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# Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon

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## SUMMARY

Animals can use fat reserves as a source of energy whenever demand exceeds intake. The size of this 'insurance' is dependent on a trade-off between storage costs and anticipated needs. Previous theoretical and empirical studies in birds have shown that fat levels are tailored to short-term needs. However, in some situations animals must match intake to longer term requirements. Here we develop a model of this situation, and compare it with experimental data from juvenile Atlantic salmon, which become anorexic and gradually deplete their energy reserves over winter. Responses to experimentally-accelerated depletion of reserves matched theoretical predictions: an elevation of appetite to restore lost reserves was dependent not on current energy state, but on projected energy state at the end of the winter. This is the first demonstration of an adaptive regulation of appetite tailored to long-term requirements for an energy insurance rather than short-term needs.

## 1. INTRODUCTION

Many animals use stored fat as an energy insurance, preferentially drawing on it (rather than protein or carbohydrate) when unable to match intake to demands. However, the means by which they regulate fat reserves through modulation of feeding is poorly understood. Recent theoretical work (for examples, see Lima 1986; reviewed by Witter & Cuthill 1993) suggests that the size of an energy reserve will vary with the relative costs and benefits of maintaining it. Thus, in winter diurnal birds should increase their fat reserves because of long nights of fasting, less predictable food supplies and increased metabolic demands. This response to short-term needs is widespread (see Witter & Cuthill 1993).

However in some situations animals may reduce appetite (and draw on stored reserves) because feeding is risky or difficult, or is in direct conflict with some other demand such as egg incubation (LeMaho 1977; Sherry *et al.* 1980), migration (Alerstam 1990), hibernation (Mrosovsky & Barnes 1974; Torke & Twente 1977) or overwinter survival (Metcalf & Thorpe 1992). The question thus arises as to how appetite should be regulated and reserves used in these situations. There is some evidence that energy levels are actively defended by feedback controls on appetite (Mrosovsky & Sherry 1980), but little is known about the ability to adjust appetite to match projected energy requirements.

The Atlantic salmon (*Salmo salar* L.) exhibits pronounced fluctuations in appetite. Juveniles preparing for seaward migration (smolting) at the end of

their first year maintain high appetite and growth rates throughout their fresh water phase (Thorpe *et al.* 1980; Higgins & Talbot 1985; Metcalfe *et al.* 1986, 1988) whereas those delaying smolting until they are at least two-years-old show a suppressed appetite over their first winter (Metcalf & Thorpe 1992). This natural anorexia commences in early autumn independent of water temperature or food availability (Metcalf *et al.* 1986) and lasts until spring, when water temperature rises and food becomes more plentiful. Food intake during the anorexic interval is insufficient to maintain energy reserves (Gardiner & Geddes 1980; Higgins & Talbot 1985).

Previous work (Metcalf & Thorpe 1992) has shown that appetite at the start of overwinter anorexia is sensitive to energy levels. Whereas glycogen and protein are used as supplementary energy stores, the most important and labile store is body lipid (Weatherley & Gill 1987), which is depleted whenever food intake is suppressed (Miglav & Jobling 1989). Here we develop a state variable model which predicts that responses to deviations from the programmed path of reserve loss should vary across the season, and provide empirical evidence to support this prediction. We thus demonstrate for the first time a connection between short-term feeding behaviour and long-term optimization of survival through projection of energy requirements.

## 2. THE MODEL

The state variable is the level of body lipids  $L(t)$  of the animal at time  $t$  within the anorexic interval ( $t = 1$  corresponds to October 1). The fish uses lipid to maintain body function, at a rate  $\alpha$  when actively foraging, but at a lower rate  $\alpha s$  when inactive. If

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foraging for an entire 24 hour period results in a lipid intake of  $q$  and the animal forages for only a fraction  $f$ , then

$$L(t+1) = L(t) - \alpha f - \alpha(1-f)s + fq. \quad (1)$$

We assume that the state  $L(t+1)$  cannot fall below a starvation level  $L_c$ . Similarly, there is a maximum value  $L_{max}$  that the lipid level cannot exceed. Bad weather (e.g. spates) may prevent the fish from foraging, so we introduce

$$p_q = \text{Prob}\{\text{the fish is able to forage on a given day}\}. \quad (2)$$

