

Density-dependent mortality is mediated by foraging activity for prey fish in whole-lake experiments

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Summary

1. Whereas the effects of density-dependent growth and survival on population dynamics are well-known, mechanisms that give rise to density dependence in animal populations are not well understood. We tested the hypothesis that the trade-off between growth and mortality rates is mediated by foraging activity and habitat use. Thus, if depletion of food by prey is density-dependent, and leads to greater foraging activity and risky habitat use, then visibility and encounter rates with predators must also increase.

2. We tested this hypothesis by experimentally manipulating the density of young rainbow trout (*Oncorhynchus mykiss*) at risk of cannibalism, in a replicated single-factor experiment using eight small lakes, during an entire growing season.

3. We found no evidence for density-dependent depletion of daphnid food in the near-shore refuge where most age-0 trout resided. Nonetheless, the proportion of time spent moving by individual age-0 trout, the proportion of individuals continuously active, and use of deeper habitats was greater in high density populations than in low density populations. Differences in food abundance among lakes had no effect on measures of activity or habitat use.

4. Mortality of age-0 trout over the growing season was higher in high density populations, and in lakes with lower daphnid food abundance. Therefore, population-level mortality of age-0 trout is linked to greater activity and use of risky habitats by individuals at high densities. We suspect that food resources were depleted at small spatial and temporal scales not detected by our plankton sampling in the high density treatment, because food-dependent activity and habitat use by age-0 trout occurs in our lakes when food abundance is experimentally manipulated (Biro, Post & Parkinson, in press).

Key-words: activity, behaviour, mortality, population consequences, trade-off.

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Introduction

A great deal of the history of population ecology has focused on understanding the causes of density-dependent growth and survival in animal populations (Sinclair 1989). The focus on density-dependent processes stems from their significant impacts on population regulation and population dynamics. For instance, density-dependent growth depression results in time-delays which can de-stabilize population dynamics whereas density-dependent mortality affects dynamics immediately and tends to stabilize

populations (Sinclair 1989). However, the processes that generate density-dependent growth and mortality in animal populations are less well understood. Several authors note that investigating behavioural trade-offs of prey at risk of predation may be key to understanding population-level patterns in prey growth and survival as a function of density, but they are currently poorly described under field conditions (e.g. Walters & Juanes 1993; Lima & Zollner 1996; Sutherland 1996; Fryxell & Lundberg 1997; Lima 1998; Luttberg & Schmitz 2000; Schmitz 2001).

The trade-off between growth and mortality rates, mediated by foraging activity, may be a viable behavioural mechanism to explain density-dependent mortality. If prey animals increase activity in response

to lower food abundance resulting from density-dependent depletion of food, then this may lead directly to higher mortality due to increased visibility and encounter rates with predators (Anholt & Werner 1995, 1998; Biro, Post & Parkinson, in press). For instance, animals that feed on relatively sedentary prey encounter more prey by searching longer and faster (e.g. Gerritsen & Strickler 1977; Norberg 1977; Gendron & Staddon 1983) but increases in activity also increase the chance of detection and attack by predators (Curio 1976; Taylor 1984; Skelly 1994; citations in Martel & Dill 1995). In fact, small increases in movement rate can cause disproportionately large increases in the likelihood of predation (e.g. Martel & Dill 1995). Therefore, we can predict that animals should reduce their foraging effort when food is abundant (McNamara & Houston 1992, 1994; Abrams 1993; Werner & Anholt 1993). Although extensive evidence shows that diverse animal taxa adjust activity rates according to food abundance and predation risk, the population-level consequences of these trade-offs in natural systems remains largely unknown (Werner & Anholt 1993; reviewed in Lima 1998). However, we have recently shown that activity- and habitat use-mediated trade-offs between growth and mortality exist at the whole-lake scale for age-0 rainbow trout (*Oncorhynchus mykiss* Mitchell), and that young trout take greater risks in low food lakes and consequently experience greater predation mortality than trout in high food lakes (Biro *et al.*, in press).

This study implemented a replicated whole-lake experiment that manipulated the density of age-0 trout to test for evidence of (i) competitive food depletion by age-0 trout at high density, (ii) resultant increases in foraging activity and risky habitat use, and (iii) increased predation mortality. Our study system is ideal for testing this hypothesis for several reasons. First, age-0 trout feed on relatively sedentary daphnid plankton that represents more than 90% of their diet (Landry 1997; Landry, Post & Parkinson 1999; Post, Parkinson & Johnston 1999). Therefore, in order for age-0 trout to increase encounter rates with prey and increase growth they must increase activity (e.g. Grant & Noakes 1987; McLaughlin, Grant & Kramer 1994; Biro & Ridgway 1995) move to deeper habitats where daphnid food is more abundant (Landry 1997; Landry *et al.* 1999; this study), or both (Biro *et al.*, in press). However, the likelihood of young trout being detected and eaten by predators increases with activity (e.g. Dill & Fraser 1984; Metcalfe, Huntingford & Thorpe 1987; Martel & Dill 1995) and with the use of deeper habitats (Landry *et al.* 1999; Post, Parkinson & Johnston 1998; Post *et al.* 1999), and consequently greater activity and use of risky habitats is linked to greater predation mortality (Biro *et al.*, in press). Second, age-0 trout confine their habitat use to shallow, food-poor habitats, due to the presence of predatory adult trout in more productive deep habitats (Biro, Post & Parkinson 2003; this confinement should result in depletion of

food resources, given that their growth is food-dependent (Post *et al.* 1999). Fourth, these are closed systems (i.e. discrete and independent replicates), and fish populations are created entirely by stocking, which allows rigorous evaluation of growth and mortality at the population-level.

