Ontogeny of energy allocation reveals selective pressure promoting risk-taking behaviour in young fish cohorts

Peter A. Biro[1,2,*], John R. Post[1] and Mark V. Abrahams[2]

[1]Division of Ecology, Department of Biological Sciences, University of Calgary, 2500 University Drive, NW Calgary, Alberta, Canada T2N 1N4
[2]Department of Zoology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2

Given limited food, prey fishes in a temperate climate must take risks to acquire sufficient reserves for winter and/or to outgrow vulnerability to predation. However, how can we distinguish which selective pressure promotes risk-taking when larger body size is always beneficial? To address this question, we examined patterns of energy allocation in populations of age-0 trout to determine if greater risk-taking corresponds with energy allocation to lipids or to somatic growth. Trout achieved maximum growth rates in all lakes and allocated nearly all of their acquired energy to somatic growth when small in early summer. However, trout in low-food lakes took greater risks to achieve this maximal growth, and therefore incurred high mortality. By late summer, age-0 trout allocated considerable energy to lipids and used previously risky habitats in all lakes. These results indicate that: (i) the size-dependent risk of predation (which is independent of behaviour) promotes risk-taking behaviour of age-0 trout to increase growth and minimize time spent in vulnerable sizes; and (ii) the physiology of energy allocation and behaviour interact to mediate growth/mortality trade-offs for young animals at risk of predation and starvation.

Keywords: predation; trade-off; lipid; starvation; behaviour

1. INTRODUCTION

Theory investigating behavioural trade-offs between growth and mortality rates incorporate background mortality (risk that is independent of behaviour), and/or a critical level of body reserves to be reached by a certain time, which promotes risk-taking in model prey (Ludwig & Rowe 1990; Rowe & Ludwig 1991; Werner & Anholt 1993; McNamara & Houston 1994). Given that state-dependent risk-taking is well documented for diverse taxa (Lima 1998), it seems reasonable to expect that one or both of these factors are what drive the evolution of risk-taking in prey. For instance, models (e.g. Ludwig & Rowe 1990; Rowe & Ludwig 1991; Houston et al. 1993; Werner & Anholt 1993; Clark 1994) and laboratory experiments (Johansson & Rowe 1999; Anholt et al. 2000; Johansson et al. 2001) show that prey take greater risks as the window of time to reach a particular state becomes smaller. Understanding the selective pressures promoting risk-taking behaviour is important given that variation in risk-taking within and among prey populations is widespread (Lima 1998) and has large population-level mortality consequences (Biro et al. 2003a,c, 2004a).

If risk-taking is promoted by either background predation risk or a time constraint to reach a particular state (or both), then how do we know which is present (or at least dominant) in nature? For example, prey living in temperate climates are probably affected by size-dependent predation risk in the short term, a short growing season to accumulate fat reserves for winter, and limited opportunity to store energy for reproduction. Examination of growth

rates relative to risk-taking behaviour does not help distinguish among these potential selective pressures in nature since larger body size confers an advantage in all cases. However, maximizing somatic growth to lower predation risk, and accumulating fat reserves for overwinter survival, are strategies that are in conflict with one another owing to the high energetic content of lipids (Brett & Groves 1979). Therefore, as the benefit of somatic energy allocation declines over time (risk declines with size), the benefit of storing lipids will correspondingly increase. The predicted switch point to storing lipids will depend upon the relative strength of predation risk, length of growing season and winter severity. Indeed, at least two field studies have shown that young fishes at risk of predation and winter starvation allocate little energy to lipids when very small, and allocate substantial energy to lipids when larger (Post & Parkinson 2001; Hurst & Conover 2003). If adaptive, these patterns suggest that size-related risk of predation is the predominant selective pressure when fishes are small, and risk of winter starvation the predominant selective pressure when fishes are larger, during their first year of life.

Examining energy allocation in relation to behaviour has the potential to reveal the selective pressure(s) that promote differences in risk-taking within and among prey populations, and reveal the interaction between physiology and behaviour in affecting growth/predation risk trade-offs. Dynamic models predict that energy resources should be allocated where selection pressures are highest, or allocated equally among body subsystems where pressures are equal (Perrin & Sibly 1993). Although it is easy to imagine how behaviourally mediated growth/predation
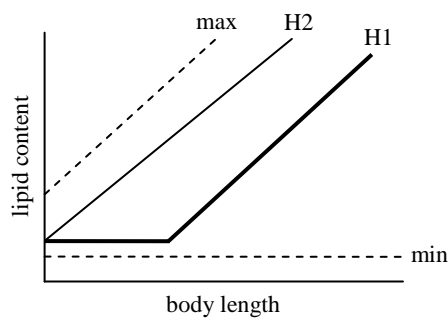
* Author for correspondence (pbiro@ucalgary.ca).

