

Compensatory Growth of Pond-reared Hybrid Striped Bass, *Morone chrysops* × *Morone saxatilis*, Fingerlings

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Abstract

Compensatory growth (CG) or “catch-up growth” is a period of super-accelerated growth following a period of suboptimal conditions (i.e., lack of prey availability or overwintering). Little is known about the CG response in pond-raised fish and whether hybrid striped bass (HSB), *Morone chrysops* × *Morone saxatilis*, might exhibit the rapid growth states or improvements in other production characteristics that may accompany the response. To evaluate the potential for CG in HSB culture, a 16-wk growth trial in twelve 0.1-ha earthen ponds was conducted. Approximately 2850 fish (mean weight ± SD = 3.2 g ± 1.1) were stocked into ponds and subjected to one of four cyclic feeding regimens. Treatment regimens included a control (0 wk, fed twice daily to apparent satiation) and cycles of 1, 2, or 4 wk of feed deprivation, followed by 1, 2, or 4 wk of feeding to apparent satiation. Fish in the 4-wk feeding regimen were offered feed twice during the feed-deprivation period (once every other week). Growth, specific growth rate (SGR), hepatosomatic index (HSI), intraperitoneal fat ratio, and condition factor (CF) were measured every other week, while overall growth, feed efficiency (FE) (FE = [weight gain/feed fed] × 100), and survival were calculated at the trial termination. The effect of these feeding regimens on water quality was examined by monitoring pH, turbidity, total ammonia nitrogen, nitrite–nitrogen, nitrate–nitrogen, soluble reactive phosphorus, and chlorophyll *a* weekly; total nitrogen and phosphorous biweekly; and dissolved oxygen and temperature twice daily. Cyclic feeding elicited CG; fish subjected to the 2-wk regimen had a significantly higher SGR than 0-wk controls during all but the final refeeding period. FE was higher for all fish in the cyclic regimens, although only FE for fish in the 2-wk regimen was statistically greater (40%) than the controls. HSI was the most responsive measure and significantly decreased in the 2- and 4-wk treatments during feed-deprivation period and overcompensated during the refeeding period. CF also varied with feeding cycle and proved to be an effective nonlethal measure of predicting a CG response. No statistical differences in water quality parameters were observed. These data suggest that CG can be effectively induced in pond-raised HSB and that the increase in FE warrants further research for practical application. Future pond studies with fingerling HSB fish should be conducted with emphasis on feed-deprivation periods of 2 wk and refeeding periods of at least twice that of the feed-deprivation period.

Hybrid striped bass (HSB), *Morone chrysops* × *Morone saxatilis*, culture is a major contributor to the US aquaculture industry, with total production for 2004 at 12 million pounds (Carlberg 2005). High costs of production and low fillet yield have slowed expansion (Carlberg 2005). Regulations on water usage and discharge could further negatively impact efforts to expand production and economic viability.

Economic sustainability will therefore rely on the development of methods to reduce production costs and minimize environmental impacts. One potential means of improving production and management of water quality is to develop methods that take advantage of compensatory growth (CG). This response, also known as “catch-up” growth, is a physiological process whereby an organism exhibits accelerated growth after a period of restricted development, usually as a result of reduced feed intake, in

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order to reach the weight of animals whose growth was never restricted (Hornick et al. 2000).

CG has been reported in terrestrial (reviewed by Wilson and Osbourn 1960) and aquatic (reviewed by Ali et al. 2003) animals. Quinton and Blake (1990) observed complete growth compensation in rainbow trout, *Oncorhynchus mykiss*, fed a cyclic regimen of 3 wk feed restriction, followed by 3 wk refeeding compared with those fed daily throughout the 12-wk study. Full growth compensation was also observed in Atlantic salmon, *Salmo salar*, subjected to an 8-wk restricted feeding regimen (50% of a predetermined optimal feeding level), followed by an 8-wk period of refeeding in excess (Johansen et al. 2001). CG has also been elicited in nonsalmonid species. Hybrid sunfish, *Lepomis cyanellus* × *Lepomis macrochirus*, doubled their growth rate and surpassed control fish (overcompensated) when subjected to 2 d of feed deprivation, followed by refeeding periods persisting until the hyperphagic response ceased (Haywood et al. 1997). This is the first and only study to report overcompensation. However, overcompensation was not reported when the study was repeated with group-housed fish as opposed to individually housed fish (Hayward et al. 2000). Channel catfish have also been shown to exhibit CG, both temporary and complete CG (Kim and Lovell 1995; Gaylord and Gatlin 2000; Chatakondi and Yant 2001; Li et al. 2005). Thus, the duration and extent of the CG response appear to be species specific and dependent on the specific feed deprivation/refeeding cycle used.

The above-mentioned studies have all been conducted in tanks, and to date, only two studies have been carried out in ponds (Kim and Lovell 1995; Li et al. 2005). In advanced catfish fingerlings, *Ictalurus punctatus*, growth rates were not significantly different between animals subjected to a restricted feeding regimen (fed every 3 d) for 3 wk and control fish fed daily at the end of an 18-wk growth trial (Kim and Lovell 1995). In addition, whole-body fat, protein, and moisture as well as dress-out percentage were similar between groups. Similarly, Li et al. (2005) reported no difference in net production between channel catfish offered cyclic

feeding regimens of 1:6, 1:4, and 2:5 (days not fed : days fed) and normally fed control fish. It is possible that production practices could be adopted in which a restricted period of feed is applied to pond-cultured fish to induce CG, increase feed efficiency (FE), and decrease costs associated with labor. Moreover, increases in FE may prove beneficial to water quality, providing additional potential for using cyclic feeding in production practices.