If the fish is unable to forage, it rests and

$$L(t+1) = L(t) - \alpha s. \quad (3)$$

We assume there is a predation rate  $m$  independent of lipid level (c.f. McNamara & Houston 1990) while the fish is foraging, so that

$$\text{Prob}\{\text{fish survives a day in which its foraging effort is } f\} = e^{-mf}. \quad (4)$$

Thus, a level of foraging effort should exist that optimizes the trade-off between starvation and predation. This level is likely to depend upon lipid level and time. For example, when close to  $L_c$ , the animal must forage regardless of predation risk, whereas towards the end of the season it may cease foraging altogether if lipid levels are high.

To determine the optimal level of foraging, introduce

$$p(l, t, T) = \text{maximum Prob}\{\text{survival between } t \text{ and } T, \text{ given that } L(t) = l\}. \quad (5)$$

The fish's survival probability at the end of the winter is  $p(l, T) = 1$  if  $L > L_c$  and 0 otherwise. Thus,  $L_c$  is a starvation value for the fish in that if its state falls below  $L_c$ , the fish is dead. An alternative would be that  $p(l, T)$  slowly decreases towards 0 as  $l$  decreases. Since we lack knowledge of the functional form of this decrease, we keep the sharper cut-off. For  $t < T$  (Mangel & Clark 1988),

$$p(l, t) = (1 - p_q) p(l - \alpha s, t+1) + p_q \max_f e^{-mf} \times p(l - \alpha f - \alpha(1-f)s + fq, t+1). \quad (6)$$

The first term on the right hand side of equation (6) arises if the fish is unable to forage. Then its state declines by  $\alpha s$  and it begins day  $t+1$  with state level  $l - \alpha s$ . With probability  $p_q$ , the fish is able to forage on day  $t$ . The optimal foraging level maximizes (hence max) expected survival, taking both starvation and predation risks into account.

The solution of equation (6) generates the survival probability and the optimal level  $f^*(l, t)$  of foraging effort for every state  $l$  and day  $t$ . To obtain predictions, parameter values must be chosen. If the anorexic interval lasts six months,  $T = 180$ . Because under-yearling salmon have peak lipid contents of about 8% (Higgins & Talbot 1985) and the lowest observed levels are approximately 1% (Gardiner & Geddes, 1980), we chose  $L_{max} = 80$  and  $L_c = 10$ . Starved fish (Metcalf & Thorpe 1992, also see below) lost about

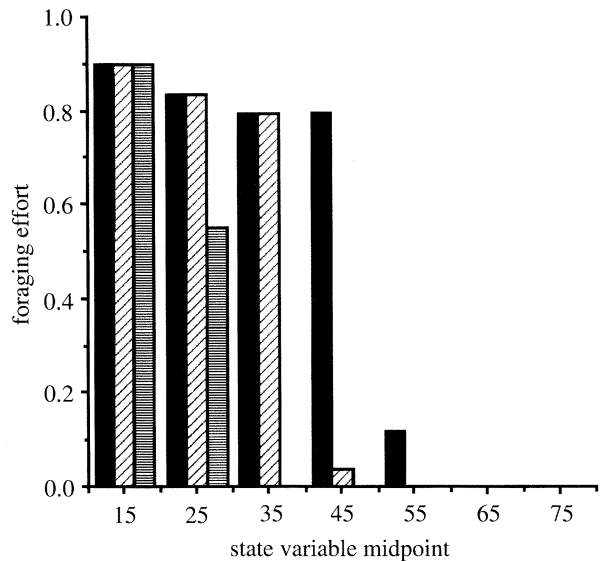


Figure 1. Predicted foraging effort depends upon lipid level and time. values of  $f^*(l, 3)$ ,  $f^*(l, 66)$  and  $f^*(l, 129)$  – stippled, slanting stripes and horizontal stripes respectively – are shown averaged over ten state variable units. Note that if the state variable is higher than 50, the foraging effort at  $t = 66$  and at  $t = 129$  is 0.

