Feeding dynamics in fish experiencing cycles of feed deprivation: a comparison of four species

Lei Wu¹, Shouqi Xie¹, Xiaoming Zhu¹ Yibo Cui¹ & R J Wootton²
¹Institute of Hydrobiology, Chinese Academy of Science, Wuhan, P R China
²Institute of Biological Sciences, University of Wales, Aberystwyth, UK Professor Y Cui: 1962–2000.

Correspondence: R J Wootton, Institute of Biological Sciences, University of Wales, Aberystwyth SY23 3DA, UK. E-mail: rjw@aber.ac.uk

Abstract
The temporal dynamics of daily food consumption were examined in individually housed fish that experienced four cycles of 1 week of feed deprivation followed by 2 weeks of feeding to satiation. Four species were compared: European minnows Phoxinus phoxinus: Cyprinidae; three-spined stickleback Gasterosteus aculeatus: Gasterosteidae; gibel carp Carassius auratus gibelio: Cyprinidae; and the longsnout catfish Leiocassis longirostris: Bagridae. The stickleback, carp and catfish showed significant compensatory increases in food intake following deprivation, with the response becoming clearer in successive cycles. The temporal pattern of consumption during the refeeding periods differed between the four species. In sticklebacks, daily intake over a refeeding period initially decreased, but then recovered. In minnows, intake tended to decline over a refeeding period. Gibel carp showed an increase in daily intake on refeeding, but this may have reflected an adverse response to weighing. Over a refeeding period, catfish had a weak tendency to show an initial decline, followed by an increase. These differences are discussed in relation to differences in experimental protocols and biological differences between the species.

Introduction
Information about temporal variations in food intake is required if models of the control of appetite in fish are to be tested. The information may also prove useful in the design of feeding regimes for fish in aquaculture and for interpreting data on estimates of consumption in natural populations. There are relatively few reports of daily variations in food intake in teleosts. Wang, Hayward & Noltie (1998) described daily food consumption of juvenile hybrid sunfish Lepomis cyanellus R. × L. macrochirus R. over 110 days. Day-to-day variation in feed demand has been investigated in goldfish Carassius auratus L. and rainbow trout Oncorhynchus mykiss (Walbaum) performing an operant response (lever biting) to obtain food (Sanchez-Vazquez, Yamamoto, Akiyama, Madrid & Tabata 1998, 1999).

A period of food deprivation is often followed by a period of hyperphagia (Miglavs, & Jobling 1989; Russell & Wootton 1992; Hayward, Noltie & Wang 1997). The temporal pattern of this hyperphagia may reflect physiological control of appetite (Toates 1986). Hayward et al. (1997) illustrated the patterns of daily food consumption of juvenile hybrid sunfish experiencing cycles of food deprivation followed by ad libitum feeding. Subsequently, Hayward & Wang (2001) described the pattern of daily consumption in yellow perch Perca flavescens (Mitchill) subjected to similar deprivation and refeeding protocols. Ali, Cui, Zhu & Wootton (2001) compared the temporal patterns of daily consumption of three species, the stickleback...
*Gasterosteus aculeatus* L.: Gasterosteidae, the European minnow *Phoxinus phoxinus* (L.): Cyprinidae and gibel carp *Carassius auratus gibelio* (L.): Cyprinidae after periods of 1 or 2 weeks of feed deprivation. For a given species, the temporal pattern was similar for both lengths of deprivation, but the pattern differed between species.

The purpose of the present study was to examine whether the interspecific differences in feeding patterns persisted when fish experienced several cycles of deprivation and refeeding. Four species were studied: the stickleback and the longsnout catfish *Leiocassis longirostris* Günther are carnivorous, whereas the gibel carp and minnow are omnivorous. The gibel carp, minnow and catfish are representatives of the superorder Ostariophysi, whereas the stickleback belongs to the Gasterosteiformes (Nelson 1994).