The present study tests whether the recently demonstrated trade-off between growth and mortality rates, mediated by behaviour of age-0 trout (Biro *et al.*, in press), provides a mechanism for understanding density-dependent mortality in young fish cohorts. Although we previously observed growth-dependent mortality in age-0 trout cohorts, neither growth nor mortality was density-dependent (Post *et al.* 1999). However, Post *et al.* (1999) did not test for potentially confounding year- and food-abundance effects which affected their ability to detect density effects. This study controls for year effects, competitive and predatory effects of adult trout, tests for food effects, and provides behavioural data to relate to population-level growth and survival estimates that is rarely done at this natural spatio-temporal scale.

Methods

EXPERIMENTAL DESIGN AND LAKES

We conducted a replicated single factor experiment using eight lakes in which we manipulated the density of age-0 trout (1500 ha⁻¹ vs. 15 000 ha⁻¹) while keeping constant the consumptive force of predatory adult rainbow trout. Density and size-structure of adult trout varied somewhat among lakes according to whether trout had survived winter anoxia. To ensure that adult trout did not differentially deplete plankton food available to age-0 trout (i.e. they are not obligate piscivores), we kept constant their consumptive potential (see Walters & Post 1993 and Post *et al.* 1999). We achieved this through a combination of spring netting to reduce densities of survivors and stocking of age-1 trout, to yield a summed (fork length)² of adult trout in each lake of 50 000 cm² (see details below). Numerical densities of adult trout varied between 250 and 400 ha⁻¹ among lakes. This small variation in adult trout density and size-structure had no effects on activity, growth or survival of age-0 trout in this experiment ($P \gg 0.05$, in all cases). In fact, variation in adult trout density much wider than in the present experiment also has no effect on age-0 trout mortality (Post *et al.* 1999). However, age-0 trout growth and survival are markedly higher when adult trout are absent from the system (Biro *et al.* 2003). In other words, adult trout appear to impose high mortality on age-0 trout whether there are few or many adult trout, at least across the range from 50 ha⁻¹ to 2000 ha⁻¹ (Post *et al.* 1999). Although piscivorous birds do frequent our lakes, we have found that they consume only a few percent of the age-0 trout over the growing season when at high density (Biro *et al.* 2003; C. Beckmann, University of Calgary,

Table 1. Lakes used, treatment allocation and morphometric statistics of the experimental lakes (n.a. indicates unavailable data)

Lake	Density treatment	Abbreviation	Surface area (ha)	Maximum depth (m)	Mean depth (m)
Bluey Pothole 1	Low	BPH 1	1.9	7	2.3
Kentucky Pothole	Low	KPH	1.9	9	3.2
Bluey Pothole 3	Low	BPH 3	1.4	6	n.a.
Cigar Lake	Low	CIG	3.9	9	4.2
Crater Pothole 1	High	CPH 1	4.1	18	10
Renee's Pothole	High	RPH	3.6	10	n.a.
Smoke Lake	High	SM	2.0	8	3.7
Bluey Pothole 2	High	BPH 2	1.4	6	2.8

unpublished data). Lastly, starvation mortality of age-0 trout has never been observed during the growing season in our lakes (Post *et al.* 1999; Biro *et al.*, in press, 2003).

We used eight lakes located within 5 km of each other in south-central British Columbia (BC), Canada (49°50'–49°56' N; 120°33'–120°34' W). The lakes are 1.4–4.1 ha in size, relatively shallow (maximum depth of 7–15 m), and have 4–6 m of pelagic habitat above the thermocline (Table 1). Deeper waters were anoxic during summer stratification and thus unavailable to fish. The littoral habitat in the lakes consisted of aquatic macrophytes (primarily *Chara* sp. and *Myriophyllum* sp.) located in small patches, open sediment, gravel, rocks, woody debris and fallen trees. The lakes are mesotrophic, based on phosphorus concentrations and total dissolved solids (Post *et al.* 1999).

FISH STOCKS

Rainbow trout were raised at the Fraser Valley Trout Hatchery (BC Fisheries Branch) using eggs collected from wild populations in Tzenzaicut Lake, BC (for age-1+ trout) and Tunkwa Lake (age-0 trout). Age-0 trout were stocked within several days of completely absorbing their yolk at a mean length of 27 mm and mean mass of 0.146 g ($n = 200$). Stocking occurred on 10 July 1998, about the time when they emerge in local wild populations. Replicate batch samples of age-0 trout were weighed and all individuals were counted to obtain a mass-density which was used to estimate the number to be stocked. Age-0 trout dispersed around the entire littoral zone of each lake and fed actively within 24 h of stocking.

