Aquaculture Research

Aquaculture Research, 2008, **39**, 1514–1523 doi: 10.1111/j.1365-2109.2008.02023.x

Effects of cyclic feeding on compensatory growth of hybrid striped bass (*Morone chrysops* × *M. saxitilis*) foodfish and water quality in production ponds

Marc J Turano, Russell J Borski & Harry V Daniels

Department of Zoology, North Carolina State University, Raleigh, NC, USA

Correspondence: M J Turano, North Carolina Sea Grant, North Carolina State University, Box 8605, 1575 Varsity Drive, Module 1, Raleigh, NC 27695, USA. E-mail: marc.turano@ncsu.edu

Abstract

An 18-week study was conducted in 12, 0.1 ha ponds to evaluate the impacts of cyclic feeding regimes on hybrid striped bass (HSB) foodfish production and pond water quality. Approximately 840 HSB [mean weight (std.); 91.08 g (8.18)] were stocked into each pond (8400 fish ha^{-1}; 3360 fish acre^{-1}) and fed according to one of three feeding regimes. The three feeding regimes included a control (fed twice daily to apparent satiation), and cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of feeding to apparent satiation (3/3 and 3/6 respectively). Compensatory growth (CG) was observed in both cyclic feeding treatments; however, the response was insufficient for the fish to completely regain lost weight. Final mean weight of control fish (477.9 g) exceeded ($P < 0.05$) that of fish receiving the two cyclic treatments: 3/6 (404.7 g) and 3/3 (353.8 g). Specific growth rate (SGR) of fish in the 3/3 treatment increased during all three refeeding periods, and was significantly greater than controls during weeks 9–12 and weeks 15–18, which represent the refeeding phase of the second and third feeding cycles. Specific growth rate for fish in the 3/6 treatment was significantly higher than controls only during the first 3 weeks of the first feeding cycle. Hepatosomatic index and condition factor were highly responsive measures that closely followed the metabolic state of fish on the feeding cycle. Of the water quality variables measured, total phosphorus was 32% lower in ponds receiving cyclic feeding versus control ponds. Soluble reactive phosphorus was 41% and 24% lower in ponds offered the 3/3 and 3/6 cyclic feeding treatments, respectively, although, significant differences ($P < 0.10$) were only observed between control and 3/3 treatment ponds. Overall, CG was observed in HSB foodfish grown in ponds, although 3 weeks of feed deprivation was excessive and did not allow for complete growth compensation. Weight loss during feed deprivation was influenced by pond water temperatures. Early season feed deprivation did not cause as much weight loss as during the second cycle later in the season. Further studies on shorter deprivation periods applied during moderate to low water temperatures are needed to identify feeding regimes that minimize weight loss and result in a complete CG response.

Keywords: compensatory growth, feed deprivation, hybrid striped bass, water quality

Introduction

Seasonal variations in food supply cause many species of fish to endure periods of starvation (Van Dijk, Hardewig & Holker 2005). Once food becomes available, some species exhibit compensatory growth (CG), or periods of accelerated weight gain exceeding that of fish not previously exposed to food shortages (Hornick, Van Eenaeme, Gerard, Dufranse & Istasse 2000). Depending on the species and experimental condition, animals have shown increased growth rates that result in partial or even complete growth compensation, while in other studies, no evidence of growth compensation was reported (see review by Ali, Nicieza & Wootton 2003). Interest in CG has increased because of its possible use in aquaculture, specifically to enhance growth and feed efficiency (FE), potentially reducing production costs and assisting in water quality management.

Cyclic feeding regimes (periods of feed deprivation followed by refeeding) in fish production attempts to mimic the natural fluctuation in prey availability and trigger CG. However, because the exact mechanisms of CG are poorly understood (Hornick *et al.* 2000), the ideal feeding cycles have not been identified. Additionally, the CG response may be species specific (Hayward & Wang 2001) and altered by factors such as sex, state of maturity, diet composition and severity of feed restriction (Quinton & Blake 1990). Hence, cyclic feeding regimes to elicit the desired CG response will likely need to be specific to the culture situation of interest.

