced trout survival by 62% (i.e. less than half as many survivors;

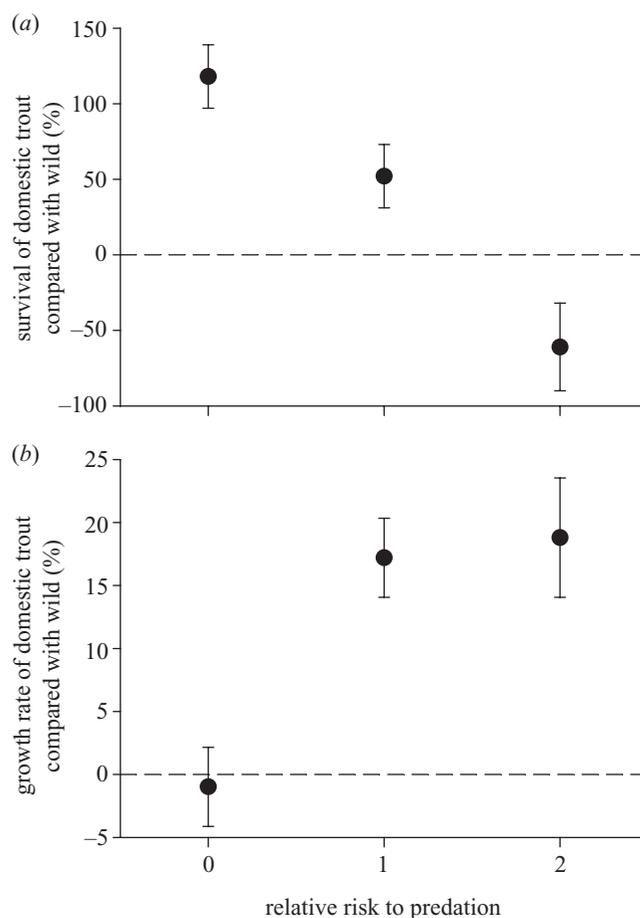


Figure 2. Percentage differences in growth rate and survival of domestic relative to wild trout in relation to level of predation risk. (a) Survival and (b) growth rate advantages of domestic trout over the wild (domestic-wild/wild). Although the relative risk value of 2 corresponds to greater loon presence than 1 (see § 2), we nonetheless treated risk as a categorical variable with three levels in our analyses to be conservative, given that surveys for loon presence were not frequent enough to justify expressing loon presence as a continuous variable. Least-squares means and associated s.e. are shown.

$\chi^2_1 = 16, p < 0.0001$). There were survival consequences for greater use of the food-rich and risky habitat by domestic trout, but this depended upon variation in predator visitation among lakes (figure 2a). Domestic trout experienced greater survival than wild trout in the absence of predators, marginally greater survival at intermediate risk, and significantly lower survival at the highest risk level ($\chi^2_2 = 5.5, p < 0.02$; figure 2a). Size at stocking and the interaction had no effect (both $p > 0.09$). Survival differences in each risk category were all significantly different from zero ($p < 0.04$).

Relative risk of predation had a significant effect on the growth advantage of domestic trout ($\chi^2_2 = 11, p < 0.005$), whereas size at stocking and the interaction had no effect ($\chi^2_1 = 0.8$ and $\chi^2_2 = 3.7$, respectively, both $p > 0.15$; figure 2b). In the absence of predators, growth of domestic trout was equal to that of the wild trout (i.e. difference did not differ from zero: $p > 0.75$). By contrast, growth rates of domestic trout were on average nearly 20% greater than

wild trout in lakes with predators present (no difference among treatment levels with risk, $p > 0.75$).

4. DISCUSSION

This experiment has shown that rainbow trout fish that have been artificially selected for high growth rates respond to predators in an appropriate manner, but are more willing to accept risk than the wild strain to gain access to abundant food resources. Consequently, greater growth rates are achieved, but with a mortality cost that is related to the level of predation risk. With increases in predation risk, there was a corresponding decline in survival advantage and an increase in growth advantage for the domestic trout. These results are consistent with theory which predicts that growing quickly and minimizing mortality represents a trade-off that is mediated through foraging behaviour (Werner & Gilliam 1984; Gilliam & Fraser 1987; Houston *et al.* 1993; Werner & Anholt 1993).