Age-1 trout were stocked on 6 June at a mean fork length (and mass) of 11.2 cm (18.3 g, $n = 300$). The size of survivors from previous experiments ranged from 15 to 45 cm in late May. By about 20 July, the mean size of age-0 trout in all populations was 32 mm (range = 24–40 mm, CV = 0.26, $n = 513$) based on beach seine catches in the nearshore littoral zone, and the mean size of stocked age-1 adults was 200 mm (range = 120–280 mm, CV = 0.40, $n = 197$). The mean size of larger adult predators is not available because we captured only a few individuals during three netting trials through the

season. The mean size of age-0 trout in all populations was 40 mm in early August (range = 27–56 mm, CV = 1.03, $n = 274$) and 52 mm in late August (range = 30–73 mm, CV = 0.73, $n = 674$).

ESTIMATION OF POPULATION ABUNDANCE

In order to re-set adult trout densities from previous experiments, all lakes were netted with a constant effort for five net-nights in May 1998. Nets were set mid-day and retrieved the following day. If no fish were caught in the first net-night, we concluded that there were no fish present (the result of a winterkill); this was confirmed during fall netting. Lakes containing survivors were netted for an additional 5–10 net-nights using 25% more gillnet. Netting ceased when the daily catch fell below five fish. The number of fish captured over the first five net-nights was used to estimate population abundance, less the additional number removed during subsequent netting (netting and abundance estimation details below).

We used lethal gillnet sampling from 1–25 October to estimate fall population size. Gillnet densities were standardized among lakes based on lake area and ranged from 400 m² ha⁻¹ night⁻¹ to 500 m² ha⁻¹ night⁻¹, following the identical netting effort and protocol used by Post *et al.* (1999) in these same lakes. We set sinking and floating experimental nets with graded mesh from 13 mm to 89 mm (stretched mesh size) for five nights in all habitats. Nets were set during the day and retrieved approximately 24 h later. The summed catch over five nights of netting was adjusted to account for the size-dependent probability of capturing fish in gillnets. We used a mean capture probability model that expresses the proportion of fish of a particular size that are captured over the five nights of netting. This function describes a steeply increasing function between 50 mm and 125 mm in length and then a constant capture probability for fish > 125 mm in length (Biro *et al.* 2003).

BEHAVIOUR OF INDIVIDUAL AGE-0 TROUT

Activity of age-0 trout was determined by direct observation of individuals in the littoral zone during mid-July,

late July and mid-August. Two lakes were sampled each day during each sampling period to minimize variation due to time or ontogenetic effects. We observed them while snorkelling during July when the young could be approached closely. Later, we observed fish from the shoreline (with the aid of polarized glasses) because the young became too wary to approach while snorkelling. A single observer (P.A.B.) observed focal animals between 10.00 and 16.30 hours during bright, relatively calm conditions. Individual fish were randomly selected for observation upon arrival at an observation location. We tried to observe a minimum of 30 individuals per lake on each visit, sampled from 4 to 10 locations evenly spaced around the shoreline. Fish were observed for 2.5 min for relatively sedentary fish, but often much less for highly active individuals that swam at speeds up to 40 cm s^{-1} . Each observation period began by noting the position of the fish and then the total time spent moving was measured using a stopwatch until the end of the observation, when the fish's final position was noted. Movement was defined as a displacement > 0.5 body length. Swimming velocity was estimated by the maximum displacement distance of each fish divided by the duration of the observation. Maximum displacement refers to the linear distance between the two farthest positions visited by the fish estimated by summing together the linear segments of the fish's path along and around the shore and shoreline debris (Biro, Ridgway & Noakes 1997). Maximum displacement is a good estimate of velocity for individuals swimming continuously because they invariably swam in a single direction.

We initially assessed the degree to which age-0 trout used shallow vs. deeper littoral habitats by direct snorkelling observation (13–16 and 26–29 July), and later used gillnets when fish became less approachable. Snorkelling observations involved an observer (P.A.B.) swimming very slowly from deep water (c. 5–6 m) towards shore counting all fish present within a 2.5-m wide strip transect. Observed fish were counted into four depth classes, ≤ 0.5 m, 0.5–1 m, 1–2 m and 2–3 m. Three meters was the maximum depth to which age-0 fish could be detected reliably on the bottom in all lakes and viewing conditions. At times, the lake bottom could be seen to depths of up to 5 m and any observations of young trout were noted. On average, 12 transects were sampled each lake-day (range = 8–18). Unfortunately, we could not estimate the density of age-0 trout equally well in all habitats due to visual obstructions in shallow habitats, and estimating numbers was exceedingly difficult in high density lakes where more > 50 individuals could be seen in a single depth class in shallow water. In addition, fish appeared to be more wary in shallow than in deep habitats, which introduced a negative bias to density estimates in shallow water. However, we could accurately determine whether young trout were present in all habitats and therefore confined our analysis to these binary data.