Few studies have evaluated cyclic feeding regimes in ponds. Kim and Lovell (1995) reported that feeding channel catfish (*Ictalurus punctatus*) every third day for 3 weeks did not significantly alter final weight, providing evidence of CG. Only dissolved oxygen (DO) was measured in the study, hence the effect of feed restriction on nutrient levels could not be evaluated. In another pond study, no difference in net production between channel catfish offered cyclic feeding regimes of 1:6, 1:4 and 2:5 (days feed deprived: days fed) and normally fed control fish was reported (Li, Robinson & Bosworth 2005). More recently, Turano, Borski and Daniels (2007) found that fingerling hybrid striped bass (HSB) that experienced periods of 2 or 4 weeks feed deprivation followed by refeeding for a similar duration resulted in partial growth compensation and improved FE. These findings are similar to what we observed with group-housed HSB raised in tanks under only partial feed restriction and refeeding (Picha, Silverstein & Borski 2006). Because pond culture is conducted in a dynamic and biologically diverse environment, as opposed to more controlled tank experiments, additional factors must be taken into consideration in the design of pond studies. Specifically, because of the availability of natural prey, extended periods of feed deprivation may be necessary to obtain a similar metabolic state as fish exposed to shorter feed deprivation periods in tanks. Additionally, seasonal fluctuations in temperature can influence the amount of time necessary to lower metabolic rate, and may also affect growth during the refeeding period. Hence, there is a need to conduct studies on CG responses in ponds independent of what may be observed with tank trials. In addition, use of cyclic feeding regimes may also have an overall effect on pond water quality, particularly if FE is increased. Enhancements in FE may help to improve overall nutrient retention, while periods of feed deprivation could be used during periods of maximum feeding to assist in management of phytoplankton. The purpose of this study was to determine the extent that periodically feed-deprived HSB could achieve growth exhibited by daily fed controls through elicitation of CG, and favourably influence pond water quality.

Methods

An 18-week growth trial was conducted at the Tidewater Research Station in Plymouth, NC. Twelve 0.1 ha ponds were stocked in May 2004 with approximately 840 fish pond^{-1} (8400 fish ha^{-1}), mean weight 78.0 g fish^{-1}. Fish were allowed to acclimate for 2 weeks during which time they were fed twice daily to apparent satiation. Following the acclimation period, each pond was assigned one of three feeding regimes; a control (fed twice daily to apparent satiation), or 3 weeks of feed deprivation followed by 3 or 6 weeks of twice daily feeding to apparent satiation (3/3 and 3/6 respectively). The 3/3 treatment fish went through three complete cycles whereas the 3/6 treatment fish completed two cycles of feed deprivation followed by satiation feeding. Each treatment had four replicates. After the 2-week acclimation period, fish were sampled from each pond to obtain an initial weight. Ten fish from each pond were sacrificed to obtain individual weights, lengths, and liver and intraperitoneal fat weights. Hepatosomatic index (HSI = [wet liver weight/body weight] × 100) and intraperitoneal fat ratio (IPF = [wet weight of fat/body weight] × 100) and condition factor [CF; (weight in grams/length^3 in mm) × 10^5] were calculated. Growth and body indices were measured every 3 weeks for 18 weeks. Specific growth rate $\{\text{SGR} = [(\ln \text{weight}_f - \ln \text{weight}_i)/(\text{Time}_f - \text{Time}_i)] \times 100\}$ was calculated based on average group weights of fish from each pond beginning at week 3, while FE [FE = (body weight/weight of feed in grams) × 100] was calculated at the end of the trial (week 18). Following the trial termination, each pond was drained approximately 45 cm, and harvested twice by seining. Growth and body indices were sampled, and total harvest weight (kg ha^{-1}) recorded.

Water quality

Water quality was measured during the trial to determine the effects of cyclic feeding on various water quality parameters. Water samples were taken weekly using a 90 cm water column sampler (Boyd

& Tucker 1992) and analysed for pH (Orion 720 A pH meter; Thermoelectron, Waltham, MA, USA), turbidity (DRT 100B turbidimeter, HF Scientific, Fort Myers, FL, USA), total ammonia-nitrogen (TAN), nitrite-nitrogen (NO_2-N), nitrate-nitrogen (NO_3-N) and soluble reactive phosphorous (SRP) (APHA 1995), and chlorophyll-*a* (Pechar 1987). Total nitrogen (TN) and total phosphorous (TP) were measured every 2 weeks (APHA 1995). Total ammonia-nitrogen and SRP were also measured 1, 3 and 5 days following each refeeding period in treatment and control ponds.