We have recently found that tank-reared juvenile HSB can undergo CG following limited feed deprivation (maintenance feeding) and that the response is accompanied by improved FE (Picha et al. 2006). It is uncertain whether this may hold true for pond-raised fingerling HSB, as pond environments and their biological processes are more variable and unpredictable relative to tank systems. In addition, the majority of HSB culture is conducted in ponds (57%). Therefore, the induction of CG through the practical application of different cyclic feeding regimens may show promise for cost savings and/or mitigating water quality problems for HSB producers. To this end, a 16-wk pond study was conducted to evaluate the effectiveness of cyclic feeding regimens to elicit a CG response and to mediate water quality problems in fingerling HSB grown in ponds.

Materials and Methods

Growth and Body Indexes

A 16-wk growth trial was conducted at the Tidewater Research Station in Plymouth, North Carolina, beginning in June 2003. Twelve 0.1-ha ponds were stocked with approximately 2850 fish/pond (28,500 fish/ha) and allowed to acclimate for 5 d. During acclimation, fish were fed twice daily at 20% body weight. Following acclimation, 30 fish, randomly chosen from three ponds, were measured for initial length (mean ± SD = 67.2 mm ± 7.1) and weight (mean ± SD = 3.2 g ± 1.1). Additionally, liver and intraperitoneal fat weights were obtained to determine hepatosomatic index (HSI) (HSI = wet liver weight × 100/body weight) and intraperitoneal fat (IPF) (IPF = wet weight of fat × 100/body weight) ratio.

Four feeding regimens consisting of alternating cycles of feed deprivation and refeeding were randomly assigned in triplicate to the 12 ponds. During all feeding periods, fish were fed to apparent satiation twice daily with a commercially available HSB diet (45% protein and 12% lipid; Melick Aquafeeds, Catawissa, PA, USA). Feeding frequency during all feeding periods was based on previous studies conducted on sunshine bass (Thompson et al. 2000; Webster et al. 2001). During the first 4 wk, fish were offered a set ration of 15% body weight because of the difficulty in determining apparent satiation. The four treatments were as follows: a control (0 wk) consisting of daily feeding; 1- and 2-wk treatments consisting of alternating equivalent periods of feed deprivation and then refeeding for 1 and 2 wk, respectively; and a 4-wk treatment of feed deprivation for 4 wk, followed by refeeding for 4 wk. During the feed-deprivation period for the 4-wk treatment, fish were fed 1 d every other week (twice during the feed-deprivation period).

Growth was measured at Week 4 and then at every 2 wk by seine sampling a section of each pond (bisecting the long axis) and obtaining a group wet weight (approximately 50 fish/pond). Specific growth rate (SGR) ($SGR = [100 \times \{\ln \text{Weight}_f - \ln \text{Weight}_i\} / \{\text{Time}_f - \text{Time}_i\}]$) was calculated based on average group weights of fish from each pond. At each sampling period, 10 fish were sacrificed to obtain individual weight, length, HSI, IPF ratio, and condition factor (CF) ($CF = [\text{weight in grams}/\text{length}^3 \text{ in mm}] \times 10^5$). Following the termination of the growth trial, each pond was drained approximately 45 cm and then fish were harvested by seining. Total harvest weight was recorded and a subsample from each pond (range: 143–200 fish/pond) taken for individual weight and length measurements and to calculate CV. Additionally, 10 fish/pond were frozen at -20°C for subsequent proximate analysis (AOAC 1995).

Water Quality

Water quality parameters were measured throughout the study to determine the effects of cyclic feeding on water quality. Temperature and dissolved oxygen (DO) were recorded twice

daily (0800 and 1600 h) with a YSI 550 (Yellow Springs Instrument Company, Yellow Springs, OH, USA). Water samples were taken weekly using a 90-cm water column sampler (Boyd and Tucker 1992) and analyzed for pH (Orion 720A pH meter; Thermoelectron Corp., Waltham, MA, USA), turbidity (DRT 100B turbidimeter; HF Scientific, Inc., Fort Myers, FL, USA), total ammonia nitrogen, nitrite–nitrogen, nitrate–nitrogen, and soluble reactive phosphorous (APHA et al. 1995). Weekly chlorophyll *a* measurements were also taken using methods described by Pechar (1987). Total nitrogen and total phosphorous were measured every 2 wk (APHA et al. 1995). Nightly aeration (2400–0830 h) was applied to each pond via 0.75-hp (6.6 hp/ha) paddlewheel aerators (Southern Machine Welding, Inc., Quinton, AL, USA). Emergency aeration was provided if DO levels in the morning were below 5 ppm until this level was reached and/or if DO levels at afternoon were below 7 ppm. Emergency hours of aeration were recorded.

Statistical Analysis

After meeting the assumption of homogeneity, mean production, survival (following arcsine transformation), CV, and mean overall water quality parameters were analyzed using a one-way ANOVA to determine significant differences ($P < 0.05$) among treatment means. Tukey's least significant difference test was used to separate significant differences between treatment means (Steel et al. 1997). Similarly, mean weight and FE were analyzed at Weeks 8 and 16 when all fish had been subjected to at least one or two complete feed deprivation/refeeding cycles, respectively. SGR, HSI, IPF ratio, and CF were analyzed at 2-wk intervals using a Student's *t*-test ($P = 0.05$) to contrast individual treatments against 0-wk control fish. All statistical analyses were conducted using the Statistical Analysis System (software version 8.2; SAS Institute, Inc., Cary, NC, USA).

Results

Results of production variables (growth and FE) were analyzed at 8 and 16 wk to coincide with

the time when all treatments had completed at least one or two production cycles, respectively.

