Group holding impedes compensatory growth of hybrid sunfish

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Accepted 6 September 1999

Abstract

An earlier study with a repeating no-feed/reefeed schedule (D2 schedule) elicited compensatory growth (CG) in age-0 hybrid sunfish (F1: female green sunfish, Lepomis cyanellus × male bluegill L. macrochirus) held individually and fed ad libitum on feeding days. Weight gain under these conditions exceeded that of daily-fed controls. The present study sought to determine whether similar growth improvement would result when hybrid sunfish were held in groups and fed to satiation on the D2 schedule. In Experiment 1, age-0 hybrid sunfish were held in groups of 10 fish per 25-l chamber at 24 ± 8°C and fed four times daily to apparent satiation on feeding days. Under this regime, fish fed according to the D2 schedule gained less weight than the controls (P < 0.10). Experiment 2 was run in an effort to duplicate the results of the previous study. When age-0 fish were held individually at 24°C and fed ad libitum on feeding days, those fed on the D2 schedule gained significantly more weight (P < 0.10) than the controls. These results indicate that group holding in combination with satiation feeding impedes the full expression of the CG capacity of hybrid sunfish. The major impediment under group holding may be the negative effects of social interactions on food consumption and growth efficiency. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Hybrid sunfish; Hybrid bluegill; Compensatory growth; Social interaction

1. Introduction

The compensatory growth (CG) response of age-0 hybrid sunfish (F1: female green sunfish Lepomis cyanellus × male bluegill L. macrochirus) can be manipulated to give
increased weight gain relative to daily fed (ad libitum) controls (Hayward et al., 1997). Although CG has been elicited in many studies on fish (Russell and Wootton, 1992; Koppe et al., 1993; Jobling, 1994), the finding of overcompensation was novel.

Overcompensation has potentially important implications for increasing fish growth rates in aquaculture, so we were interested in whether weight gains could be increased under conditions mimicking those in aquaculture. Fish are usually reared in groups and fed periodically to satiation, whereas in our previous study, we held fish individually and fed them ad libitum. The holding of fish in groups may result in reduced food consumption, growth, and growth efficiency despite apparent ample food provisioning (Purdom, 1974; Jobling and Reinsnes, 1986; Jobling and Baardvik, 1994). Feeding regime can also influence food consumption and growth (Jobling, 1994; DeSilva and Anderson, 1995; Wang et al., 1998a). The ability of the fish to consume large amounts of food after deprivation periods was critical to the overcompensation response observed in our previous study, so we aimed to examine whether fish held in groups and fed to satiation would also display overcompensation and outgrow controls.

2. Materials and methods

Two experiments, designed to be comparable to our previous study (Hayward et al., 1997), were conducted. Each involved control fish fed meal worms (Tenebrio molitor) every day, and a treatment group fed meal worms on a repeating no-feed/ refereed schedule (hereafter, the D2 schedule). For the treatment groups, no-feed periods were fixed at 2 days while refeeding periods were continued until mean specific daily consumption (percentage body weight) no longer exceeded that of the controls (one-tailed t-test, \( P < 0.05 \), plus two additional days needed to analyze consumption data. Both experiments were run at 24 ± 1℃ with a 15 h light:9 h dark photoperiod regime.

2.1. Experiment I

Age-0 hybrid sunfish, obtained from a local producer in September 1997, were held in two 945-l tanks, equipped with biofiltration, water recirculation, and temperature control systems. Over 4 weeks, fish were exposed to water that was gradually increased from 20℃ to 24℃, a 15 h light:9 h dark photoperiod, and daily provision of meal worms.

Subsequently, 80 fish were placed into eight, perforated plastic chambers (43 × 30 × 43 cm\(^3\)), 10 fish per chamber, with four replicate chambers each for the control and treatment group. Fish were size-selected so that their mean weights and size ranges were similar among the eight chambers. The chambers were submerged to about one-half of their height, two control and two treatment chambers being in each of the two 945-l tanks. Water volumes were approximately 25 l per chamber. Tank water could move through the perforated chambers and open tops allowed fish to be fed and observed. The fish were hand-fed meal worms to apparent satiation four times daily (at 0800, 1200, 1600, and 2000 h), as described by Wang et al. (1998a).
The experiment began in October 1997, 2 weeks after the fish had been placed into the chambers, and was continued for 64 days. Starting mean weights of hybrid sunfish (and weight ranges across all fish) in the control and treatment groups, were 7.4 (3.7–13.5) and 7.5 g (4.0–13.3), respectively. Food consumption (g) by fish in each chamber was estimated daily by subtracting the weight of food remaining in a food can at the end of the day from the initial food weight. Daily food consumption (g) for an individual fish within a chamber was estimated by dividing combined daily food consumption by 10. Combined weights of fish in chambers were determined every week; this allowed for expression of food consumption as percentage body weight, so that control and treatment groups could be routinely compared, and stop dates determined for feeding periods of the D2 schedule Hayward et al., 1997. Weights of individual fish within each chamber were determined (nearest 0.1 g) on the first and last day of the experiment. For these weighings, fish were deprived of food for 24 h, blotted with a towel and transferred to a tared water-filled container.