1% of their weight wet in lipid (i.e. a change in  $L$  of ten units) over a three-week deprivation period, so that we choose  $21\alpha s = 10$ . Thus,  $\alpha$  is approximately 0.5/s. The additional parameters,  $q$ ,  $s$ ,  $m$ , and  $p_q$ , are harder to estimate, so after describing the main pattern, we consider a sensitivity analysis. For presentation of results, set  $s = 0.2$ ,  $p_q = 0.5$  and  $m = 0.01$ . If the overwintering fish can meet its daily requirements by foraging for a fraction  $d_r$  of the 24 hour interval, the parameter  $q$  satisfies  $d_r\alpha + (1 - d_r)\alpha s = d_r q$ ; for presentation of results, we assumed  $d_r = 0.2$ .

The optimal foraging effort increases as lipid levels decline and decreases as the end of winter approaches (see figure 1). From this, we predict that early in the winter, fish in good condition will forage little or not at all, so that there will be an initial decline in weight. We also predict that fish in poor condition will forage with great intensity regardless of the time of year.

We can describe the results in figure 1 by a threshold state for foraging. If its state is above this threshold, the fish does not forage; otherwise it forages. Thus, the main pattern is one in which the threshold state for foraging decreases as the season progresses. To examine the robustness of the pattern in figure 1, we modified parameters one at a time. For example, if the end condition is changed so that  $p(l, T)$  is an increasing function of terminal state, the pattern is not observed. Instead, foraging effort increases as  $T$  is approached. When mortality rate  $m = 0$ , the threshold state becomes independent of time; however if  $m = 0.001$  (i.e. ten times smaller than the value used to generate figure 1), the pattern is maintained. Hence, we conclude that some mortality (so that there is a starvation risk-predation risk trade-off) is required to generate the pattern in figure 1. If  $p_q = 1$ , so that the fish are always able to forage, the pattern disappears and the fish forages in mid or late season only if the

Table 1. *Predicted relative foraging effort of control and deprived fish after deprivation periods in the early, middle and late winter*

time of deprivation	average foraging effort over 14 days from the end of deprivation	
	control	deprived
early	0.13	0.33
mid	0.11	0.13
late	0.06	0.06

state is near the critical value. However, the pattern is maintained for  $p_q = 0.7, 0.4$  or  $0.3$ . Hence, we conclude that some level of uncertainty about the foraging environment is needed to generate the pattern. It is maintained (although the particular values change) if  $s = 1.0$  or  $s = 0.2$  or if  $d_r = 0.4$  or  $0.6$ . Hence, we conclude that these values (which describe the energy dynamics of the animal) generate the pattern over a wide range of values. Finally, the pattern is maintained as  $L_c$  is varied around its value in the base case. We thus conclude that the model predictions shown in figure 1 are robust to changes in parameter values or functional forms. The cases in which the pattern is not maintained are ones in which the biology is different from that underlying the model (e.g. no mortality risk or uncertainty in the foraging environment, or terminal fitness that is increasing with state).

Next, we used forward iteration (Mangel & Clark 1988) to ask how fish will respond to food deprivation at different times in the season. We considered deprivation lasting 21 days and starting at  $t = 3$  (early season), 66 (mid winter), or 129 (late winter), and computed the average foraging effort for 14 days after the deprivation period (table 1), using the empirical value of lipid content at the start of the deprivation period ( $L = 51, 45$  or  $35$  respectively). From this, we predict that fish deprived early in the winter will work much harder after deprivation ends than ones deprived in mid or late winter. Our sensitivity analysis showed that the qualitative features of this table are also robust to changes in parameter values, although the quantitative response changes. For example, if  $p_q = 0.3$ , the control vs. deprived foraging levels predicted by the model are 0.09 versus 0.71, 0.09 versus 0.33 and 0.07 versus 0.08 for the early, mid and late deprivation periods respectively. Both the qualitative pattern of figure 1 and the qualitative results in table 1 are maintained for other changes in parameter values.