Weeks 0–8

Fish readily adapted to the feeding regimens, with no effect on overall survival. Mean total production for ponds assigned the 0-wk regimen (control) was 62.3% higher than that for all other treatments (Table 1); but there were no significant differences among treatments. Following the first 8 wk of the study, no significant differences were observed in weight gain (Fig. 1). SGRs were calculated following the first 4 wk of the trial since a set ration was offered during feeding periods for this duration (Table 2). Fish in the 2-wk treatment had a significantly higher SGR than control fish and 1-wk-cycled fish at Week 8. SGR of fish in the 4-wk regimen was significantly higher than all other treatments at 6 wk; however, this difference was not observed at 8 wk.

FE during the first 8 wk was notably improved for all cyclic-fed fish ranging from 101.5 to 117.0% compared to 88% for the 0-wk fish (Table 2); however, only fish in the 4-wk treatment had significantly higher FE than control fish.

Weeks 8–16

During the final 8 wk of the trial, fish subjected to the control-feeding regimen were significantly larger (Fig. 1). Fish in the 2-wk treatment had a significantly higher SGR than the controls at Week 12 (Weeks 10–12; 2-wk after refeeding) (Table 2). An increase in SGR was observed for fish in the 4-wk regimen during the second complete cycle (Weeks 14 and 16); however, the effect was not statistically dif-

ferent from controls during this period. Similar to the first 8 wk, FE of all treatment fish was improved; however, only fish in the 2-wk regimen displayed statistically higher FE (98.3%) than control fish (70.2%).

In order to monitor fish health and energy partitioning, HSI and IPF ratio were measured throughout the study. Based on the rapid fluctuations in HSI levels following feed deprivation and refeeding, the liver appeared to be a highly responsive organ to variations in feed consumption (Fig. 2). Liver weights of fish subjected to cyclic feeding regimens decreased and reached their lowest mass within 2 wk of feed deprivation and exceeded that of 0-wk fish upon refeeding. As shown by fish offered the 4-wk regimen, liver weights reached control levels by the fourth week of refeeding. The rapid liver response in both treatments was similar during all complete feeding cycles. IPF ratio was not as responsive to the feeding regimens as HSI levels. Figure 3 shows variations in IPF ratios for all treatments during the trial. Although IPF ratio varied early for the 2- and 4-wk treatments, as fish grew larger, fluctuations in fat deposition stabilized.

CF was calculated during the study as a nonlethal means of evaluating the effect of cyclic feeding on fish. CF of fish in the 2-wk treatment decreased significantly with feed deprivation and recovered during refeeding (Fig. 4). A maximum of 2 wk of refeeding was necessary for the CF to return to levels similar to those in control fish, as indicated by fish in the 2- and 4-wk regimens. Cyclic feeding did not seem to affect overall body composition. No significant differences were observed in fish for whole-body percent dry matter (range: 31.7–33.3%), protein

TABLE 1. Mean production variables (\pm SEM) of fingerling hybrid striped bass (*Morone chrysops* \times *Morone saxatilis*) fed daily to satiation (control) or equal periods of feed deprivation/refeeding during a 16-wk study in ponds.¹

| Treatment | Production (kg/ha) | Survival (%) | CV for fish weight (%) |
|----------------|---------------------------------|------------------------------|-----------------------------|
| 0 wk (control) | 2149.6 \pm 479.2 ^a | 81.7 \pm 12.0 ^a | 31.0 \pm 4.2 ^a |
| 1 wk (1/1) | 1174.1 \pm 146.5 ^a | 67.3 \pm 1.6 ^a | 28.0 \pm 0.8 ^a |
| 2 wk (2/2) | 1322.4 \pm 43.9 ^a | 79.7 \pm 5.5 ^a | 32.0 \pm 8.0 ^a |
| 4 wk (4/4) | 1450.1 \pm 100.3 ^a | 85.2 \pm 9.1 ^a | 26.0 \pm 1.7 ^a |

¹ Values are means of three replicates per treatment. Means within columns with different superscript letters are significantly different ($P < 0.05$).