Figure 1. Hypothesized relationships between whole-body lipid content and body length for age-0 trout responding only to the risk of lipid-dependent overwinter starvation mortality (H2) or to the size-dependent risk of predation when small and vulnerable, and risk of overwinter starvation when larger (H1). Maximum and minimum lipid contents in relation to body size bound the range of possible outcomes for fishes' lipid content with body size (actual observed minimum and maximum lipid allometries are shown in figure 3).

risk trade-offs interact with an animals' physiology and life history, few studies link them together in a single study (Stoks & McPeek 2003). Further, energy allocation is frequently studied as a trade-off between gonads and soma, but rarely as a trade-off between soma and energy storage as lipids (Metcalfe et al. 2002). In fact, we know of no study that has directly related patterns of energy allocation with prey behaviour in order to understand the proximate basis for risk-taking behaviour, and its population-level effects on mortality (Walters & Juanes 1993; Werner & Anholt 1993; Biro et al. 2003a,c, 2004a).

In this study, we examine the ontogeny of energy allocation of individual age-0 rainbow trout (Oncho-rhynchus mykiss) in relation to known differences in food-dependent risk-taking among populations, using fish samples collected from that same study (Biro et al. 2003a). This allowed us to (i) infer the selective pressure promoting risk-taking behaviour, and (ii) examine the interaction between their physiology and behaviour in mediating the growth/predation risk trade-off. Previous research has shown that size-dependent risk of cannibalism (Johnsson 1993; Landry 1997; Parkinson et al. 2004) and lipid-dependent risk of overwinter survival (Biro et al. 2004b) are both strong selective pressures affecting mortality of young trout in our lakes. We predicted that size-dependent (background) predation risk is the selective pressure promoting rapid growth and increased risk-taking behaviour in these experimental prey fish populations. We based this expectation upon the rapid increase in survival of young trout with size (Parkinson et al. 2004). If so, trout should allocate the maximum energy to somatic growth, within the constraint of a minimum lipid concentration needed for survival (first segment of hypothesis 1 (H1), figure 1). Later in the season, when fishes are larger (and risk is diminished), trout should allocate significant energy to lipids in anticipation of winter (second segment of H1, figure 1). Under H1, the two segments represent fish samples obtained early and later in the season. We did not expect energy allometries of age-0 trout to differ according to food abundance given that observed growth rates were equal between food treatments (Biro et al. 2003a) and the expectation of maximum growth rates during much of the summer (Biro et al. 2003b). Conversely, if risk-taking by

trout is promoted only by the need to accumulate lipid reserves for winter survival, then trout should allocate significant energy to lipids throughout the season. If so, a single lipid allometry should describe allocation of energy to lipids, where the slope will depend upon winter severity (e.g. Schultz & Conover 1997) and be bounded by a maximum lipid allometry (H2, figure 1).

2. METHODS

Samples of age-0 trout for lipid analysis were obtained from an earlier experiment that manipulated food abundance available to age-0 trout by fertilizing four of nine lakes (located in British Columbia, Canada) in order to manipulate their foraging effort (risk-taking; Biro et al. 2003a). Specifically, we examined the allometry of the ratio of storage/structure (lipid mass/lipid-free dry mass) and lipid concentration (% lipid) and tested for the effects of date, food treatment and interactions. Changes in the allometry of storage/structure and lipid content (i.e. an interaction between body size and date) indicate changes in energy allocation between energy storage and somatic growth (Post & Parkinson 2001).

The experiment was conducted over an entire growing season from 12 July 1999 to early October that year. However, we sampled age-0 trout during the last week of July (18 days post stocking) and again the last week of August (48 days post stocking). We chose this timing for obtaining samples for two reasons. First, this timing brackets the period when antipredator behaviour is greatest (late July when fishes are less than 45 mm in fork length; FL) and a period when predation risk is much reduced owing to their rapid growth rates and larger body size (late August when fishes are 55–100 mm; see Landry 1997; Biro et al. 2003b; Parkinson et al. 2004). In fact, when age-0 trout exceed 90 mm FL, they often inhabit the riskiest habitat, the pelagic zone (Biro et al. 2003b). Second, the timing corresponded with behavioural observations on activity rates and habitat use of age-0 trout between refuge and high-risk, high-reward habitats (Biro et al. 2003a).