Gillnet sampling in August involved daytime sampling with gillnets of different heights to sample from 0.5 m to 5 m depth. However, few fish were captured with this method and none were caught at > 3 m depth, even though snorkelling observations clearly indicated their presence. Consequently, we did not use this gillnet data.

EVALUATION OF FOOD ABUNDANCE

To quantify food abundance potentially available to age-0 trout, we sampled zooplankton from six permanent sampling sites in the nearshore and deep littoral habitats, and also at the lake's centre. Zooplankton were sampled bi-monthly from 13 July until 30 August in all lakes, over a 4 day sampling period. Additional pelagic samples were taken 22–25 September. Zooplankton were also sampled during the 4 days prior to stocking age-0 trout in order to detect depletion of daphnid prey by young trout. We used a 12-L Schindler trap as its small size (height = 0.3 m) allowed sampling in shallow water. Owing to the small volume of the trap, two 12-L samples were taken adjacent to each another (separated by approximately 1.5 m) and pooled. Nearshore littoral samples were taken at 0.50–0.75 m of water. The deep littoral habitat was sampled at 1 m depth along the 2-m depth contour. The pelagic habitat was sampled at 1, 3, and 5 m depths which represents the depth region available to trout because the lakes were generally anoxic below 5 m. The six nearshore, six deep littoral and three pelagic samples of zooplankton were combined to yield a single sample for each of the three habitats for each lake-day. Analysis involved randomly sub-sampling at least 300 zooplankton which were identified to family or genus and counted. The first 30 individuals of a given taxon encountered were measured with an eyepiece micrometer to the nearest 0.04 mm. Biomass was estimated using density estimates and mean individual mass obtained from genus-specific regressions of length vs. wet-mass (Post 1984). We report only daphnid biomass estimates because $> 90\%$ of age-0 trout diet is comprised of daphnia (Landry 1997; Landry *et al.* 1999).

DISTRIBUTION OF PREDATORS

The spatial distribution of large and small adults among populations was assessed by sampling the nearshore littoral zone and offshore pelagic areas of each lake with gillnets (described above). Lakes were sampled in late July, late August and late September. On each visit, one sinking and one floating gillnet were simultaneously set adjacent to one another in the littoral and pelagic zones; the same net sites were used for the three trials. The sinking gillnet (2.4 m deep) was set in broad s-shaped curves parallel to shore, such that it sampled depths ranging from 0.5 m to 4 m. The floating gillnet (6 m deep) was set along the centreline of the lake, adjacent to the sinking net. Nets were left in the water until

either it appeared that at least 30 individuals had been captured or 2 hours had elapsed, in order to sample two lakes each day. Sampling duration varied with the size of the lake, adult fish density and the variable sampling effort among lakes. The catch in each net was corrected for net area and proportional netting effort in each lake. In addition, we noted whether adult trout were captured in portions of the gillnet shallower than 1.5 m in order to estimate spatial variation in predation risk within lakes.

STATISTICAL ANALYSIS

Working at the scale of whole-systems, with few replicates, results in the loss of statistical power and an increased type II error rate using traditional parametric statistics. Therefore, for analysis of activity, growth and mortality, where each datum represents an estimate for a single lake, we used maximum likelihood techniques and AIC statistics to find the most likely model given the data rather than relax the traditional (and arbitrary) level of significance of $\alpha = 0.05$ (Hilborn & Mangel 1997; Burnham & Anderson 1998). AIC statistics allow one to rank competing models against one another and take into account parsimony by penalizing model fit (the log-likelihood) by the number of parameters (k), where $AIC = -2(\log\text{-likelihood}) + 2k$ (Burnham & Anderson 1998). The model with the smallest value of AIC thus represents the most likely model, given the data; all other competing models can then be ranked relative to the most likely model, where $\Delta_i = AIC_{\text{observed}} - AIC_{\text{minimum}}$. Therefore, the most likely model has $\Delta_i = 0$. The null hypothesis in such an analysis is $Y = \text{constant}$, which is identical to the null hypothesis in regression analysis. We did not use AICc statistics (Burnham & Anderson 1998) because this selection criterion is highly conservative, especially given our small sample size. In addition to our likelihood analyses, we also present parametric R^2 values to express effect sizes for likely models. Age-0 trout mortality, the proportion of time spent moving by young trout, and the proportion of each cohort moving continuously, were analysed assuming normally distributed errors on arcsine-square-root transformed data. Mean autumn mass was log-transformed. We used PROC GENMOD for maximum-likelihood analyses and PROC GLM to obtain R^2 values (SAS v. 8).