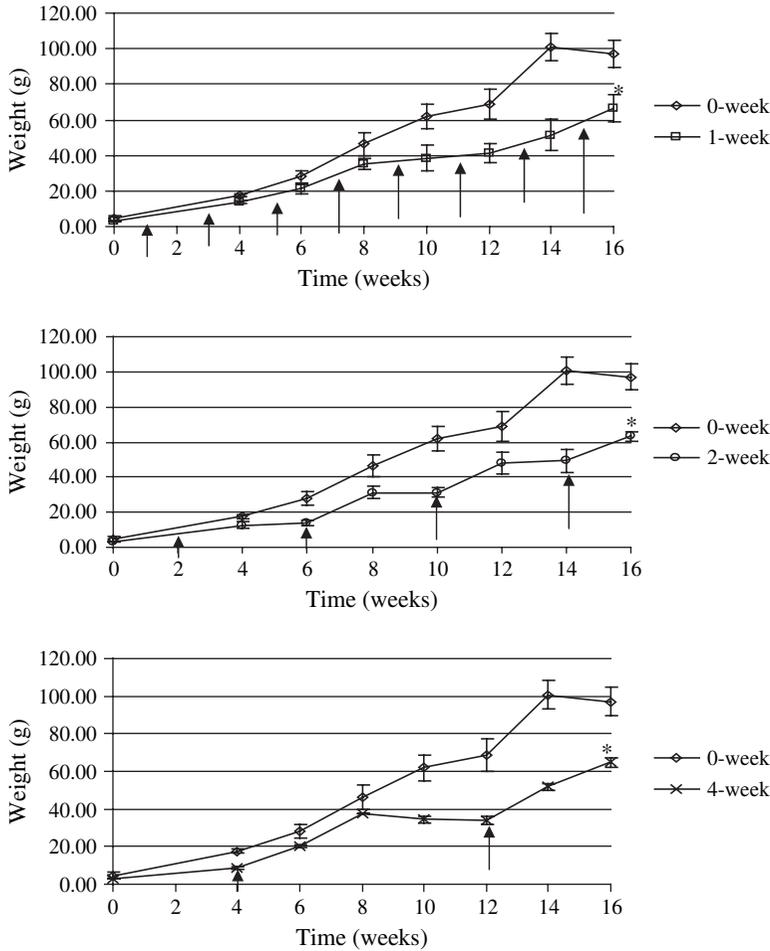


FIGURE 1. Weight (g) of fingerling hybrid striped bass (*Morone chrysops* × *Morone saxatilis*) fed twice daily to satiation (0-wk control) or consecutive cycles of equal periods of feed deprivation, followed by twice daily feeding to satiation (1, 2, and 4 wk). Arrows indicate start of refeeding period. The symbol “*” represents significant difference from 0-wk controls; $P < 0.05$.

(range: 47.0–49.2%), and fat (range: 35.1–37.3%) (Table 3). The different feeding strategies also did not influence size variation in fish because there were no differences in CV among fish in each treatment relative to the control group (Table 1).

Discussion

Fish respond to periods of feed deprivation by increasing SGR and/or FE during the refeeding period (reviewed by Ali et al. 2003). These responses in various fish species resulted in partial or complete growth compensation, with one study reporting overcompensation (Hayward

et al. 1997). Following the first 8 wk of the current trial, no significant differences in growth were observed between cycled fish, despite being fed only 50% of the total feed offered to control fish. However, the mean FE for the 1-, 2-, and 4-wk feeding regimens was 24.5% higher than that of the control group. This improved FE along with similar body sizes observed by 8 wk in treatment versus control fish suggests that the cyclic feed regimen was effective in inducing a CG response, characterized by increased SGR. It also appears that fish on the cyclic feed regimen may have better used pond resources by increasing the consumption

TABLE 2. Mean growth parameters of fingerling hybrid striped bass (*Morone chrysops* × *Morone saxatilis*) fed daily to satiation (control) or equal periods of feed deprivation/refeeding during a 16-wk study in ponds.

| Parameter | Treatment | Week | | | | | | |
|---------------------|----------------|------|------|---------------------|-----|------|-----|--------------------|
| | | 4 | 6 | 8 | 10 | 12 | 14 | 16 |
| SGR ¹ | 0 wk (control) | 5.4 | 3.2 | 3.6 | 2.1 | 0.7 | 2.8 | 0.0 |
| | 1 wk (1/1) | 5.2 | 3.0 | 3.6 | 0.5 | 0.6 | 1.6 | 1.9* |
| | 2 wk (2/2) | 4.8 | — | 5.7* | — | 3.0* | — | 1.9* |
| | 4 wk (4/4) | 3.5 | 6.1* | 4.4 | — | — | 3.0 | 1.6 |
| | 0 wk (control) | | | 88.8 ^a | | | | 70.2 ^b |
| FE (%) ² | 1 wk (1/1) | | | 101.5 ^{ab} | | | | 77.8 ^{ab} |
| | 2 wk (2/2) | | | 115.8 ^{ab} | | | | 98.3 ^a |
| | 4 wk (4/4) | | | 117.0 ^b | | | | 90.4 ^{ab} |
| | <i>P</i> value | | | 0.0442 | | | | 0.0414 |

FE = feed efficiency; SGR = specific growth rate.

¹ SGR = $(100 \times [\ln \text{Weight}_f - \ln \text{Weight}_i]) / [\text{Time}_f - \text{Time}_i]$. An “*” indicates significant differences from 0-wk control fish.

² FE = $(\text{weight gain}/\text{feed fed}) \times 100$. Means within columns with different superscript letters are significantly different ($P < 0.05$).

of natural productivity. Gut content analyses indicated the presence of both plant matter and zooplankton in addition to feed pellets.

Similar to the first 8 wk, FE of fish on the 1-, 2-, and 4-wk feeding regimens was higher than that of control fish at the completion of the trial. FE of fish offered the 2-wk feeding regimen was 40% higher ($P < 0.05$) than the control regimen. The elevated FE has important cost-saving implications, although the increased FE came at the expense of lost growth. Final weights of control fish were significantly higher than those of all cyclic-fed animals at the end of the trial, even though no growth was observed in control fish during the final 2 wk of the trial. It is unclear as to the reasons for the lack of growth in control fish; however, final sampling was conducted during the harvest, when fish were weighed in baskets rather than in buckets of water. Regardless, the overall difference between control and treatments groups remained.

The lack of complete growth compensation indicates that the CG response, as indicated by increases in SGR, was too brief to overcome lost weight. Additionally, it seems that when feed-deprivation cycles are repeated, the CG response becomes successively less dramatic. Similar findings with group-housed HSB raised in tanks were observed after a second cycle of 4 wk of limited feed deprivation (Picha et al. 2006). Temporary increases in growth rates have

also been observed in channel catfish (Gaylord and Gatlin 2000), where it was suggested that the period of feed deprivation may have been excessive, not allowing complete catch up. Similarly, in this study, the extent and duration of accelerated growth (CG response) were not sufficient to overcome lost growth.