Initial density of age-0 rainbow trout was set at 15 000 ha^{-1} and the density of adult rainbow trout predators was set between 300 and 365 ha^{-1} for all lakes. Age-0 trout were raised from eggs obtained from wild trout in nearby Tunkwa Lake (similar elevation and latitude to the experimental lakes) and were stocked within several days of completely absorbing their yolk on 12 July 1999, at a mean length and mass of 27 mm and 0.152 g (n ≈ 200). Trout predators were 10–35 cm in length when stocked in early June. The small variation in adult trout density and size structure among lakes has no effect on the behaviour of age-0 trout (Biro et al. 2003a), beyond the avoidance of pelagic habitats when adult trout are present (Biro et al. 2003b). Details of lake preparation, stocking, fertilization and study site descriptions are given in Biro et al. (2003a). Whole-lake fertilization was successful in creating significant differences in daphnid plankton abundance (Biro et al. 2003a), which are the primary food item for age-0 trout (Landry 1997; Post et al. 1999).

We sampled age-0 trout for analysis of lipid concentration and to estimate growth rates in all lakes during a 4 day period, 18 and 48 days post stocking, using a 20 m

long beach seine made of 4 mm mesh. We sampled fishes from all habitats where they resided (0.5–4 m depth; details in Biro et al. 2003a). We sampled fishes from several locations around the shoreline of each lake that typically yielded a total of not less than 1000 fishes; 200 individuals were then randomly subsampled for length and mass measurement, and 100 individuals were frozen for lipid analysis. We compared the observed mean masses with the maximum predicted mean mass for our cohorts using a relationship developed for hatchery rainbow trout fed to satiation (Iwama & Tautz 1981) by using the mean observed littoral water temperatures for each growth period from temperature data loggers placed at 0.75 m depth.

Age-0 trout for lipid analysis were placed on ice immediately after capture, and frozen within 8 h. We used a stratified random sampling procedure to select 30 fishes from each lake and date for analysis. We used 5 mm FL size bins to ensure an even distribution of fish lengths across the range observed in that particular lake at the time of sampling. A methanol and chloroform procedure were used to extract lipids (details of this methodology are outlined in Post & Parkinson 2001; Biro et al. 2004b). The methodology requires approximately 0.3–0.5 g of powdered fishes, which necessitated pooling up to 10 of the smallest individual trout to make a single composite sample. Therefore, the lipid concentration of fishes less than 55 mm FL represents an integrated sample of between 2 and 10 individuals, yielding a single datum (sample), with an average FL of the particular individuals in that size bin. Analytical error in lipid determination is low, with an average coefficient of variation of less than 5% for repeated measurements taken from the same sample (Post & Parkinson 2001).

We assessed the allometry of total wet mass, whole-body lipid concentration (g lipid per g wet mass), and the ratio of storage to structure (g lipid per g lipid-free dry mass), using general linear models with lake as a repeated measures effect. To satisfy normality assumptions, the percentage of lipid and the storage/structure ratio were arcsine-square root transformed, and wet mass was log transformed. Fork length was log transformed to ensure linearity. Analysis was implemented using PROC MIXED in SAS whereby we first identified the most probable covariance structure for the repeated measurements within lakes, using maximum likelihood and AICc statistics (Burnham & Anderson 1998) (SAS Institute, v. 8.1). We then fixed the covariance structure in the analysis and conducted type III sums of squares tests of significance of each experimental factor (fork length, date and food treatment), and all possible interaction terms in a fully saturated model. In light of the fact that data points under 55 mm FL represented between 2 and 10 individual fishes, we weighted each sample by the number of fishes comprising each. This approach is conservative in the sense that it accounts for the number of fishes in each datum but does not inflate the degrees of freedom in the analysis.