**Materials and methods**

Experiments on minnows and sticklebacks were carried out in Aberystwyth (Wales, UK) in winter 1999–2000. Young-of-the-year sticklebacks and minnows were collected from a small, upland reservoir, Llyn Frongoch, in autumn 1999. They were held in single-species groups in communal tanks at 14 °C and fed once per day on a mixture of live whiteworm (Enchytraeids) (mean composition percentage dry matter: crude protein 37.8%, crude lipid 17.6%, ash 4.5%, dry matter 21.8% of wet weight) and crushed commercial fish flake (Aquarian, Waltham, Melton Mowbray, UK). In December 1999, minnows and sticklebacks were selected at random and placed individually in 10-L tanks, which were arranged in four, filtered, recirculating systems, housed in two constant-environment rooms. The temperature was 14 °C and the photoperiod 10L:14D. This photoperiod was used to maintain the fish in a sexually immature state. The fish were fed on live whiteworm for 1 week *ad libitum* so food was continually present. They were then deprived of food for 24 h, blotted of superficial water, weighed to the nearest mg and measured (total length) to the nearest 0.1 mm. Individuals were then assigned at random to two groups. The mean (SE) weights at the start of the experiment were 0.391 (0.037) g for sticklebacks and 0.140 (0.046) g for minnows. Controls were fed *ad libitum* on live whiteworm daily, except for the 24 h that preceded weighing and measuring. Deprived fish experienced four cycles, each consisting of 1 week of food deprivation followed by 2 weeks of *ad libitum* feeding. On feeding days, the fish were given a weighed excess of live whiteworm; uneaten worms were removed 24 h later and reweighed. Food intake was calculated by difference (after a small correction for the weight change shown by whiteworm immersed for 24 h). At the end of each week of deprivation and each period of refeeding, the fish were reweighed and remeasured. The experiment on the two species was run concurrently. Final numbers for each species were: stickleback (controls) *n* = 6; stickleback (deprived) *n* = 6; minnow (controls) *n* = 9; minnow (deprived) *n* = 9.

The experiment on the gibel carp and longsnout catfish was conducted at the Institute of Hydrobiology (P R China) in summer 2000. Longsnout catfish were obtained from a hatchery in Guandong, and gibel carp came from the hatchery at the Institute of Hydrobiology about 1 month after hatching. The fish were held in a recirculation system for 1 month before the start of the experiment. Sixty longsnout catfish and 60 gibel carp were transferred to 60 perforated Plexiglas containers (surface area 650 cm², water volume 26 L), with two conspecifics per container. Four containers were housed in each of 15 300-L fibreglass tanks on a recirculating system, with two catfish and two gibel carp containers per tank. The temperature was 29 °C and the photoperiod 12L:12D. Before the start of the experiment, the fish were fed to satiation twice per day, during the light phase, at ~10.00 and 15.00, on formulated pellets (mean composition as percentage of dry matter: crude protein 42.6%, crude lipid 5.9%, ash 21.5%, with water 1.4% of total weight). At the start of the experiment, fish were deprived of feed for 1 day to empty the gut. Thirty catfish of mean weight (SE) 13.38 (0.402) g and 30 gibel carp of mean weight 9.87 (0.231) g were chosen at random. (The remaining 60 fish were used for analyses of proximate composition.) Each fish was blotted of excess water, weighed to the nearest 0.01 g and placed individually in a Plexiglas container. Fish from each species were randomly assigned to two groups. Controls (*n* = 15) were fed to satiation twice a day. The deprived group (*n* = 15) experienced four cycles of 1 week of deprivation and 2 weeks of refeeding. When feeding the control and deprived fish, a small weighed quantity of food was dropped into each tank every few minutes until the fish no longer accepted food. Feeding of each fish was completed within 1 h, and food intake was recorded as g dry weight.
Fish were weighed once a week after 22 h of deprivation, and fish were not fed on the day of weighing.

Repeated measures ANOVA was used to analyse the temporal patterns in daily food intake, with the factor of days nested within the factor of refeeding periods and the between-subjects factor of treatment. To compare overall food intake during the refeeding periods, a mean daily food intake was calculated for each fish for each refeeding period and analysed by repeated-measures ANCOVA, with period as the within-subjects factor, treatment as the between-subject factor and weight at the start of the refeeding period as the covariate after a log transformation of the data.

To compare the temporal trends in daily consumption in the control groups of the four species, consumption was standardized as \( (X_i - X) / SD \), where \( X_i \) is consumption on day \( i \). \( X \) is mean daily consumption over the experiment and SD is the standard deviation. Cross-correlations were calculated between the time series for daily consumption of the pairs of species that shared the same housing conditions: stickleback and minnow, gibel carp and longsnout catfish.

**Results**

**Stickleback**

Both groups grew over the experimental period. The weight trajectory of the deprived fish converged on that of the control fish, although each week of deprivation had caused a reduction in weight. At the end of the experiment, there was no significant difference in mean weight between control and deprived groups (\( F_{1,8} = 2.333; P = 0.17 \)). The mean (SE) specific growth rates over the experiment were 1.15 (0.152)% day\(^{-1}\) and 1.00 (0.122)% day\(^{-1}\) for control and deprived groups respectively.