2.2. Experiment 2

A second batch of age-0 hybrid sunfish was obtained in December 1997. These fish were held for 4 weeks in 945-l tanks at 24°C, fed daily with meal worms, and exposed to the same photoperiod as in Experiment 1. Two weeks before Experiment 2 began, 20 hybrid sunfish were selected on the basis of size similarity and placed individually into perforated, 3.25-l plastic chambers (20 × 12.5 × 13 cm³) submerged in one of the two 945-l tanks, 10 fish and chambers per tank. Each fish was then provided with meal worms ad libitum.

Experimentation began in February 1998 and continued for 68 days. Ten fish, five in each tank, comprised the control group in which fish were fed every day; the remaining 10 fish comprised the treatment group that was fed according to the D2 schedule. On all feeding days, the fish were fed ad libitum as described by Hayward et al. (1997): meal worms were provided once daily in amounts that substantially exceeded what fish could eat in 24 h. Starting mean weights (and ranges) were 15.2 (11.6–20.1) and 15.7 g (10.8–19.5) in the control and treatment groups, respectively. Daily food consumption (g) for individual fish was estimated as described by Hayward et al. (1997). Weights of individual fish were determined at the start of the experiment and then weekly.

2.3. Calculations

The number of feeding days in relation to the number of days of food deprivation (FD/DD) was calculated for the treatment group in each experiment to indicate the persistence of hyperphagia following the 2-day periods of food deprivation. Specific growth rate (SGR), gross growth efficiency (GGE), weight gain and cumulative consumption were each calculated as the average response among fish in a chamber in Experiment 1, and for individual fish in Experiment 2. Specific growth rate was calculated as SGR (%/day) = [100(ln W_f − ln W_i)/t], where W_f is the final weight, W_i is the initial weight, and t is the number of days in an experiment. GGE was estimated as weight gain/CC, where weight gain (g) = W_f − W_i, and CC is cumulative consump-
tion (g) over the experiment. Differences between control and treatment groups were determined by t-tests where P-values < 0.10 were considered to indicate significant differences. A value of P < 0.10 was chosen because previous work with hybrid sunfish has revealed pronounced inter-individual and among-replicate-group variation in consumption and growth responses (Hayward et al., 1997; Wang et al., 1998b), which reduces statistical power. Larger sample sizes were impractical in the present study due to the intensity of effort that would have been required.

3. Results

3.1. Experiment 1

Hybrid sunfish held in groups and fed to satiation on the D2 schedule performed less well than the controls, with weight gain, SGR and GGE all being lower for the treatment group (P < 0.10; Table 1). Fish fed according to the D2 regime exhibited some hyperphagia after the no-feed periods, so mean cumulative consumption was not significantly different from the controls (P = 0.194; Table 1) over the 64 days. The FD/DD value showed that 2-day no-feed periods in the treatment group, were followed by a hyperphagia that persisted for 2.9 days on average (Table 1).

3.2. Experiment 2

In this experiment, the D2 group gained 38% more weight than the controls (P < 0.10; Table 1), while GGE was no different (P = 0.35). Mean cumulative consumption by the D2 group exceeded that of the controls by 32% (P < 0.10; Table 1), and a FD/DD value of 3.9 indicated longer periods of hyperphagia than in Experiment 1 (Table 1).

Table 1

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Treatment</th>
<th>N</th>
<th>FD/r DD Variable</th>
<th>Cumulative consumption per fish (g)</th>
<th>Weight gain (g)</th>
<th>SGR (g/day)</th>
<th>GGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hayward et al. (1997)</td>
<td>Control</td>
<td>7</td>
<td>2.7</td>
<td>27.5 (4.1)</td>
<td>9.3 (6.1)</td>
<td>0.44 (0.07)</td>
<td>0.31 (0.04)</td>
</tr>
<tr>
<td>D2</td>
<td>7</td>
<td>3.7</td>
<td>48.7 (9.8)**</td>
<td>18.7 (11.9)*</td>
<td>0.74 (0.13)*</td>
<td>0.35 (0.03ns)</td>
<td></td>
</tr>
<tr>
<td>Experiment 1</td>
<td>Control</td>
<td>4</td>
<td>2.9</td>
<td>21.1 (0.9)</td>
<td>6.4 (0.4)</td>
<td>0.97 (0.04)</td>
<td>0.30 (0.01)</td>
</tr>
<tr>
<td>D2</td>
<td>4</td>
<td>2.9</td>
<td>18.4 (1.6ns)</td>
<td>4.9 (0.6)*</td>
<td>0.79 (0.08)*</td>
<td>0.27 (0.01)***</td>
<td></td>
</tr>
<tr>
<td>Experiment 2</td>
<td>Control</td>
<td>10</td>
<td>3.9</td>
<td>25.5 (2.5)</td>
<td>10.5 (1.2)</td>
<td>0.78 (0.07)</td>
<td>0.40 (0.02)</td>
</tr>
<tr>
<td>D2</td>
<td>9</td>
<td>3.9</td>
<td>34.3 (3.8)*</td>
<td>14.5 (1.7)*</td>
<td>0.94 (0.07)*</td>
<td>0.42 (0.01ns)</td>
<td></td>
</tr>
</tbody>
</table>

The FD/DD variable was based on the first 70 days of experimentation in Hayward et al. (1997) and the full experimental periods in Experiments 1 and 2 (64 and 68 days, respectively).