3. RESULTS
(a) Patterns of risk-taking and growth
In late July, age-0 trout used the shallow refuge habitat almost exclusively in fertilized (high-food) lakes, whereas
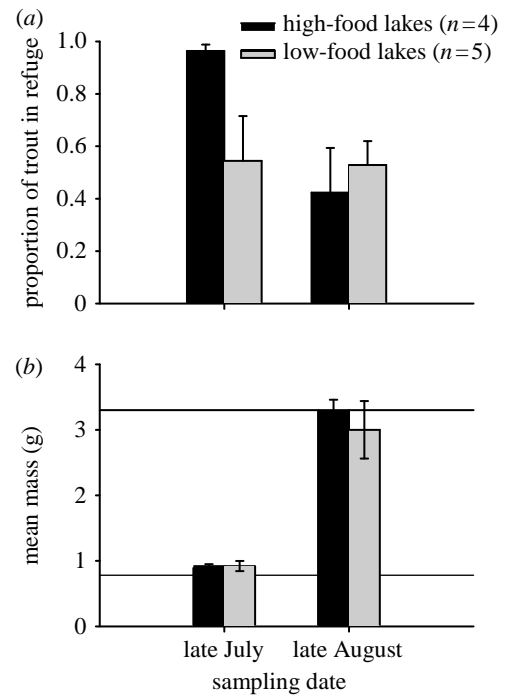

Figure 2. (a) Relative use of the refuge habitat (areas less than 1.5 m depth) by age-0 trout and (b) population mean mass of age-0 trout, in relation to food treatment and sampling date. Each datum represents the response observed in a single lake ($n = 9$ lakes). Mean ($\pm$s.e.m.) for each is shown. Refuge use by age-0 trout is significantly higher in high-food lakes than in low-food lakes in late July; all other differences in refuge use and mean mass between food treatments are not different ($p > 0.05$; data redrawn from Biro et al. 2003a). Food-dependent differences in habitat use by age-0 trout are similarly accompanied by food-dependent differences in individual activity rates (see Biro et al. 2003a). Areas less than 1.5 m deep represent refuges because adult rainbow trout are typically only observed in deeper habitats (Biro et al. 2003a). Thin horizontal lines in (b) represent the predicted maximum mean mass of rainbow trout (see §2).

trout in unfertilized (low-food) lakes used refuge habitats significantly less (figure 2a; Biro et al. 2003a). By late August, use of refuge habitats by age-0 trout was relatively low and did not vary among lakes differing in food abundance (figure 2a). Age-0 trout grew rapidly over the summer, although the mean mass of age-0 trout did not differ between food treatments in July or August (figure 2b; Biro et al. 2003a). Trout had growth rates just above the predicted maximum growth rates for rainbow trout in late July, and equal to the maximum in late August (figure 2b). Age-0 trout had mean instantaneous growth rates in wet mass of 10% day^{-1} over the first 18 day in the lake, and 6.3% day^{-1} during the subsequent 30 day interval. Individual age-0 trout accumulated mass at a constant rate with increases in fork length, regardless of date, food treatment or possible interaction effects (effect of fork length: $F_{1,296} = 18\,436$, $p < 0.0001$; other effects: all $p > 0.10$).

(b) Patterns of energy allocation
Age-0 trout allocated energy to soma in late July (when trout used risky habitats more in low-food lakes) and to lipids in late August (when trout used risky habitats equally in high- and low-food lakes; figure 3). Lipid concentration of age-0 trout increased at a low rate with
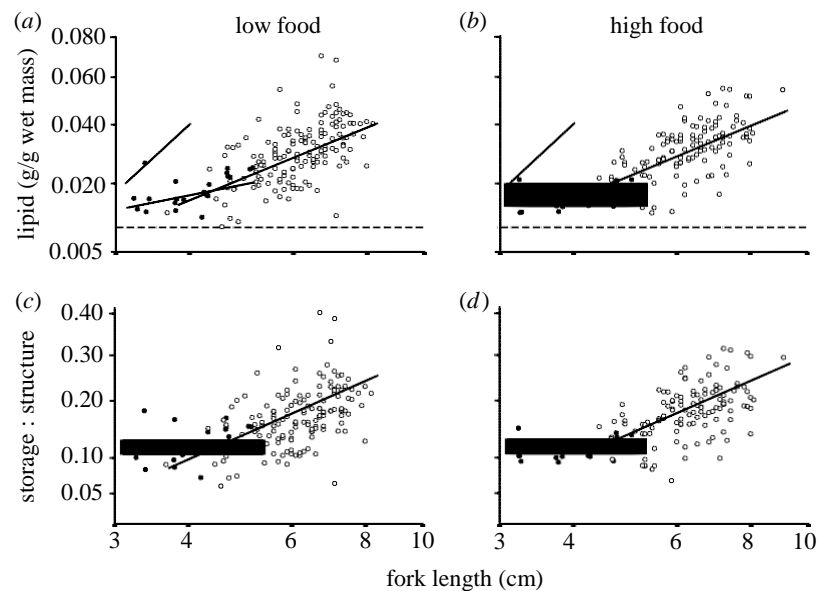
Figure 3. Allometric relationships between fork length of individual age-0 trout from low- and high-food lakes and (a, b) their lipid concentration (g lipid g wet mass ^{K1}) and (c, d) ratio of storage/structure (g lipid per g lipid-free dry mass). Solid symbols represent late July samples (18 days post stocking) and open symbols represent late August samples (48 days post stocking). Regression lines represent the significant interaction effect between sampling date and fork length, and the dashed line in the upper panels represents the minimum lipid concentration for survival in age-0 rainbow trout (Biro et al. 2004a,b). The heavy solid lines (a, b) represent the lipid allometry of rainbow trout raised in the hatchery (in the absence of predator cues) and fed to satiation for approximately two weeks following hatching (data from Biro et al. 2004a,b).