The probability of observing age-0 trout in different depth-habitats were modelled according to a repeated measures model by assuming normally distributed errors on logit transformed data (i.e. $\log_e(p/1-p)$) using PROC MIXED (SAS v. 8), because this particular procedure in SAS is not affected by frequent values of either 0 or 1 that are present in our data. To meet the assumptions of standard one-way and repeated-measures ANOVAs used in all other analyses, we arcsine-square root or \log_{10} transformed independent variables expressed as proportions or continuous, respectively.

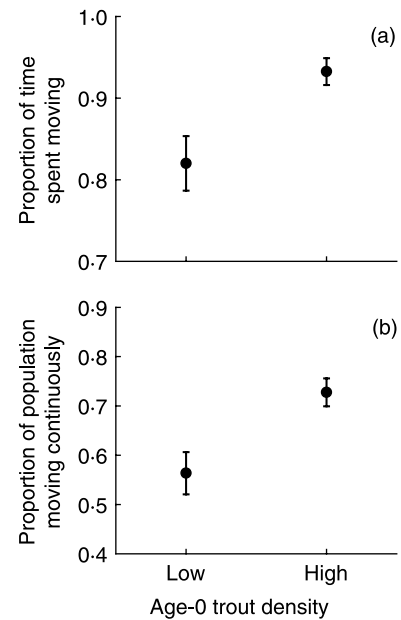


Fig. 1. (a) Proportion of time spent moving by age-0 individuals and (b) proportion of cohort swimming continuously, in relation to their own density. Plot shows mean (\pm SE) of raw data aggregated across sampling trials ($n = 4$ lakes in each treatment).

Results

ACTIVITY AND HABITAT USE OF AGE-0 TROUT

Age-0 trout were more active foragers in high density populations than in low density populations, consistent with our prediction for increased foraging effort in response to depleting food resources (Fig. 1). Young trout spent a greater proportion of time moving in high density populations than in low density populations (Table 2, model 2, $R^2 = 0.63$; Fig. 1a). Differences in daphnid food abundance among lakes had no effect on activity, because models which included food as predictors were not likely (Table 2, models 3–5).

A relatively high proportion of age-0 trout swam continuously in all populations (Fig. 2). However, a greater proportion of age-0 trout swam continuously in high density populations (Table 2, model 2, $R^2 = 0.63$; Fig. 1b). As in the previous analysis, models that included food abundance were not likely (Table 2, models 3–5). Age-0 trout that swam continuously had high and variable swimming velocity that was not related to density or to food abundance in any way (Table 2, models 2–5). Continuously active age-0 trout therefore swam at a mean speed of 0.134 m s^{-1} (95% CI = $0.112\text{--}0.155 \text{ m s}^{-1}$).

Age-0 trout used only those areas less than 2 m deep in low density populations, whereas trout were frequently observed as deep as 3 m (Fig. 3) and less frequently as deep as 5 m in high density populations (pers. obs.). The likelihood of observing young trout was higher in high density populations ($F_{1,4} = 23.0$,

Table 2. Goodness-of-fit measures for models predicting measures of age-0 trout activity, growth and mortality. Each row represents a single model where β_0 represents a constant, D represents age-0 trout density, and f represents food abundance, estimated by nearshore daphnid biomass. Model selection criterion AIC, and parametric R^2 for each model is given, for $n = 8$ lakes. Smaller values of the AIC indicate more likely models, given the data. AIC values in bold indicates the most likely model explaining variation in mortality of age-0 trout. Values for Δ_i express the difference in AIC between each model and the most likely model

Model	Proportion of time spent moving			Proportion of population continuously active			Velocity of continuously active individuals			Growth			Mortality		
	AIC	Δ_i	R^2	AIC	Δ_i	R^2	AIC	Δ_i	R^2	AIC	Δ_i	R^2	AIC	Δ_i	R^2
1. β_0	-10.5	6	0	-10.8	6	0	-27.1	0	0	3.30	3	0	-3.28	2	0
2. $\beta_0 + D$	-16.5	0	0.63	-16.9	0	0.63	-25.1	2	0.01	0.46	1	0.45	-3.30	2	0.22
3. $\beta_0 + D + f$	-15.9	1	0.68	-15.0	2	0.64	-24.0	3	0.11	-0.06	0	0.60	-5.44	0	0.54
4. $\beta_0 + D + f + D \times f$	-14.0	3	0.70	-13.1	4	0.65	-22.0	5	0.12	1.48	2	0.62	-4.32	1	0.58
5. $\beta_0 + f$	-10.8	6	0.04	-10.8	6	0.01	-25.9	1	0.10	3.9	4	0.16	-4.48	1	0.33

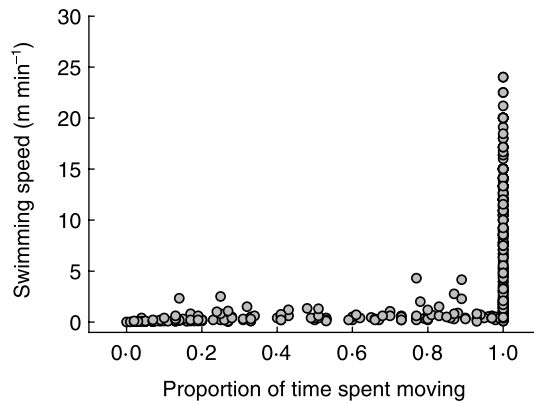


Fig. 2. Swimming speed of individual age-0 trout in relation to the proportion of time spent moving. Data is aggregated across sampling trials and age-0 density treatments ($n = 455$).