Temperature and DO were recorded twice daily (08:00 and 16:00 hours) with a YSI 550 (Yellow Springs Instrument Company, Yellow Springs, OH, USA). Nightly (24:00–08:30 hours) aeration was applied to each pond via 0.75-hp paddlewheel aerators (Southern Machine Welding, Quinton, AL, USA). Additional hours of aeration were provided if morning DO levels were below 5 mg L^{-1} until this level was reached and/or if afternoon DO levels were below 7 mg L^{-1}. Additional hours of aeration were recorded.

Statistical analysis

All values are expressed as mean ± SEM. All test variables were analysed for differences from controls using a one-way analysis of variance (ANOVA) followed by a Tukey's HSD test to separate the means (Steel, Torrie & Dickey 1997). Additionally, pre-planned contrasts were conducted to compare each treatment separately against the control. Survival data were arcsin transformed before analysis. Significant differences were determined at the $P<0.05$ level for all growth and body indices data, while water quality parameters were considered significant at the $P<0.10$ level. The *P*-value used for water quality analyses was chosen as a result of increased variance between ponds commonly observed in pond water quality studies (Boyd 1990; Queiroz & Boyd 1998). All statistical analyses were conducted using the Statistical Analysis System (SAS; v8.2, Cary, NC, USA).

Upon initial data analyses, it was found that one pond assigned the control treatment was incorrectly stocked. Hence, all data analyses were conducted based on three replicates for the control treatment, and four replicates for each cyclic treatment.

Results

Growth and body indices

All experimental fish adapted well to the feeding regimes. No significant differences were found for survival (%), overall production (kg ha^{-1}) and FE (%). Production was the highest for the control treatment (2528.2 kg ha^{-1}) followed by the 3/6 (2485.9 kg ha^{-1}) and 3/3 (1703.9 kg ha^{-1}) treatments respectively (Table 1). Fish in the control group were significantly larger (477.9 g) than fish in the 3/6 (404.7 g) and 3/3 (353.8 g) treatments respectively (Fig. 1). During the first 3 weeks, fish in both cyclic feeding treatments gained an average of 5 g, despite the lack of feed. During subsequent feed deprivation periods, 3/3 treatment fish lost 0.5% and 13.3% body weight, and 3/6 treatment fish lost 12.2% body weight. Fish in the 3/3 treatment had a significantly higher SGR than control fish during all refeeding periods, while the SGRs of fish in the 3/6 treatment were only statistically higher than controls during the first 3 weeks of the first refeeding period (Fig. 2).

Liver weight closely followed changes in nutritional input associated with the feeding cycles (Fig. 3). Hepatosomatic indices for all cyclic fed fish decreased significantly compared with control fish after each 3-week feed deprivation period. During refeeding, overcompensation of the liver was observed for fish

Table 1 Mean production variables (± SEM) for hybrid striped bass foodfish subjected to twice daily feeding to satiation (control) or cycles of 3 weeks feed deprivation followed by 3 or 6 weeks twice daily feeding to satiation during an 18-week compensatory growth study in ponds*

Treatment	Initial weight (g)	Final weight (g)	Production (kg ha^{-1})	Survival (%)	Feed efficiency† (%)	Total feed (kg)
Control ($n=3$)	90.4 ± 2.4	477.9 ± 10.3^a	2528.2 ± 99.7	78.1 ± 1.8	71.9 ± 1.3	3511.9 ± 79.7^a
3/3 ($n=4$)	94.2 ± 7.6	353.8 ± 7.8^c	1703.9 ± 76.1	81.3 ± 3.4	76.9 ± 2.7	2218.8 ± 80.5^b
3/6 ($n=4$)	89.5 ± 1.0	404.7 ± 7.7^b	2485.9 ± 407.3	88.8 ± 4.5	78.0 ± 2.6	3148.5 ± 403.8^a
Pr> *F*	$P=0.7690$	$P<0.0001$	$P=0.1651$	$P=0.2068$	$P=0.2742$	$P=0.0243$

*Means followed by different letters indicates a significant difference ($P<0.05$).

†Feed efficiency [FE = (weight gain/food fed) × 100)].