Shorter feed-deprivation periods and longer refeeding periods have been shown to result in full growth compensation (Miglavys and Jobling 1989; Kim and Lovell 1995; Chatakondi and Yant 2001; Hayward and Wang 2001; Johansen et al. 2001). In this study, the shortest period of feed deprivation (1 wk) did not result in a significant increase in SGR upon refeeding when compared to normally fed fish (0-wk treatment). However, fish offered the 2-wk cyclic regimen displayed both increased SGR during the refeed and significantly higher FE at the end of the trial. Hence, 2 wk of feed deprivation is sufficient to trigger a measurable CG response that leads to improved FE in fingerling HSB. Because the final weight of fish in the 2-wk feeding regimen did not reach that in the 0-wk treatment, it would seem that although a CG response was elicited by 2 wk of feed deprivation, the increase in growth rate was not of sufficient magnitude or duration to compensate for lost growth. It is well known that growth, measured as a percentage of body weight, is more rapid in smaller fish than in larger ones

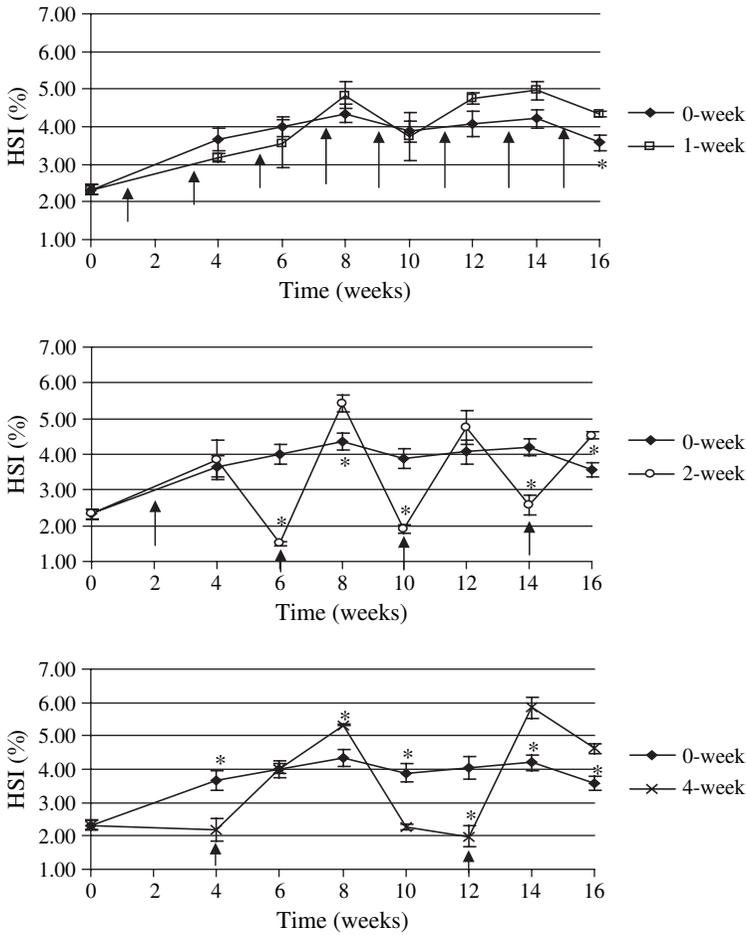


FIGURE 2. HSI (=liver weight \times 100/fish weight) of fingerling hybrid striped bass (*Morone chrysops* \times *Morone saxatilis*) fed twice daily to satiation (0-wk control) or consecutive cycles of equal periods of feed deprivation, followed by twice daily feeding to satiation (1, 2, and 4 wk). Arrows indicate start of refeeding period. The symbol “*” represents significant difference from 0-wk controls; $P < 0.05$. HSI = hepatosomatic index.

(Mommsen 2001). Therefore, it is possible that the rapid growth rates of smaller fish used in this study may have precluded the ability to elicit even greater growth rates through manipulation of feeding practices. Perhaps, a better CG response and hence full catch-up growth can be achieved in larger, slower growing fish or in production of market-sized animals. This is supported, in part, by previous studies by our group, where full growth compensation of individually tank-reared HSB was observed following 4 wk of feed deprivation (Skalski et al. 2005). Nevertheless, strategies to increase the length of the CG response in fast-growing fingerlings, such as regimens that incorporate longer refeeding

periods, may result in a more complete CG response.

Variations in the magnitude and duration of CG seen in studies of various fish suggest that the response is species specific (Hayward and Wang 2001) and highly dependent on the life history of the species being examined. The exact mechanisms underlying the CG response are yet to be elucidated (Ali et al. 2003). Broekhuizen et al. (1994) suggested a two-part model that describes an attainment of an optimal ratio between reserve and structural tissue. During feed deprivation, the ratio falls below this “ideal” level, at which time appetite increases but maintenance is steady. If feed deprivation