One fish died in the D2 group during Experiment 2.
4. Discussion

A previous study (Hayward et al., 1997), found that a particular, repeating no-feed/refeed schedule (the D2 schedule) elicited episodes of CG in age-0 hybrid sunfish, and it produced weight gains averaging twice that of controls fed every day (Table 1). This occurred because cumulative food consumption by the treatment fish substantially exceeded that of the controls, while growth efficiency remained similar.

In Experiment 1, hybrid sunfish held in groups and fed according to the D2 schedule did not outgrow the controls, but grew less when fed to satiation on scheduled feeding days. Although periods of hyperphagia did occur in the treatment group (indicating some CG), cumulative food consumption did not exceed that of the controls and growth efficiency was slightly lower. The low FD/DD value for the treatment group in Experiment 1, relative to those of the previous study (Hayward et al., 1997) and Experiment 2 (Table 1), indicates that cumulative food consumption did not exceed controls, in part, because hyperphagia persisted for fewer days. The results of Experiment 2 demonstrated the repeatability of applying the D2 schedule to induce overcompensation of CG in hybrid sunfish held individually and fed ad libitum. Weight gains in excess of controls were less in Experiment 2 (38%) than in the previous study (100%) (Hayward et al., 1997), but this difference is probably related to the shorter duration of Experiment 2 (68 vs. 105 days). Overall, our results indicate that the full potential to increase weight gain through CG may not be realized when fish are reared in groups.

Group rearing has been shown to reduce fish growth rates when competitive social interactions diminish food consumption and growth efficiency (McComish, 1971; Purdom, 1974; Jobling and Reinsnes, 1986; Jobling and Baardvik, 1994). For example, McComish (1971) found that food consumption of age-0 bluegill sunfish declined by more than 50% and growth efficiency by approximately 30% when fish were fed ad libitum every day in groups, vs. when they were held individually. It is possible that similar effects were operating for hybrid sunfish in Experiment 1, preventing all fish from reaching satiation and resulting in less than full achievement of CG. The reason why growth efficiency of the treatment fish was lower than for controls in Experiment 1 is not known. Conceivably, episodes of hyperphagia may have intensified energy expenditure among treatment fish (see Jobling and Wandsvik, 1983; Christiansen et al., 1991) relative to controls. We found, however, no difference in the development of size variation within the treatment group and the controls (t-test on percentage increase in CV, \( P = 0.14 \)), suggesting that any intensification relating to competition and social interactions was of minor proportions (cf. Jobling and Koskela, 1996). An inability of the treatment fish to achieve satiation during hyperphagic periods, could, however, have given rise to a lower growth efficiency because the D2 schedule seemed to produce submaximal CG responses that failed to match the growth of the controls even though cumulative consumption was similar.

With regard to feeding regime, Wang et al. (1998a) found that food consumption and growth of juvenile hybrid sunfish increased as the number of feedings per day increased from one to three (each feeding was to apparent satiation); no further increases occurred with four feedings per day. We fed fish to apparent satiation four times daily on
scheduled feeding days in Experiment 1 and consider it unlikely that food consumption was restricted by feeding in this manner.

Finding ways to reduce the effects of social interactions on food consumption and growth may be necessary in order to gain maximum growth benefits from CG in aquaculture settings. Holding fish at high densities, for example, has reduced the effects of social interaction on food consumption and growth in some cases (Jørgensen et al., 1993; de March, 1997). It is possible that the effect of group holding may be slighter in fish that are less aggressive and competitive than hybrid sunfish (Brunson and Robinette, 1986; R. Hayward, unpubl. data). Nonetheless, we suggest that individually held fish should represent the sample units in laboratory studies seeking to maximize fish growth with CG.

Acknowledgements

Primary funding for this study was provided by a grant from the North Central Regional Aquaculture Center. Additional support came from the Missouri Agricultural Experiment Station, the Missouri Aquaculture Council, and the Missouri Cooperative Fish and Wildlife Research Unit. This publication is a contribution from the Missouri Cooperative Fish and Wildlife Research Unit (the US Geological Survey, Missouri Department of Conservation, The School of Natural Resources of the University of Missouri-Columbia, and the Wildlife Management Institute cooperating).

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