$P < 0.01$) and fish generally avoided deeper habitats in all populations ($F_{3,12} = 8.8$, $P < 0.005$). However, there was greater avoidance of deep habitats in low density populations (density \times depth interaction effect, $F_{3,12} = 5.2$, $P < 0.02$; Fig. 3) and it was the complete absence of young trout from 2 m to 3 m depths in low density populations that accounts for the interaction (Fig. 3). Date had no effect on the likelihood of observing age-0 trout nor did any of the remaining possible main or interaction effects, including food abundance ($P > 0.17$ in all cases).

DISTRIBUTION AND ABUNDANCE OF FOOD RESOURCES AND ADULT TROUT PREDATORS

The increased activity rates and use of risky habitats by age-0 trout in high density populations probably represent a trade-off between growth and mortality rates, given that deeper habitats have greater food abundance, but also greater likelihood of encountering adult trout. Within individual lakes, mean daphnid biomass was approximately seven-fold greater in the deep-littoral habitat than in the nearshore littoral zone (paired t -test; mean difference = $1130 \mu\text{g L}^{-1}$, $t_7 = 2.8$,

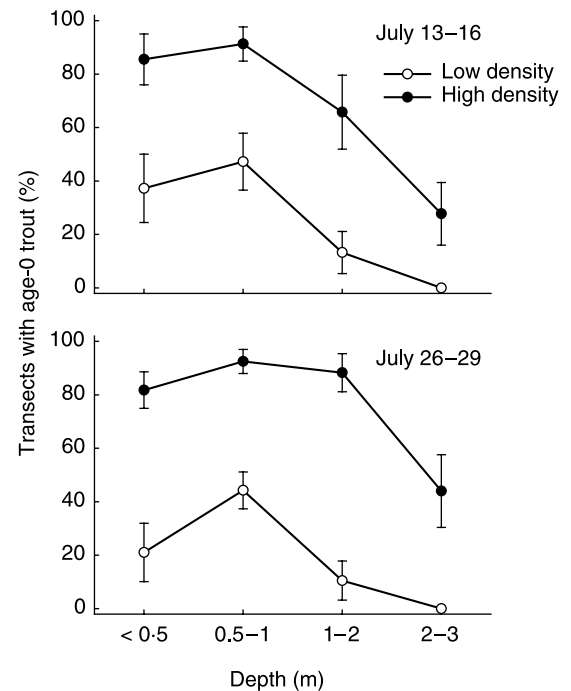


Fig. 3. Percentage of snorkelling transects with age-0 trout present, in relation to water depth, density and sampling date. Plot shows mean (\pm SE) of raw data ($n = 4$ lakes for each data point).

$P < 0.03$), and daphnid biomass in the pelagic zone was twice that in the deep-littoral habitat (mean difference = $1004 \mu\text{g L}^{-1}$, $t_6 = 4.5$, $P < 0.005$).

Given the small variation in adult trout numerical density, it was not surprising that catch rates of adult trout in the littoral zone did not differ among populations nor were there any temporal trends within lakes (repeated measures ANOVA, $P > 0.38$ in all cases). We noted that no adult trout were captured in areas < 1.5 m deep, confirming that risk to predation varies spatially within the littoral zone and suggesting that the two shallowest habitat categories (Fig. 3) represent at least partial refuge from predation. The mean (\pm SE) proportion of the total catch within lakes, in late July

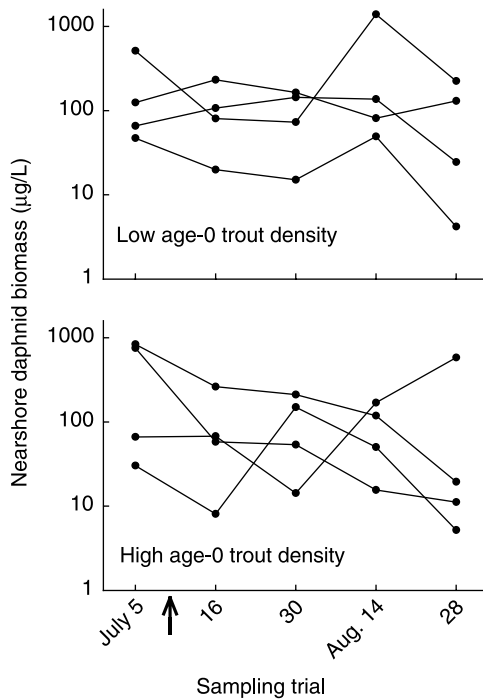


Fig. 4. Biomass of nearshore daphnid food in eight experimental lakes in relation to sampling date and density of age-0 trout. Each time series represents one lake. Arrow indicates when age-0 trout were stocked into the lakes.

and late August, in areas < 1.5 m deep, 1.5–4 m deep and pelagic habitats, was 0, 0.46 (0.06) and 0.54 (0.06), respectively.