### 3. MATERIAL AND METHODS

Offspring of sea-run adults from the River Almond, Perthshire were reared at the SOAFD Almondbank hatchery prior to experiments at the University Field Station, Rowardennan, Loch Lomond. Fish (40) of fork length less than 70 mm (to maximize the proportion that would delay smolting for another year; Metcalfe *et al.* 1988), were selected on 28 September, 1994 and given individual combinations of alcian blue dye marks (Metcalfe *et al.* 1988) on their undersides. They were divided into two size-matched groups of 20. The control group was maintained in a 1 m<sup>2</sup> holding tank and experienced ambient water temperatures (see figure

2a), simulated natural photoperiod and excess food (dispensed every ten minutes by automatic feeder) except during feeding trials.

All fish in the experimental group experienced three separate three-week periods of food deprivation (termed early, mid- and late winter) commencing on 3 October, 5 December and 6 February respectively. We have previously shown that this period of deprivation produces a measurable drop in lipid reserves at winter temperatures without causing undue stress (Metcalfe & Thorpe 1992; see also Weatherley & Gill 1981). During deprivation fish were held without food in a 1 m<sup>2</sup> tank inside a controlled temperature cabinet (with simulated natural photoperiod) kept at  $6.0 \pm 1.0$  °C, ensuring a constant temperature during each period. We measured wet weight (to 0.01 g), forklength (to the nearest millimetre) and body fat content of all fish immediately before, and 0 and 30 days after each deprivation period. To measure fat content repeatedly on the same fish it was estimated (c.f. Simpson *et al.* 1992) from a combination of body weight ( $m$ ), forklength ( $f$ ) and standardized body widths at leading edge of dorsal ( $w_d$ ), pelvic ( $w_p$ ) and anal fins ( $w_a$ ) measured to nearest 0.1 mm with vernier callipers:

$$\text{Lipid (g)} = 0.0976m - 0.00413f + 6.11w_d + 10.9w_p - 7.93w_a - 0.125 \quad (r^2 = 0.637, n = 55, p < 0.001). \quad (7)$$

We derived equation (7) using a separate sacrificed sample of salmon of similar size subjected to Soxhlet solvent extraction (see Simpson *et al.* 1992). Individual fat reserves were expressed as a percentage of wet weight to control for variation in body size.

At the end of each deprivation period, the appetite of all experimental and control fish was monitored by placing them singly in compartments (25 cm × 10 cm, water depth 5 cm) of long raceways, through which water at ambient temperature flowed at a slow rate. Each compartment contained a small opaque overhang under which fish could hold station. Fish were assigned compartments at random and were left to settle for four days during which bloodworms (*Chironomidae* sp. larvae) were hand fed to excess twice a day, so that any subsequent observed differences in appetite between groups were not caused by differences in gut fullness before trials.

Appetite trials were then conducted between 10h00 and 12h00 every second day for the next three weeks. We scored each fish's response to five bloodworms per day (presented singly ca. 10 cm upstream of the fish at intervals of at least 20 min) as a measure of foraging effort. Responses were disregarded (and an extra bloodworm introduced later) if the fish was obviously disturbed or if the bloodworm did not come within 2 cm of its head. Because fish were allocated to compartments at random and as their dye marks were only visible during handling, all appetite data were collected blind. The responses were scored as: no response = 0; orientation = 1; turn back after initially moving towards prey = 2; miss bloodworm = 3; ingest but subsequently reject bloodworm = 4; consume bloodworm = 6 (*sensu* Metcalfe *et al.* 1986). A minimum of four responses were used to calculate an individual's mean appetite score each day. This scoring system is a better measure of foraging effort (and its associated predation risk) than simply measuring intake rate because it includes all movements associated with feeding. Each fish was presented with a minimum of 20 bloodworms following each trial, and on days between trials, to ensure they received *ad lib.* rations.

At ten and 20 days since establishment in the raceway all fish were moved to a new randomly-allocated compartment to control for variations in water flow between compartments. Following the final appetite trial all fish were transferred to

a 1 m<sup>2</sup> holding tank where they were fed excess pelleted food. Two weeks later, fish in the experimental group experienced the next period of food deprivation and the cycle was repeated. Any dead fish were replaced at this point ( $n = 5$  experimental).

#### 4. RESULTS

Two fish grew throughout the winter (increasing to more than 20 mm in length) and underwent smolt

metamorphosis; these were omitted from analyses. No other fish gained more than 5 mm.