Domestication has proved that salmonid fishes are physiologically capable of elevated growth rates that are not observed in nature (Gross 1998; Devlin *et al.* 2001). The absence of such elevated growth rates in nature (and the fitness benefits associated with greater body size) would suggest strong selection against such traits in nature. We have shown here that there is strong selection against elevated growth rates through predation, which is mediated by risky foraging behaviour required to achieve rapid growth when food is limiting. In other words, behaviourally mediated trade-offs between growth and mortality rates explain the positive correlation between growth and mortality rates predicted by theory. It was surprising that the domestic fish did not outgrow the wild in predator-free lakes. However, it may have been impossible for the domestic fish to realize their full growth potential while feeding primarily upon plankton, as compared with feeding in the hatchery. It was also interesting to observe that the domestic fish, while less risk-averse than wild fish, did show appropriate antipredator behaviour (reduced use of the pelagic habitat) despite no experience with predators for at least 25 generations within the hatchery system. We speculate that the large variation in growth potential that is commonly observed within fish populations is an adaptation that permits individuals with low appetite to survive high predation regimes, and those with high appetite to take advantage of situations when predator populations decline. However, theory also predicts that trade-offs between growth and mortality can lead to maintenance of individual variation in growth rates that yield similar lifetime fitness (Mangel & Stamps 2001).

Studies of the trade-off between growth and mortality rates usually focus on variation among populations, not within populations (Arendt 1997; Mangel & Stamps 2001). Here, we use two phenotypes of the same species that differ genetically in their growth rates, which in turn affects their behaviour and contrasts their relative performance within populations that differ in predation intensity. Consequently, the mortality consequences of risk-taking behaviour, and the associated elevated growth rates as a function of predation risk observed here, provide rare and highly realistic support for theories that predict such trade-offs between growth and mortality (Werner & Gilliam 1984; Houston *et al.* 1993; Werner & Anholt 1993). In

addition, the direct manipulation of behaviour in this experiment provides a direct link between risk-taking behaviour and mortality, and the contribution of behaviour to populations (Anholt 1997). This study adds to an accumulating body of empirical evidence suggesting that the behaviour of individuals while under risk of predation may be a key determinant of population and community dynamics (e.g. Turner & Mittelbach 1990; Huang & Sih 1991; Werner & Anholt 1996; Beckerman *et al.* 1997; Lima 1998; Peckarsky & McIntosh 1998; Schmitz 1998; Biro *et al.* 2003a,b,c). Previous tests of the contribution of behaviour to populations usually involved indirect manipulations of prey behaviour through variations in food and/or predator abundance (Anholt 1997). While this is a valid approach, it also has problems. For instance, augmenting food abundance for prey fish in small lakes by fertilization can affect water clarity (reducing predator-prey encounter rates) and also increase food for predators that share food resources with prey fish (Biro *et al.* 2003a). These spin-off effects can confound, at least in part, the lower predation mortality observed at low food abundance and thus overestimate the contribution of risk-taking behaviour to mortality (Biro *et al.* 2003a).

We have identified in our study the predation conditions that affect survival of farmed salmonids that escape into wild, and the behavioural mechanism that underlies it. Combining a simple behavioural theory with knowledge of the life-history attributes of this potential invader provided an *a priori* basis from which to predict the likelihood of initial invasion. Our data indicate that the probability of initial invasion of wild populations by growth-enhanced fishes will be greatest when predators are few or absent, but low when predation risk is relatively higher. Hence, the likelihood of invasion is dependent upon an interaction between animal phenotype and the biotic environment. We predict that, in situations where there are few or no predators, significant numbers of domestic survivors will survive, compete and hybridize with wild fish. Wild stocks are likely to dwindle in this scenario (Muir & Howard 1999), owing to the low fitness of hybrids (Fleming *et al.* 2000; McGinnity *et al.* 2003). When predators are common, however, few domestic fish will survive and then compete and mate with wild fish, their progeny will also have high mortality, and invasion will be less likely. Thus, the level of hybridization and natural selection against them (predation environment) will determine the degree to which domestic fishes will invade. Because many commercially exploited fish species are also major predators (Christensen *et al.* 2003), a consequence of commercial exploitation may be increased vulnerability of ecosystems to invasion. Our study represents, to our knowledge, the first field experiment to directly quantify the likelihood of escapees surviving to potentially reproduce after release, and the conditions that affect their survival. These results should also apply to the potential risk of growth hormone transgenic salmon, which are currently being considered for net-cage aquaculture use, and to bio-invasions in general where an invading species has high intrinsic growth rates relative to native species. We believe, as do others (Kareiva *et al.* 1996; Rissler *et al.* 2000), that a mechanistic understanding of the initial stages of an invasion is critical to predicting whether exotic

species or genetic strains establish themselves, but that this understanding is currently lacking.