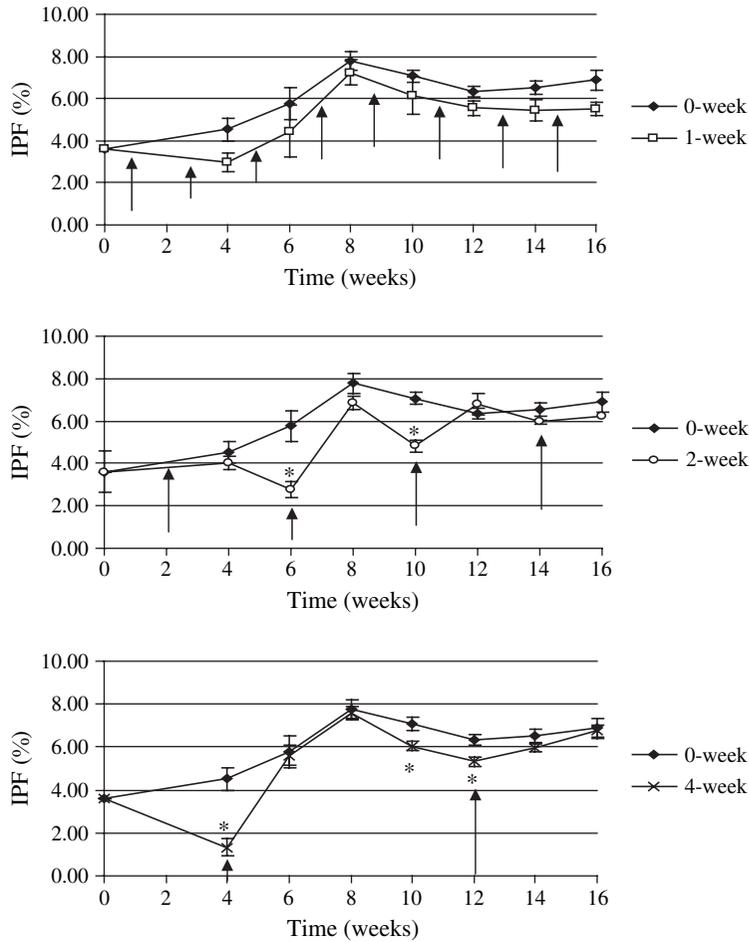


FIGURE 3. IPF ratio ($IPF = \text{fat weight} \times 100/\text{fish weight}$) of fingerling hybrid striped bass (*Morone chrysops* \times *Morone saxatilis*) fed twice daily to satiation (0-wk control) or consecutive cycles of equal periods of feed deprivation, followed by twice daily feeding to satiation (1, 2, and 4 wk). Arrows indicate start of refeeding period. The symbol "*" represents significant difference from 0-wk controls; $P < 0.05$. IPF = intraperitoneal fat.

persists, fish will minimize maintenance costs to increase chances of survival. Upon locating food, consumption is increased beyond the normal maintenance level in order to replenish the ratio; however, the maintenance cost stays at a minimum. The resulting increase in nutrient intake and decreased maintenance costs allow for more rapid growth, particularly in the form of muscle tissue. In this study, HSI levels were monitored in an attempt to estimate metabolic condition and provide an indication of sufficient feed deprivation (reserve tissue). Hepatic tissue responded rapidly to feed deprivation and reached a minimum level after 2 wk. Further re-

ductions in HSI were not observed even after 4 wk of feed deprivation. The reduction in liver size was likely because of glycogen depletion and may represent a maintenance state of metabolism. Gaylord and Gatlin (2000) observed a decrease in liver glycogen levels in channel catfish after 14 d of feed deprivation. In this study, HSI levels rebounded above those in control fish during the refeeding period. The rapid overcompensation of the liver could be a response mechanism where fish store excess glycogen in anticipation of future periods without feed. In this study, overcompensation of HSI (increase in liver mass) coincided with rapid

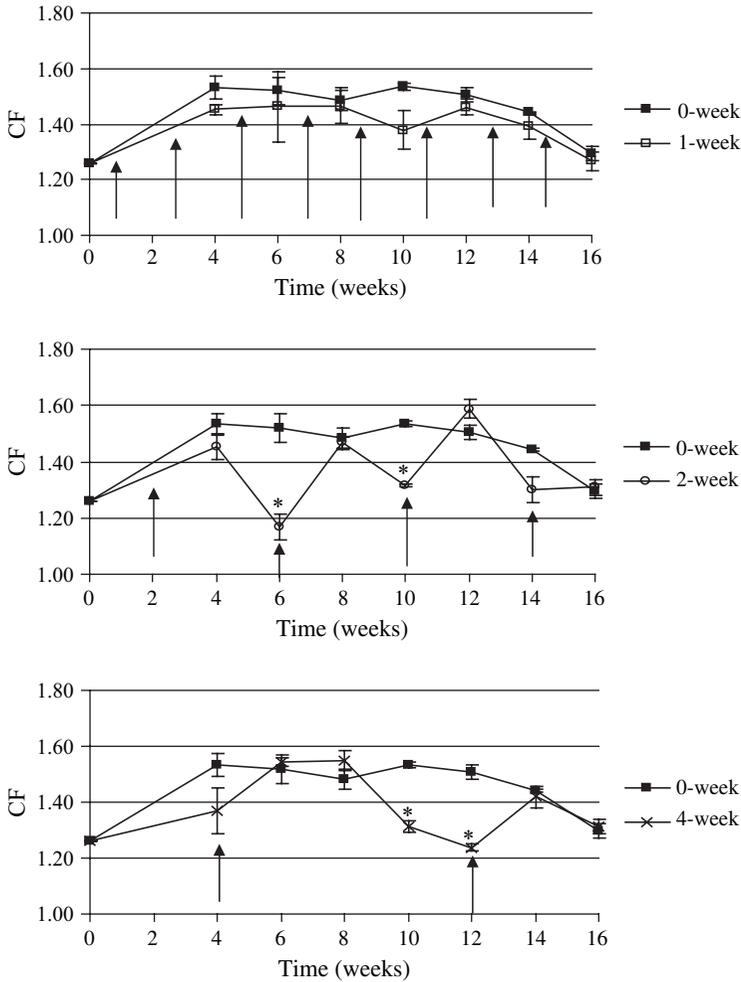


FIGURE 4. $CF (= [fish\ weight/length^3] \times 10^5)$ of fingerling hybrid striped bass (*Morone chrysops* \times *Morone saxatilis*) fed twice daily to satiation (0-wk control) or consecutive cycles of equal periods of feed deprivation, followed by twice daily feeding to satiation (1, 2, and 4 wk). Arrows indicate start of refeeding period. The symbol “*” represents significant difference from 0-wk controls; $P < 0.05$. CF = condition factor.

increases in SGR during the refeeding period and partly contributed to the rapid weight gain. Reduction of the HSI to 1.5 in fish in the 2-wk treatment and 2.2 in fish in the 4-wk treatment

led to significant increases in SGR during refeeding. Hence, a reduction in liver size may be an important indicator for a potential CG response. However, the transient nature of the