Control fish entered anorexia in early winter (figure 2*a*), and their body lipid levels consequently dropped from  $5.32 \pm 0.42\%$  of body weight ( $n = 18$ ) in September to  $2.63 \pm 0.40\%$  ( $n = 18$ ) in April (figure 3*a*), despite food always being in excess.

The three deprivation periods caused significantly accelerated lipid depletion: the mean reductions in fat during the early, mid, and late winter periods were

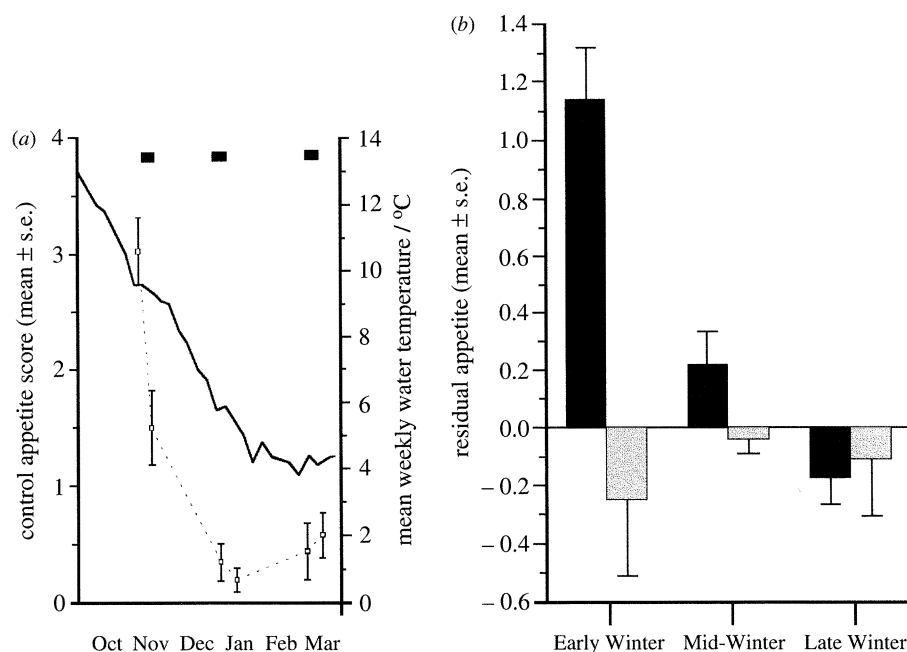


Figure 2. (*a*) Seasonal decline in appetite of control fish for days 1–14 and 15–28 of trials in early, mid- and late winter; the solid line shows ambient water temperature and the solid bars indicate periods of food deprivation for experimental fish. (*b*) Changes in appetite of experimental fish following deprivations (means  $\pm$  s.e. for days 1–14 (dark bars) and 15–28 (light bars) during refeeding). Experimental fish appetite was significantly higher than controls following early winter deprivation ( $t_{33} = 3.11$ ,  $p < 0.01$ ), and was greater following early winter deprivation than either mid- or late (Kruskal-Wallis ANOVA, ( $\chi^2 = 14.61$ , d.f. = 2,  $p < 0.001$ ).