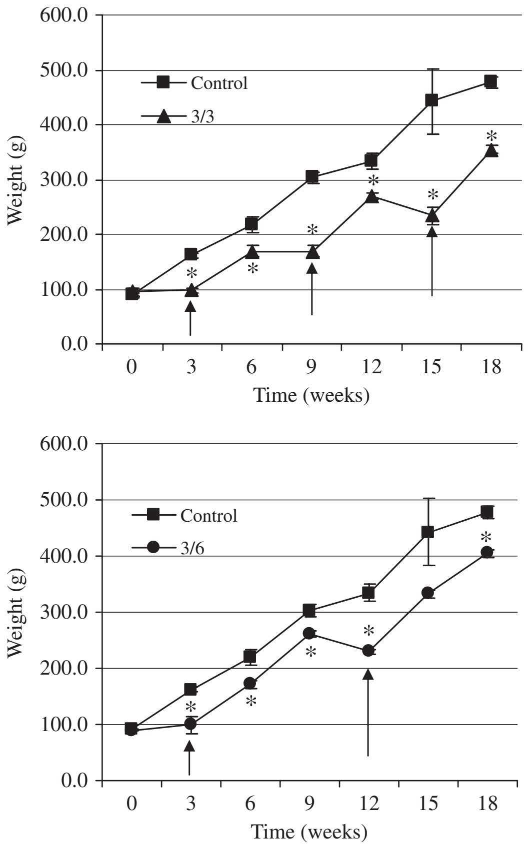

Figure 1 Weight (g) of foodfish hybrid striped bass fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively. Arrows indicate start of refeeding (* significant difference from controls, $P<0.05$).

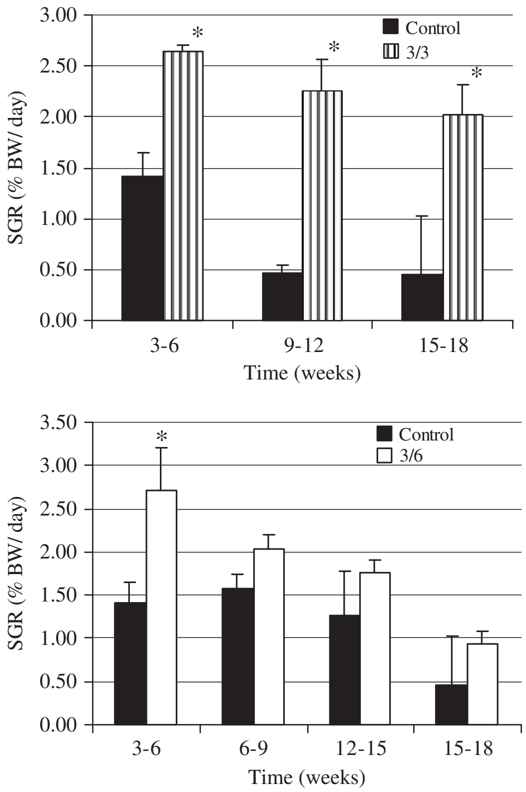

Figure 2 Specific growth rate $\{\mathrm{SGR} = [\,(\ln \mathrm{Weight}_f - \ln \mathrm{Weight}_i)/(\mathrm{Time}_f - \mathrm{Time}_i) \times 100]\,\}$ of hybrid striped bass during the refeeding phase of the cyclic feeding regime versus that of control fish during the same time period. Fish were fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively (* significant difference from controls, $P<0.05$).

in both cyclic treatments. Hepatosomatic index was restored to control levels following 6 weeks of refeeding as observed in 3/6 treatment fish.

Intraperitoneal fat levels varied early in the trial, however this variation diminished after week 9 (Fig. 4). Following the first 3 weeks of feed deprivation, the IPF ratio of fish in both cyclic treatments significantly decreased, and then rebounded to control levels after 3 weeks of refeeding. Changes in IPF levels of fish in the 3/3 treatment during the second feeding cycle followed a similar pattern to that of the first cycle. By the third cycle, however, there was no significant reduction in IPF during feed deprivation as seen at week 15 (Fig. 4).

Condition factor varied with the feeding cycle for both treatments (Fig. 5). Fish subjected to the cyclic feeding regimes showed a significant decrease in CF during each feed deprivation period, which returned to levels similar to that of control fish during the 3 weeks of refeeding. The additional 3 weeks of refeeding offered to fish in the 3/6 treatment resulted in a statistically higher CF relative to control fish (overcompensation), but only during the first refeeding period. All CF measurements were statistically similar at the end of the trial.

Water quality

Significant differences ($P<0.10$) were found in overall TP, SRP and chlorophyll-*a* (Table 2). Ponds in the 3/3 and 3/6 treatments had 38% and 25% less TP than the controls. Chlorophyll-*a* was 28% and 12% lower in the 3/3 and 3/6 treatments than in control ponds, and SRP was 41% and 24% lower than controls in the 3/3 and 3/6 treatments respectively.