In the analysis of the temporal pattern of daily food intake, there was a highly significant treatment \( \times \) period \( \times \) day interaction (\( F_{16,720} = 1.977; P = 0.00007 \)) (Fig. 1). In the first refeeding period (weeks 2 and 3), although the control fish showed a variable daily intake, the deprived fish showed an initial decline in consumption, followed by a recovery. In period 2 (weeks 5 and 6) and period 4 (weeks 11 and 12), the patterns of daily consumption for the control and deprived fish were similar to those in the first period. There was a different daily pattern for period 3 (weeks 8 and 9), during which daily intake of deprived fish was relatively stable over the refeeding period.

In the first period of refeeding, there was no significant treatment effect (\( F_{1,15} = 0.0008; P = 0.93 \)) on mean daily consumption. In the other three periods, the mean daily consumption was significantly higher for deprived than for control fish (period 2: \( F_{1,12} = 9.377; P = 0.02 \); period 3: \( F_{1,12} = 13.31; P = 0.003 \); period 4: \( F_{1,12} = 19.41; P = 0.0009 \)) (Table 1).

In the first, second and fourth periods of refeeding, the deprived fish showed an initial decline in daily consumption (Fig. 1), and this temporal pattern was similar for periods in which there were both no (period 1) and highly significant compensatory increases (periods 2 and 4) in consumption (Table 1). The third period of refeeding had an anomalous pattern, although the response was compensatory.

**Minnow**

Both groups increased in weight, albeit slowly, but the weight trajectory of the deprived minnows diverged from that of the control fish. Mean specific growth rates were 0.71 (0.123)% day\(^{-1}\) and 0.36 (0.036)% day\(^{-1}\) for control and deprived minnows respectively. At the end of the experiment, the deprived fish were lighter than the control fish, with the difference marginally significant (\( F_{1,15} = 4.208; P = 0.06 \)).

In the analysis of the pattern of daily intake, the treatment \( \times \) period \( \times \) day interaction was not significant (Fig. 2). There was a significant treatment \( \times \) day interaction (\( F_{12,768} = 3.397; P = 0.00007 \)). In periods 1–3, the patterns for control and deprived groups were similar but, in period 4, the control group showed an increase in consumption not matched by the deprived group. The period \( \times \) day interaction was significant (\( F_{16,768} = 4.620; P < 10^{-6} \)), with the overall pattern of consumption varying between periods.

There was no significant difference in mean daily consumption between the control and deprived groups in any of the four refeeding periods (Table 1). Thus, the deprived minnows did not show a compensatory increase in consumption.

**Gibel carp**

Both groups increased in weight, and the mean daily specific growth rates were 1.86 (0.062)%
day$^{-1}$ and 1.40 (0.046)\% day$^{-1}$ for control and deprived carp respectively. The weight trajectory of the deprived fish diverged from that of controls and, at the end of the experiment, the deprived group was significantly lighter than the control group ($F_{1,28} = 36.52; P = 0.00002$).

For the pattern of daily consumption over the refeeding periods, the treatment $\times$ period $\times$ day interaction was significant ($F_{31,924} = 2.0544; P = 0.00005$), although there were similarities between periods (Fig. 3). Consumption tended to be low on the day immediately after the fish were weighed and then increased until the next weighing. The treatment $\times$ day interaction was significant ($F_{1,308} = 9.8025; P < 10^{-6}$) because of a tendency for the rate of increase to be higher for the deprived group.

Over period 1, the mean daily consumption did not differ between control and deprived fish but, in the three succeeding periods, the mean rate of consumption (after covariance adjustment) was significantly higher in the deprived group (period 1: $F_{1,27} = 1.5969; P = 0.22$; period 2: $F_{1,27} = 7.2883; P = 0.01$; period 3: $F_{1,27} = 6.2628; P = 0.02$; period 4: $F_{1,27} = 29.27; P = 0.00001$) (Table 2).
Table 1 Mean daily consumption (with 95% CI) during four refeeding periods of 2 weeks after 1 week of deprivation of stickleback and minnow