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REFERENCES

- Anholt, B. R. 1997 How should we test for the role of behaviour in population dynamics. *Evol. Ecol.* **11**, 633–640.
- Anholt, B. R. & Werner, E. E. 1995 Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* **76**, 2230–2234.
- Anholt, B. R. & Werner, E. E. 1998 Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. *Evol. Ecol.* **12**, 729–738.
- Arendt, J. D. 1997 Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* **72**, 149–177.
- Beckerman, A. P., Uriarte, M. & Schmitz, O. J. 1997 Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc. Natl Acad. Sci. USA* **94**, 10735–10738.
- Biro, P. A., Post, J. R. & Parkinson, E. A. 2003a From individuals to populations: risk-taking by prey fish mediates mortality in whole-system experiments. *Ecology* **84**, 2419–2431.
- Biro, P. A., Post, J. R. & Parkinson, E. A. 2003b Population consequences of behaviour: density-dependent risk-taking mediates mortality in young fish cohorts. *J. Anim. Ecol.* **72**, 546–555.
- Biro, P. A., Post, J. R. & Parkinson, E. A. 2003c Population consequences of a predator-induced habitat shift by trout in whole-lake experiments. *Ecology* **84**, 691–700.
- Christensen, V., Guenette, S., Heymans, J. J., Walters, C. J., Watson, R., Zeller, D. & Pauly, D. 2003 Hundred-year decline of North Atlantic predatory fishes. *Fish Fisheries* **4**, 1–24.
- Devlin, R. H., Giagi, C. A., Yesaki, T. Y., Smailus, D. E. & Byatt, J. C. 2001 Growth of domesticated transgenic fish. *Nature* **409**, 781–782.
- Fleming, I. A., Hindar, K., Mjølnerod, I. B., Johsson, B., Balstad, T. & Lamberg, A. 2000 Lifetime success and interactions of farm salmon invading a native population. *Proc. R. Soc. Lond. B* **267**, 1517–1523. (doi:10.1098/rspb.2000.1173)
- Fleming, I. A., Agustsson, T., Finstad, B., Johsson, J. I. & Björnsson, B. T. 2002 Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). *Can. J. Fisheries Aquat. Sci.* **59**, 1323–1330.
- Gilliam, J. F. & Fraser, D. F. 1987 Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* **68**, 1856–1862.
- Gross, M. R. 1998 One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. *Can. J. Fisheries Aquatic Sci.* **55**, 131–144.
- Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993 General results concerning the trade-off between gaining energy and avoiding predation. *Phil. Trans. R. Soc. Lond. B* **341**, 375–397.
- Huang, C. & Sih, A. 1991 Experimental studies on direct and indirect interactions in a three trophic-level system. *Oecologia* **85**, 530–536.
- Johansson, J. I. & Abrahams, M. V. 1991 Domestication increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. *Can. J. Fisheries Aquat. Sci.* **48**, 243–247.
- Johansson, J. I., Petersson, E., Jonsson, E., Björnsson, B. T. & Jarvi, T. 1996 Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Can. J. Fisheries Aquat. Sci.* **53**, 1546–1554.
- Kareiva, P., Parker, I. M. & Pascual, M. 1996 Can we use experiments and models in predicting the invasiveness of genetically engineered organisms? *Ecology* **77**, 1670–1675.
- Lima, S. L. 1998 Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Study Behav.* **27**, 215–290.
- McGinnity, P. (and 11 others) 2003 Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proc. R. Soc. Lond. B* **270**, 2443–2450. (doi:10.1098/rspb.2003.2520)
- Mangel, M. & Stamps, J. 2001 Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evol. Ecol. Res.* **3**, 583–593.
- Muir, W. M. & Howard, R. D. 1999 Possible ecological risks of transgenic organism release when transgenes affect mating success: sexual selection and the Trojan gene hypothesis. *Proc. Natl Acad. Sci. USA* **96**, 13853–13856.
- Peckarsky, B. L. & McIntosh, A. R. 1998 Fitness and community consequences of predator-induced changes in mayfly behavior. *Oecologia* **113**, 565–576.
- Post, J. R., Parkinson, E. A. & Johnston, N. T. 1999 Density-dependent processes in structured fish populations: assessment of interaction strengths in whole-lake experiments. *Ecol. Monogr.* **69**, 155–175.
- Rissler, L. J., Barber, A. M. & Wilbur, H. M. 2000 Spatial and behavioral interactions between a native and introduced salamander species. *Behav. Ecol. Sociobiol.* **48**, 61–68.
- Rowe, L. & Ludwig, D. 1991 Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* **72**, 413–427.
- Schmitz, O. J. 1998 Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.* **151**, 327–342.
- Turner, A. M. & Mittelbach, G. G. 1990 Predator avoidance and community structure: interactions among piscivores, planktivores and plankton. *Ecology* **71**, 2241–2254.
- Walters, C. J. & Juanes, F. 1993 Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can. J. Fisheries Aquat. Sci.* **50**, 2058–2070.
- Werner, E. E. & Anholt, B. R. 1993 Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* **142**, 242–272.
- Werner, E. E. & Anholt, B. R. 1996 Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* **77**, 157–169.
- Werner, E. E. & Gilliam, J. F. 1984 The ontogenetic niche shift and species interactions in size-structured populations. *A. Rev. Ecol. Syst.* **15**, 393–425.