DID AGE-0 TROUT DEplete FOOD AT HIGH DENSITY?

Abundance of daphnid food in the nearshore littoral zone (where most age-0 trout resided) varied considerably among lakes, but did not vary significantly with the density of trout from one week before stocking to late August (repeated measures ANOVA, all effects $P > 0.3$ for each habitat; Fig. 4). However, daphnid biomass did increase in two of four lakes in low density treatments, in contrast to high density lakes where none increased and three of four lakes declined by at least 50% by the second sampling period (Fig. 4). Differences in nearshore daphnid abundance between lakes were largely the result of inherent differences in lake productivity, rather than differential predation rates by adult trout, because daphnid biomass did not vary with adult trout density or size-structure in the nearshore littoral, deep-littoral or pelagic habitats (repeated measures ANOVA, all effects $P > 0.3$ for each habitat).

MORTALITY CONSEQUENCES OF DENSITY-DEPENDENT ACTIVITY

Mortality of age-0 trout over the growing season was greater in high density populations, and in lakes with

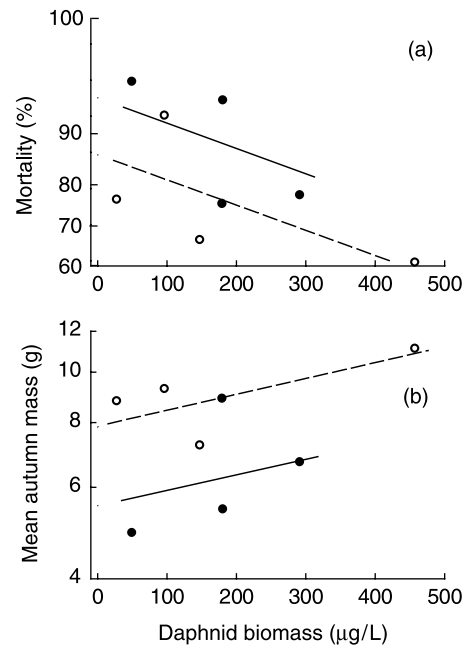


Fig. 5. (a) Percentage mortality estimates and (b) autumn mean mass of age-0 trout in eight experimental lakes as a function of their own density, and biomass of nearshore daphnid food. Solid (high density) and dashed (low density) lines represent the predictions of the best-fit models predicting mortality and autumn mass (Table 2).

less food, consistent with our prediction that depleting food resources at high fish density will result in greater risk-taking behaviour and greater susceptibility to predation (Fig. 5a, Table 2, model 3). This model (model 3) was the most likely of the set of models (models 1–5) that include density, food abundance or both to predict mortality (Table 2, model 3, $R^2 = 0.54$). The addition of daphnid biomass to the model containing density increased the proportion of mortality variance explained from 0.22 to 0.54, indicating that differences in lake productivity has an relatively large effect on mortality.

Mean autumn mass of age-0 trout was lower in high density populations and in lakes with less food, consistent with the prediction for lower growth in high density populations owing to depleted food and greater activity, the strength of which depending on lake productivity (Fig. 5b; Table 2, model 3; $R^2 = 0.60$).

Discussion

We predicted that age-0 trout at high density would reduce the abundance of food resources in shallow and safer habitats, less food would result in compensating increases in their activity and use of riskier habitats, leading to increased susceptibility to adult trout, and greater predation mortality. We expected this process because age-0 trout growth is food-dependent in our lakes (Post *et al.* 1999), they mostly inhabit the shallowest habitats, and their activity rates and habitat use affect food intake rates and vulnerability to predation

(Landry 1997; Post *et al.* 1998; Biro *et al.*, in press, 2003). As expected, most age-0 trout resided in the shallowest habitats that was relatively safe, but food-poor. Activity and use of risky habitats by age-0 trout was greater in high density populations, which is consistent with the prediction for increased foraging effort with declining food resources. Differences in average food abundance between lakes, a potential surrogate for lake productivity, had no effect on activity or habitat use. However, age-0 trout did not significantly reduce nearshore food resources at the whole-lake scale when at high density, although daphnid biomass declined by at least 50% shortly after fish stocking in three of four high density lakes. Population-level mortality was greater in populations at high density, and in lakes with lower food abundance, consistent with our expectations for food-dependent risk-taking behaviour. Mean autumn mass of age-0 trout was similarly affected by density, and by differences in average food abundance between lakes. In aggregate, we have shown that (i) age-0 trout increase activity and use of risky habitats when at high density, (ii) this increased foraging effort probably provides access to more food, but at greater predation cost, and (iii) mortality is density- and food-dependent, and therefore linked to density-dependent behavioural variation that increases susceptibility to predation.