TABLE 3. Final proximate composition (mean \pm SEM) of fingerling hybrid striped bass (*Morone chrysops* \times *Morone saxatilis*) fed daily to satiation (control) or equal periods of feed deprivation/refeeding during a 16-wk study in ponds.¹

| Treatment | Protein (%) | Lipid (%) | Dry matter (%) |
|----------------|------------------------------|------------------------------|------------------------------|
| 0 wk (control) | 47.50 \pm 0.4 ^a | 37.27 \pm 0.6 ^a | 33.27 \pm 0.3 ^a |
| 1 wk (1/1) | 49.22 \pm 1.3 ^a | 35.14 \pm 1.2 ^a | 35.14 \pm 0.9 ^a |
| 2 wk (2/2) | 47.02 \pm 0.9 ^a | 35.45 \pm 0.8 ^a | 35.45 \pm 0.7 ^a |
| 4 wk (4/4) | 47.96 \pm 0.8 ^a | 36.54 \pm 0.6 ^a | 36.54 \pm 0.4 ^a |

¹ Means within columns with different superscript letters are significantly different ($P < 0.05$).

CG response observed in this study seemingly corresponds to the restocking of nutrients in the liver and return to normal growth. It is possible that identification of feeding regimens that sufficiently reduce HSI levels but do not lead to rapid overcompensation in the liver upon refeeding could result in a more sustained CG response and possibly complete growth compensation. A similar pattern of rapid decline during feed deprivation and overcompensation after refeeding was observed in IPF ratios of Arctic Charr (Miglav and Jobling 1989). Arctic Charr fed a restricted diet for 8 wk, followed by satiation feeding for 8 wk did not completely compensate for lost growth when final weights were compared to control fish. Whole-body lipid to lean body mass ratios were similar for both groups at the trial completion, leading the authors to suggest that the depletion of lipid stores led to a halt in the CG response and the failure to fully compensate for lost growth.

As a nonlethal measure of the effect of feeding regimen on the fish, CF was monitored throughout the study. CF values coincided with the feeding cycle for fish subjected to the 2- and 4-wk treatments. During feed deprivation, CF decreased significantly in both 2- and 4-wk treatment fish and was subsequently restored to control values within 2 wk of refeeding. This restoration accompanied the CG response, thereby allowing CF measurements to be used as a nonlethal predictor of CG.

Cyclical feeding of fish could promote hierarchical feeding and hence variation in fish size if the largest, more dominant fish consume a greater amount of feed during the refeeding period. This does not appear to be the case in this study because there were no significant variations in final weights of fish among treatment and control groups. This suggests that feed offered during the refeeding periods was enough to allow for equal access to the entire fish population. These results are similar to those of tank-raised HSB on 4-wk cycles of limited feed deprivation and satiation feeding, where feed consumption in group-housed individuals was tracked with lead-oxide-impregnated feed (Picha et al. 2006). Additionally, results of proximate composition indicated that all fish were similar in

whole-body protein, lipid, and moisture at the end of the study, further indicating no negative effects of the feeding cycles. Similar results were obtained with rainbow trout (Miglav and Jobling 1989; Quinton and Blake 1990; Kim and Lovell 1995; Wang et al. 2000). These results have further implications for commercial production in that implementation of cyclic feeding strategies do not have negative effects on overall body composition of the fish.

The increases in FE observed in cyclic-fed fish in the current study would not only reduce feed costs but may also have positive impacts on water quality. Only 25–30% of the nitrogen and phosphorus applied to ponds in feeds is recovered during the harvest (Boyd and Tucker 1998). Hence, a large amount of potential waste remains in the pond and must be assimilated. Despite differences in FE between treatments, significant differences in water quality variables were not observed in this study. Although stocking was similar to that of commercial fingerling production (Hodson 1995), average total feed input did not reach problematic levels. Cole and Boyd (1986) reported that feeding rates up to 56 kg/ha required relatively little aeration, whereas ponds with feeding rates of 112 kg/ha required almost constant nightly aeration. In this study, the highest maximum daily feeding rate reached 63.87 kg/ha, below the level requiring constant nightly aeration.

Summary and Conclusions

Cyclic feeding was successful in eliciting a CG response in fingerling HSB grown in ponds. Fish offered the 2-wk cyclic feeding regimen had a significantly higher SGR during refeeding periods and higher overall FE compared to other treatment groups and control fish. Based on the feeding regimens in this study, complete growth compensation was not observed. When compared to other studies, it seems that although 2 wk of feed deprivation was sufficient to cause a CG response, the subsequent 2 wk of refeeding was insufficient to allow complete catch up. A longer refeeding period is likely needed to allow fish to regain lost growth. The HSI was a highly responsive measure of feed deprivation; feeding strategies

to gradually replenish energy stores during refeeding could result in a longer period of growth compensation. Improvements in water quality were not observed in this study, likely because of reduced stocking density and feed inputs. Future pond studies with fingerling HSB should be conducted with emphasis on feed-deprivation periods of 2 wk and refeeding periods of at least twice that of the feed-deprivation period. Additional studies should also be conducted with larger fish to observe whether the CG response in slower growing individuals is enhanced and if pond water quality is impacted to a greater extent. Furthermore, the use of HSI as an indicator of metabolic condition seems promising, and future studies should be directed toward hepatic function and the mechanisms that control nutrient partitioning.