<table>
<thead>
<tr>
<th>Refeeding period</th>
<th>Stickleback (mg ww)</th>
<th>Minnow (mg ww)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control (n = 6)</td>
<td>Treat (n = 6)</td>
</tr>
<tr>
<td>1</td>
<td>59 (19)</td>
<td>61 (18)</td>
</tr>
<tr>
<td></td>
<td>62</td>
<td>62</td>
</tr>
<tr>
<td>2</td>
<td>47 (12)</td>
<td>64 (13)</td>
</tr>
<tr>
<td></td>
<td>53</td>
<td>89</td>
</tr>
<tr>
<td>3</td>
<td>50 (13)</td>
<td>65 (15)</td>
</tr>
<tr>
<td></td>
<td>52</td>
<td>88</td>
</tr>
<tr>
<td>4</td>
<td>47 (11)</td>
<td>58 (11)</td>
</tr>
<tr>
<td></td>
<td>51</td>
<td>80</td>
</tr>
</tbody>
</table>

Adjusted mean after covariance analysis with fish weight at beginning of refeeding period as covariate given in italics.

Figure 2 Daily consumption (appetite) of minnow during refeeding periods (2 weeks) after deprivation (1 week). Control (●): deprived (■).
**Table 2** Mean daily consumption (with 95% CI) during four refeeding periods of 2 weeks after 1 week of deprivation of gibel carp and catfish

<table>
<thead>
<tr>
<th>Refeeding period</th>
<th>Gibel carp (g dw)</th>
<th>Longsnout catfish (g dw)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control (n = 15)</td>
<td>Treat (n = 14)</td>
</tr>
<tr>
<td>1</td>
<td>0.78 (0.07)</td>
<td>0.74 (0.04)</td>
</tr>
<tr>
<td></td>
<td>0.70</td>
<td>0.80</td>
</tr>
<tr>
<td>2</td>
<td>0.88 (0.07)</td>
<td>0.89 (0.04)</td>
</tr>
<tr>
<td></td>
<td>0.78</td>
<td>0.99</td>
</tr>
<tr>
<td>3</td>
<td>0.83 (0.10)</td>
<td>0.89 (0.05)</td>
</tr>
<tr>
<td></td>
<td>0.70</td>
<td>0.98</td>
</tr>
<tr>
<td>4</td>
<td>1.01 (0.12)</td>
<td>1.15 (0.07)</td>
</tr>
<tr>
<td></td>
<td>0.82</td>
<td>1.37</td>
</tr>
</tbody>
</table>

Adjusted mean after covariance analysis with fish weight at beginning of refeeding period as covariate given in italics.

**Figure 3** Daily consumption (appetite) of gibel carp during refeeding periods (2 weeks) after deprivation (1 week). Control (●); deprived (■).
Longsnout catfish

Both groups increased in weight, but the weight trajectory of the deprived catfish diverged from that of controls so, by the end of the experiment, fish in the deprived group were significantly smaller than those in the control group at the end of the experiment ($F_{1,27} = 8.616; P = 0.007$). Mean specific growth rates were 1.38 (0.071)\% day\(^{-1}\) and 1.09 (0.075)\% day\(^{-1}\) for the control and deprived groups.

For the pattern of daily consumption, the only significant interaction term was period $\times$ days ($F_{13,891} = 5.4190; P < 10^{-5}$), indicating that the daily pattern of consumption over the refeeding periods was similar for both control and treatment groups, but that the daily pattern did vary between periods (Fig. 4).

For period 1, there was no significant difference in mean daily consumption between control and deprived catfish ($F_{1,26} = 2.9998; P = 0.10$). In subsequent refeeding periods, mean daily consumption (after covariance adjustment) was significantly higher in deprived fish (period 2: $F_{1,26} = 8.0457; P = 0.009$; period 3: $F_{1,26} = 12.548; P = 0.002$; period 4: $F_{1,26} = 26.695; P = 0.00002$) (Table 2).

Pattern in controls

The daily consumption (standardized means) of the control groups for the two pairs of species that shared the same rearing conditions was compared.
For the gibel carp and catfish controls, there was a significant cross-correlation between the mean daily consumption of the two species at lags of 6 and 7 days (lag 6, \( r = 0.29, P < 0.05 \); lag 7; \( r = 0.28, P < 0.05 \)). This pattern of cross-correlations probably reflects the disturbance associated with weighing and measuring of the fish during the experiment, with both species tending to have relatively low rates of consumption on the day after weighing. There were no significant cross-correlations for the minnow and stickleback.

**Discussion**

The aim of the study was to examine whether four teleost species displayed consistent temporal patterns in weights of food consumed per day when subjected to recurrent periods of food deprivation. Ali et al. (2001) observed interspecific differences in the temporal response of appetite after 1 or 2 weeks of feed deprivation.