body size in July ($b_1 Z 0.118$), and increased at twice that rate in August ($b_2 Z 0.242$; interaction between fork length and date: $F_{1,295} Z 16.8$, p ! 0.001; figure 3a,b). The food treatment and remaining interactions had no effect on age-0 trout lipid concentration (all $pO0.50$). There was some overlap in fish lengths and lipid concentrations between July and August fish samples, with more overlap occurring in low-food lakes.

Lipid concentrations of age-0 trout in July were only slightly higher than the minimum lipid concentration needed for survival in this species, and well below lipid concentrations observed for very small trout raised in the hatchery (figure 3). To explore this further, we used the observed daily mass increases, combined with mass-specific energy content, to calculate the amount of somatic growth in length that could have been achieved by trout if all increases in energy were allocated to soma. We found that if trout allocated all energy acquired during the first 18 days to soma, they would only increase growth by 0.1 mm day^{K1} (less than 2 mm total over the first 18 days) in addition to the observed growth rate of approximately 1.3 mm day^{K1}.

Low accumulation of lipid reserves by age-0 trout in July favoured somatic growth at the expense of lipids, and rapid accumulation of lipids in August came at the expense of somatic growth (figure 3c,d). The allometry of storage/structure ratio had a low slope for age-0 trout in July ($b_1 Z 0.189$), and an almost 3.5 times greater slope in August ($b_2 Z 0.648$), indicating a switch to lipid allocation in August (fork length ! date interaction: $F_{1,295} Z 13.4$, p ! 0.005; figure 3b,c). The food treatment and remaining interactions had no effect on relative proportions of storage and structure (all $pO0.50$). The allometry of storage/structure also suggested a switch from a strategy favouring somatic growth to one favouring lipid accumulation at approximately 50 mm FL. Thus, the low allocation of energy to lipids by age-0 trout in July, just

above the minimum required for survival in this species, corresponded with very rapid growth rates that did not differ between populations taking greater versus lesser risks while foraging (figures 2 and 3). By late August, there was substantial allocation of energy to lipid storage, corresponding with equal use of risky habitats by age-0 trout that had achieved a large body size.

4. DISCUSSION

We predicted that if the size-dependent risk of predation is the dominant selective pressure when age-0 trout are small, then energy should be allocated to soma at the expense of lipids. Because these fishes grow quickly, we expected that fishes would quickly outgrow high vulnerability to predation and then allocate significant energy to lipids for winter. We found that energy was allocated to somatic growth in July, which corresponded with differences in risk-taking behaviour, and to energy storage in August when use of risky habitats were equal among populations. Trout in all lakes allocated near-maximum energy to somatic growth and grew at maximum rates during July. At that time, fishes possessed lipid levels just above the minimum required for survival, such that any additional allocation to soma would provide little additional growth benefit. The intersection of the two lipid allometries (July versus August) at a fork length of approximately 45 mm suggests a size- rather than time-dependent switch in energy allocation strategies. Together, these results suggest that the size-dependent risk of predation selects for increased risk-taking and energy allocation to soma (at the expense of lipids) to maximize somatic growth rates and therefore minimize time spent in a highly vulnerable size range.

The correspondence between elevated risk-taking by age-0 trout in low productivity lakes and somatic energy allocation in July suggests that trout accept greater

behaviour-related risk to maximize growth rates and minimize background predation risk. Early in the summer, trout grew at maximum rates in all lakes. However, trout in low-food lakes achieved maximum growth rates by foraging more actively and by using risky habitats to a greater extent than fishes in high-food lakes (figure 2), resulting in greater mortality (only 25% survival; Biro et al. 2003a). In contrast, fishes in high-food lakes could not benefit from increased foraging activity, took fewer risks, and reduced predation mortality (42% survival; Biro et al. 2003a). If the observed patterns of behaviour and energy allocation are adaptive, then background (size-dependent) predation risk must be greater than risk due to more conspicuous foraging behaviour. We therefore suggest that the two major components comprising predation risk—the probability of capture given detection and the probability of detection—correspond with size-dependent background predation risk and foraging behaviour, respectively. By late summer, most trout had outgrown much of their potential size-related risk to predation, were still growing at maximum rates, but achieved this level of growth through similar use of food-rich, previously high-risk habitats in all lakes.