Acknowledgments

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Literature Cited

- Ali, M., A. Nicieza, and R. J. Wootton. 2003. Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries* 4:147–190.
- AOAC. 1995. Official methods of analysis. Association of Official Analytical Chemists International, Arlington, Virginia, USA.
- APHA, American Water Works Association, and Water Pollution Control Federation. 1995. Standard methods for the analysis of water and wastewater, 19th edition. American Public Health Association, Washington, D.C., USA.
- Boyd, C. E. and C. S. Tucker. 1992. Water quality and pond soil analysis for aquaculture. Alabama Agricultural Experimental Station, Auburn University, Auburn, Alabama, USA.
- Boyd, C. E. and C. S. Tucker. 1998. Pond aquaculture water quality management. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Broekhuizen, N., W. S. C. Gurney, A. Jones, and A. D. Bryant. 1994. Modeling compensatory growth. *Functional Ecology* 8:770–782.
- Carlberg, J. M., M. J. Massingill, R. J. Chamberlain, and J. C. Van Olst. 2005. Production and sales of farm-raised hybrid striped bass from 1987–2004. Aquaculture America Conference, New Orleans, Louisiana, USA.
- Chatakondi, N. G. and R. D. Yant. 2001. Application of compensatory growth to enhance production in channel catfish *Ictalurus punctatus*. *Journal of World Aquaculture Society* 32:278–285.
- Cole, B. A. and C. E. Boyd. 1986. Feeding rate, water quality, and channel catfish production in ponds. *The Progressive Fish Culturist* 48:25–29.
- Gaylord, T. G. and D. M. Gatlin, III. 2000. Assessment of compensatory growth in channel catfish *Ictalurus punctatus* and associated body changes in body condition indices. *Journal of the World Aquaculture Society* 31(3):326–336.
- Hayward, R. S. and N. Wang. 2001. Failure to induce overcompensation of growth in maturing yellow perch. *Journal of Fish Biology* 59:126–140.
- Hayward, R. S., D. B. Noltie, and N. Wang. 1997. Notes: use of compensatory growth to double hybrid sunfish growth rates. *Transactions of the American Fisheries Society* 126:316–322.
- Hayward, R. S., N. Wang, and D. B. Noltie. 2000. Group holding impedes compensatory growth of hybrid sunfish. *Aquaculture* 183:299–305.
- Hodson, R. G. 1995. Farming a new fish: hybrid striped bass. North Carolina Sea Grant, Publication UNC-SG-95–10. North Carolina Sea Grant, Raleigh, North Carolina, USA.
- Hornick, J. L., C. Van Eenae, O. Gerard, I. Dufranse, and L. Istasse. 2000. Mechanisms of reduced and compensatory growth. *Domestic Animal Endocrinology* 19:121–132.
- Johansen, S. J. S., M. Ekli, B. Stagnes, and M. Jobling. 2001. Weight gain and lipid deposition in Atlantic salmon, *Salmo salar*, during compensatory growth: evidence for lipostatic regulation? *Aquaculture Research* 32:963–974.
- Kim, M. K. and R. T. Lovell. 1995. Effect of feeding regimens on compensatory weight gain and body tissue changes in channel catfish, *Ictalurus punctatus* in ponds. *Aquaculture* 135:285–293.
- Li, M. H., E. H. Robinson, and B. G. Bosworth. 2005. Effects of periodic feed deprivation on growth, feed efficiency, processing yield, and body composition of channel catfish *Ictalurus punctatus*. *Journal of the World Aquaculture Society* 36(4):444–453.
- Miglavs, I. and M. Jobling. 1989. The effects of feeding regimen on proximate body composition and patterns of energy deposition in juvenile Arctic charr, *Salvelinus alpinus*. *Journal of Fish Biology* 35:1–11.
- Mommsen, T. P. 2001. Paradigms of growth in fish. *Comparative Biochemistry and Physiology Part B* 129:207–219.
- Picha, M. E., J. T. Silverstein, and R. J. Borski. 2006. Discordant regulation of hepatic IGF-I mRNA and

- circulating IGF-I during compensatory growth in a teleost, the hybrid striped bass (*Morone chrysops* X *M. saxatilis*). *General and Comparative Endocrinology* 147:196–205.
- Pechar, L.** 1987. Use of an acetone:methanol mixture for the extraction and spectrophotometric determination of chlorophyll-a in phytoplankton. *Algological Studies* 78(1):99–117.
- Quinton, J. C. and R. W. Blake.** 1990. The effect of feed cycling and ration level on the compensatory growth response in rainbow trout, *Oncorhynchus mykiss*. *Journal of Fish Biology* 37:33–41.
- Skalski, G. T., M. E. Picha, J. F. Gilliam, and R. J. Borski.** 2005. Variable intake, compensatory growth and increased growth efficiency in fish: models and mechanisms. *Ecology* 86(6):1452–1462.
- Steel, R. G. D., J. H. Torrie, and D. A. Dickey.** 1997. Principles and procedures of statistics. A biometrical approach. McGraw-Hill, New York, New York, USA.
- Thompson, K. R., C. D. Webster, A. M. Morgan, and E. J. Grisby.** 2000. Effects of different feeding frequencies on growth, body composition, and fillet composition of juvenile sunshine bass, *Morone chrysops* x *M. saxatilis*, grown indoors. *Journal of Applied Aquaculture* 10(2):55–65.
- Wang, Y., Y. Cui, Y. X. Yang, and F. S. Cai.** 2000. Compensatory growth in hybrid tilapia, *Oreochromis mossambicus* x *O. niloticus*, reared in seawater. *Aquaculture* 189:101–108.
- Webster, C. D., K. R. Thompson, A. M. Morgan, E. J. Grisby, and S. Dasgupta.** 2001. Feeding frequency affects growth, not fillet composition, of juvenile sunshine bass *Morone chrysops* X *M. saxatilis* grown in cages. *Journal of the World Aquaculture Society* 32:79–88.
- Wilson, P. N. and D. F. Osbourn.** 1960. Compensatory growth after undernutrition in mammals and birds. *Biological Review* 35:324–363.