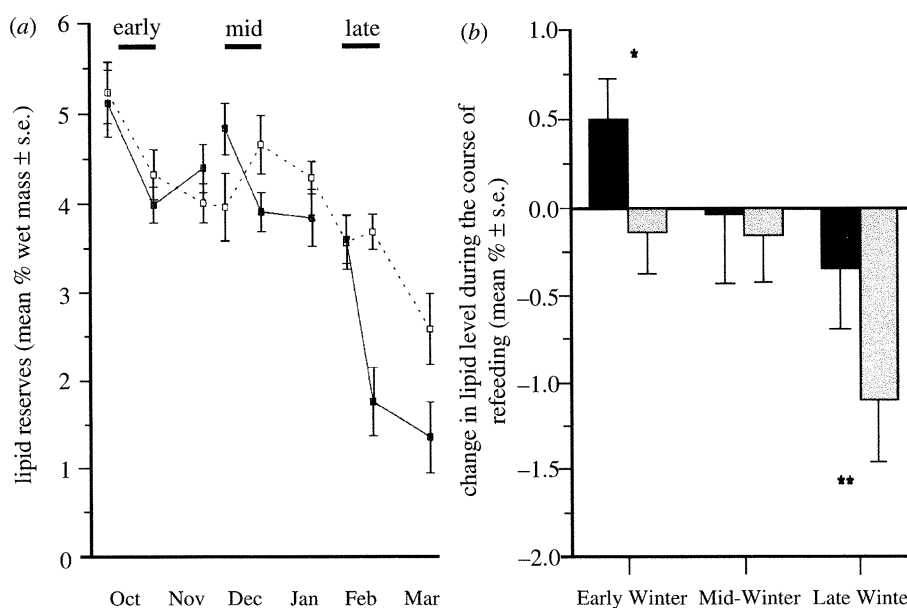


Figure 3. (*a*) Changes in lipid level during the course of the experiment (solid squares represent experimental fish and open squares represent controls; periods of food deprivation indicated by black bars). (*b*) Changes in lipid during refeeding following deprivation in early, mid- and late Winter for experimental (dark bars) and control fish (light bars). Asterisks indicate  $t$ -tests comparing treatments; \* $p < 0.05$ , \*\* $p < 0.01$ .

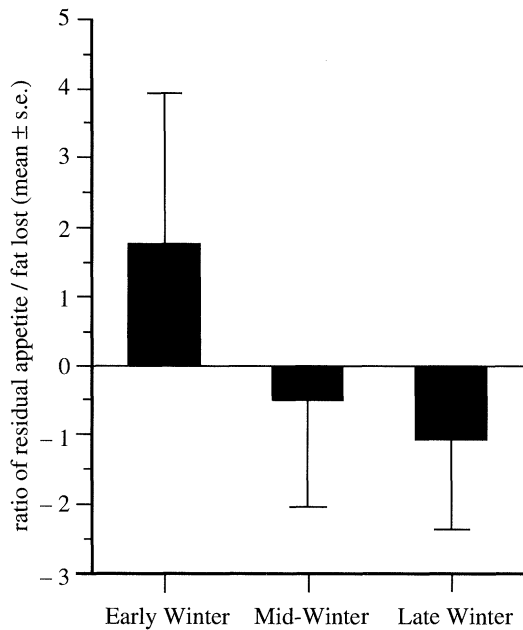


Figure 4. Values of  $R$  (elevation of appetite per unit loss of fat; see text) following deprivation periods in early, mid- and late winter. The appetite response to accelerated lipid loss declined over the course of the winter (Kruskal-Wallis ANOVA between times ( $\chi^2 = 6.53$ , d.f. = 2,  $p < 0.05$ )).

$1.12 \pm 0.22\%$  of body weight (paired  $t$ -tests,  $t_{19} = 2.83$ ,  $p < 0.01$ ),  $1.00 \pm 0.33\%$  ( $t_{18} = 3.03$ ,  $p < 0.01$ ) and  $1.94 \pm 0.31\%$  ( $t_{19} = 6.18$ ,  $p < 0.001$ ) respectively. These reductions were significantly greater than the concurrent changes in control fish during the mid- and late winter deprivations ( $t$ -tests on fat change between treatments,  $t_{33} = 2.60$ ,  $p < 0.05$ ;  $t_{33} = 4.56$ ,  $p < 0.001$  respectively) but not during the early winter period, owing to a reduction in control fat levels ( $t_{34} = 1.07$ , N.S.).

Individual daily appetite scores for experimental fish during refeeding were calculated as residuals from the mean value for control fish on that day; elevated or reduced appetites were indicated as positive or negative values respectively. This eliminated variation caused by parallel fluctuations in appetite in the two treatment groups of fish between trials. Following deprivation in early winter, experimental fish exhibited a marked elevation in appetite relative to controls over the first 14 days of refeeding. However no such effect was apparent after periods of deprivation in mid- or late winter (figure 2*b*), despite their body lipids being lower by this time. The results thus match the model predictions (table 1). The early winter elevation in appetite was short-lived: appetite scores over the period 16–28 days of refeeding were no different from controls, regardless of season (figure 2*b*). These appetite responses resulted in fat levels of experimental fish increasing during the refeeding period in early winter (mean increase of  $0.49 \pm 0.23\%$  of body weight; paired  $t$ -test between sampling dates,  $t_{18} = 2.11$ ,  $p < 0.05$ ), but not following mid- and late winter deprivations (mean reduction  $0.05 \pm 0.39\%$ ,  $t_{18} = 0.13$ , N.S.;  $0.37 \pm 0.34\%$ ,  $t_{18} = 1.08$ , N.S. respectively; figure 3*b*).