Accepting increased risk and allocation of energy to somatic growth to minimize time spent in highly vulnerable small size classes is adaptive if size-dependent predation risk is severe. Several facts and observations point to this background predation risk in promoting risk-taking and the observed somatic energy allocation. First, there is a significant trade-off between somatic growth and lipid storage. For example, injecting growth hormone into young trout increases RNA levels (indicating higher protein synthesis; Johnsson et al. 1996) and accelerates growth in mass and length, but at the expense of fat (Johnsson et al. 2000). Second, we found that trout in nature allocated nearly all energy to somatic growth when small, and maintained lipid levels just above the minimum required to survive, yet are physiologically capable of allocating significant energy to lipids in culture situations (figure 2; Biro et al. 2004b). Third, we observed a size-dependent switch in energy allocation. If the switch in energy allocation was dependent upon time remaining until winter, then we would expect that small (less than 50 mm) fishes at the end of the summer would possess more lipid than large (greater than 50 mm) fishes in July, which was not the case. This switch point corresponds, if only in a qualitative way, to much diminished risk of predation for young trout greater than 50 mm in length. For instance, age-0 rainbow trout stocked at 25 mm in length are expected to experience only about 25% survival in contrast to 65% survival when stocked at 50 mm (Parkinson et al. 2004; estimates generating this relationship were obtained from the same set of research lakes containing a range of cannibal density and size-structure similar to the present experiment). The scope for additional size-dependent mortality beyond 50 mm in length is further reduced given that survival of larger trout reaches an asymptote at 90% in our lakes (Parkinson et al. 2004). Based on this pattern of size-dependent risk, the risk of overwinter starvation should be the dominant selective pressure for larger (greater than 50 mm) age-0 trout, and we did observe significant lipid accumulation in trout larger than 50 mm. In fact, we estimate that trout allocated only 12% of energy to lipids when 30 mm in

length, 15% of energy to lipids at the switch point (45 mm) and then dramatically increasing energy to lipids reaching 33% at 80 mm in length in August. Expressed as rates of increase before and after the switch, trout allocated 0.19% of energy to lipids per mm increase in length before, compared with 0.53% after the switch point.

Our study has shown that flexible behaviour and size-dependent energy allocation both contribute to mediating the trade-offs between growth and mortality rates for young animals under risk of predation and overwinter starvation. Few studies link physiology/life history with behaviour to understand growth/predation risk trade-offs (Stoks & McPeek 2003) or examine energy allocation trade-offs between soma and lipid storage (but see Post & Parkinson 2001; Metcalfe et al. 2002; Hurst & Conover 2003). However, two previous laboratory studies with salmonid fishes have shown flexible behaviour, growth and energy allocation in response to changing selective pressures and individual state (Bull et al. 1996; Metcalfe et al. 2002). Metcalfe and colleagues' (2002) study found that young salmon that were deprived of food responded by allocating resources to growth in length as well as lipids in summer, and to restoring lipid reserves but not increasing in length in winter. Flexibility in the allocation of resources to different body subsystems, while not shown here, appears to be a widespread and significant component of adaptive behaviour, but is often ignored (Piersma & Lindstrum 1997; Metcalfe et al. 2002).

Previous studies with young fishes suggest a switch from somatic to lipid energy allocation strategies, but none have directly linked this physiological trade-off with behaviour and mortality. Post & Parkinson (2001) found evidence for a sigmoid lipid allocation pattern in age-0 rainbow trout sampled at the end of the growing season in October. In contrast, Hurst & Conover (2003) examined seasonal energy allocation and found that small striped bass early in the season allocated little energy to lipids, grew quickly and then abruptly switched to lipid allocation prior to winter. As in our study, there was little variation in energy allocation among populations in the early part of the season, but large within- and among-population (different year classes) variation during the period was observed when bass were accumulating lipids (Hurst & Conover 2003). Finally, we would suggest that future studies would greatly benefit by more forceful integration of physiological trade-offs with behaviour to understand how individuals deal with multiple selective pressures and their population-level consequences.

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