A comparison of the results of the present study with those of Ali et al. (2001) is possible for the stickleback, minnow and gibel carp. The comparison shows that the patterns observed after one period of deprivation tend to recur when the species are subjected to cycles of deprivation and refeeding. In the stickleback, daily consumption declined initially and then increased. In the minnow, consumption tended to decline over the refeeding period, whereas in the gibel carp, consumption tended to increase over the refeeding period. Of the four species investigated in the present study, only in the stickleback was the pattern shown by deprived fish strongly delineated from that shown by controls.

Three factors are relevant to an interpretation of the patterns of consumption observed. There were differences in the protocols between the experiment on minnows and sticklebacks and that on gibel carp and longsnout catfish. Secondly, fish were weighed at intervals during the experiments, and the patterns of consumption suggested that this caused some disruption, particularly for the gibel carp and catfish, which reduced food intake after weighing. The disruptive effect of weighing is also suggested by some synchrony in daily intake between control groups of gibel carp and catfish related to the timing of the weighings. Thirdly, there is the response to deprivation.

Three of the four species, stickleback, gibel carp and longsnout catfish, showed a compensatory increase in daily food consumption as a response to deprivation, but the increase was only significant in the second, third and fourth periods of refeeding. A similar lag had previously been observed in sticklebacks deprived for 1 or 2 weeks (Zhu, Cui, Ali & Wootton 2001), but not in gibel carp (Xie, Zhu, Cui, Wootton, Lei & Wang 2001). Grouped rainbow trout experiencing 3 weeks of deprivation followed by 3 weeks of feeding had the highest growth rates in the third week of refeeding (Quinton & Blake 1990). This may indicate that there was also a lag in the development of the compensatory increase in consumption in this species. Zhu et al. (2001) noted a brief compensatory increase in consumption by minnow in the second week of refeeding after 1 week of deprivation, but this was not seen in the present experiment. Russell & Wootton (1992) observed a compensatory growth response in minnows deprived of food for 14 days, but not when fish were deprived for 4 days. For stickleback, gibel carp and catfish, the trends in daily consumption suggest the possibility that the hyperphagia would have continued into a third week of refeeding.

In gibel carp and longsnout catfish, hyperphagia tended to be present throughout the refeeding period but, in the stickleback, the hyperphagia was most developed in the latter half of the refeeding period (Fig. 1). Indeed, over the first week of refeeding, the consumption of the deprived group tended to fall below that of the controls.

In sunfish hybrids and in yellow perch, hyperphagia tended to be highest on the first day of refeeding. There was then a sharp decline in consumption on the second day of refeeding followed by a recovery to a second peak, and this was succeeded by a decline back to control levels of consumption (Hayward et al. 1997; Wang et al. 1998; Hayward & Wang 2001). Both sunfish and yellow perch are Perciformes. A somewhat similar pattern was observed in the minnow, a cyprinid, refeed after feed deprivation for 2 weeks, but a sharp decline on the second day was not observed (Zhu et al. 2001). In the present experiment, the minnow failed to develop a consistent hyperphagia in response to deprivation of 1 week.

These interspecific differences may be artifacts of the experimental protocols. The interspecific comparisons of the stickleback and minnow as one pair and of the gibel carp and longsnout catfish as the other are more valid, because the housing conditions for each member of a pair were identical. Even under identical housing conditions, there may be a differential sensitivity of species to the
disturbance caused by weighing and measuring. However, it is also possible that the different patterns reflect interspecific differences in the control of appetite in relation to periods of high and low food availability. Such differences may reflect morphological and physiological variation in the digestive systems, different priorities of somatic growth and acquisition of reserves and different temporal patterns of feeding associated with carnivorous, herbivorous or omnivorous diets. Carnivores such as the stickleback and longsnout catfish are more likely to experience periods without food than are omnivores, such as the minnow and gibel carp, which can exploit algae and detritus. There have been too few comparative studies to evaluate the relative importance of artfact and adaptive biological differences in generating interspecific differences as observed here. Hosn, Dutilleul & Boisclair (1997) identified short rhythms in the growth rates of grouped brook trout Salvelinus fontinalis (Mitchill). The relationship between such growth cycles and temporal patterns in appetite needs to be investigated using experimental protocols that avoid disturbance caused by intrusive measurements of fish size.

Acknowledgments

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References