We can compare seasonal variation in appetite

responses by considering a ratio expressing the elevation in appetite over the first 14 days of refeeding per unit loss of fat:

$$R = \frac{\text{Mean residual appetite}}{\% \text{ fat lost during deprivation period}} \quad (8)$$

As predicted, fish showed a relatively far greater elevation of appetite in response to an accelerated loss of lipid in early winter than later in the year (figure 4), despite their body lipid levels being higher; their appetite therefore reflected future needs rather than current state.

## 5. DISCUSSION

Despite excess food, all fish showed a depletion of energy reserves over the winter (figure 3*a*), in agreement with other studies (Egglisshaw & Shackley 1977; Gardiner & Geddes 1980; Higgins & Talbot 1985). We conclude that the fish were following seasonal trajectories towards a low target level of lipid early in the spring, when the expected improvement in conditions would allow rapid replenishment (Cunjak & Power 1986). The seasonal variation in the appetite response to deviations from this lipid trajectory (figure 2*b*) suggests that the fish facultatively responded not to their current reserve level, but to their projection of whether they would be above or below the target level at the end of the winter: thus they foraged harder to restore lost lipids earlier in the winter despite having greater reserves at the time. It might be argued that the colder temperatures later in the winter would prevent fish from expressing any increase in appetite after a period of deprivation. However, the fish would be physiologically capable of feeding at a higher rate since controls are feeding at a much lower rate than predicted from equations relating food intake by juvenile salmonids to temperature (Elliott 1976). The magnitude of the change in appetite response between early and late winter (see figure 4) is therefore much greater than any metabolic constraints imposed by decreasing temperatures. Many juvenile salmonids exhibit a rapid decline of body lipid early in the winter (Egglisshaw & Shackley 1977; Gardiner & Geddes 1980; Cunjak 1988), and this is predicted by our model. However, whereas the model predicts a continued decline, we observed a relatively constant level between mid-October and January (figure 3*a*). A possible explanation is that the stable low water temperatures reduce the costs of metabolism and temperature acclimatization (Cunjak & Power 1987; Cunjak 1988), thus leading to a balance between assimilable energy and maintenance requirements.

An alternative explanation is that the fish are more cautious than characterized by the model. Whereas salmon respond to photoperiod as a cue for change of season (Villareal *et al.* 1988), the arrival of better feeding conditions in spring is still unpredictable because of substantial interannual variation in spring temperatures. Studies with birds show that individuals faced with unpredictable feeding opportunities carry higher levels of fat as insurance (Rogers 1987; Ekman & Hake 1990; Ekman & Lilliendahl 1993). Thus, if the

salmon continued to lose fat at the early winter rate, the chances of survival when faced with a late spring might be minimal. A more cautious strategy (i.e. the maintenance of greater fat reserves in mid-winter) requires a higher foraging effort, and thus the acceptance of a greater predation risk, because escape responses are slowed by low water temperatures (Webb 1978). As water temperatures drop below 10 °C, salmon switch from diurnal to nocturnal foraging, hiding during the day in streambed refuges (Fraser *et al.* 1995). This behavioural switch is controlled solely by temperature and is consistent with the idea of reducing foraging risks: nocturnal foraging may allow the maintenance of a higher lipid insurance without increased predation costs.

Our empirical results would not have been predicted from previous studies on the dynamics and function of fat reserves. Indeed it would appear counter-intuitive that the animals exerted greater foraging effort when their lipid levels were higher. Our model predicts this behaviour if the fish are anticipating future energy requirements. Thus, by appropriate regulation of energy reserves, the fish are able to maximize over-winter survival, a key component of their life history.

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