Greater activity and use of risky habitats by age-0 trout were likely to be the result of lower food abundance caused by a combination of food depletion and inherent differences in productivity among lakes. First, density-dependent increases in foraging activity and greater use of risky but productive habitats, and corresponding density-dependent predation mortality, is consistent with the prediction that increased foraging effort is a response to declining or depleted food resources. Second, it is unlikely that age-0 trout would increase activity and use of risky habitats if it were not a response to lower food abundance, given the substantial mortality consequences of such risky behaviours that we observed. Indeed, there is a significant reduction in activity, and therefore mortality, of young trout when food abundance is experimentally augmented by whole-lake fertilization (Biro *et al.*, in press). Third, there was quantitative (but not statistically significant) evidence that food was in fact being depleted in high density lakes. Daphnid biomass declined by at least 50% immediately after fish stocking in three of four high density lakes, whereas food resources increased in half of the low density lakes. Therefore, our failure to demonstrate statistically significant declines in food abundance in the high density treatment probably results from a combination of our small sample size ($n = 8$), relatively large inherent differences in food abundance among lakes, and plankton sampling that was conducted at a temporal and spatial scale that was likely to be insufficient to detect depletion that can occur at the scale of habitat patches. Similarly, we feel that our failure to detect an effect of mean food abundance on measures of behaviour probably result

from small behavioural samples from within populations that display extremely wide variation in activity (Fig. 3), few lakes, and the fact that we did not experimentally manipulate food abundance directly in our lakes.

We did not test for the direct effect of mean autumn mass (a surrogate for seasonal growth rate) on the mortality of age-0 trout because we have previously shown that differences in mean autumn mass among lakes arises from food-dependent growth late in the growing season when fish are no longer highly vulnerable to predation (Biro *et al.*, in press). This is not say that size-dependent risk of predation is irrelevant, but rather that differences in mortality among populations is due to risk-taking behaviour *per se* by individuals attempting to maintain high growth rates to minimize time spent in vulnerable size classes. Lower autumn mass of age-0 trout at high density is likely to have resulted from a combination of competitive effects and the increased metabolic costs of higher activity, which can be large for young salmonid fishes (Trudel & Boisclair 1996). The positive effect of food abundance on autumn mass, that is in addition to the negative density effect, suggests that differences in lake productivity affect changes in the strength of density effects and confirms that age-0 trout growth is food-limited. More importantly, variation in autumn mass among populations may also have longer-term effects on the likelihood of overwinter survival, and therefore another tier of population regulation that is in addition to that occurring during the growing season. Lower mass in autumn is likely to increase overwinter mortality given the close association between size, lipid concentration and overwinter mortality (Post & Parkinson 2001). If so, we can expect that differences in mortality between high density (lower growth) and low density (higher growth) populations to become even greater after their first winter, resulting in even stronger density-dependent population regulation.

Theory (e.g. Werner & Anholt 1993) and experiments (Anholt & Werner 1995, 1998; Biro *et al.*, in press) suggest that behaviourally mediated trade-offs between growth and mortality rates may be a general mechanism to explain mortality in prey populations. If so, animals which deplete their food resources in a density-dependent manner are also expected to increase activity rates and use of risky habitats resulting in greater predation mortality. As such, this trade-off presents a novel mechanism for the mortality of prey populations (Anholt & Werner 1995, 1998). This study appears to be the first experimental test of whether such trade-offs might also explain density-dependent mortality in animal populations, and provides evidence in support of it. This mechanism for density-dependent mortality has the potential to be a powerful and very general predictor of mortality in prey populations given that most animals are prey for others, and many animals are active foragers. We suspect the failure to detect density effects in cohorts of age-0 trout in earlier experiments (Post *et al.* 1999), was due to confounding variation in

food abundance among lakes, and among years within a lake, that were not accounted for in their statistical models.

Our results are consistent with previous studies on young lake-dwelling salmonids, showing high activity rates and low overt aggression, which conclude that the territorial model of population regulation for stream resident salmonids does not hold in lakes (Biro & Ridgway 1995; Biro *et al.* 1997). Our results parallel those for young stream salmonid fishes in which territorial behaviour can explain density-dependent growth and emigration and/or mortality from stream reaches (Elliott 1989, 1990a,b). In streams, territorial individuals remain in a reach and increase territory size over time to maintain intake rates, whereas non-territorial individuals are forced out, and presumably emigrate or die. So, survival at the scale of a stream reach is dependent on behaviour. In lakes, as closed systems, emigration is of course not possible, but we did see evidence of increased activity and habitat expansion into riskier habitats at high density which was linked to increased mortality. It is not clear how the behaviours play out at the population level in stream systems because the fate of the emigrants remains unknown. So, it may be that density-dependent individual behaviours in young salmonids, although different in detail in lotic and lentic systems, act through growth and survival in similar ways to result in density compensation. This should lead to reduced interannual recruitment variability and population regulation in salmonids.

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