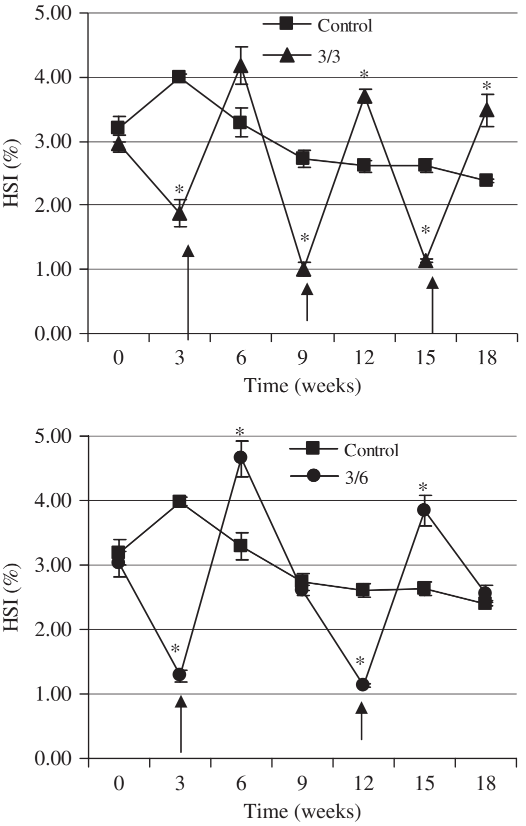

Figure 3 Hepatosomatic index (HSI = [liver weight/fish weight] × 100) of hybrid striped bass fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively. Arrows indicate start of refeeding (* significant difference from controls, $P < 0.05$)

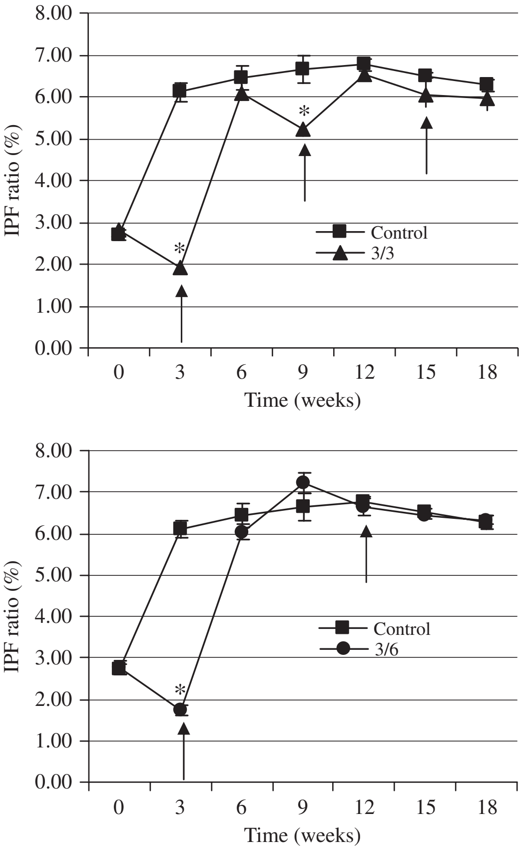

Figure 4 Intraperitoneal fat (IPF) ratio (IPF = [fat weight /fish weight] × 100) of hybrid striped bass fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively. Arrows indicate start of refeeding (* significant difference from controls, $P < 0.05$).

Chlorophyll-*a* and SRP levels in ponds in the 3/3 group were statistically lower than control ponds. Total phosphorus was significantly lower in the 3/3 treatment compared with control ponds at all sampling periods except time 0 (Fig. 6). The 3/6 ponds had lower TP levels than control ponds throughout the study, however, statistical differences were only observed at weeks 3 and 5. Soluble reactive phosphorus concentrations varied with feeding cycle for the first 9 weeks of the study, decreasing with feed deprivation and increasing with refeeding for ponds in both cyclic regimes (Fig. 7). Statistical differences were only observed, however, between control and 3/3 treatment ponds at 12 and 15 weeks. Soluble reactive phosphorus was significantly lower in the 3/6 treatment ponds than control ponds at 18 week. Following week 9, SRP in cyclic fed ponds remained below that of control ponds for the remainder of the study, although this trend was not statistically significant. Finally, chlorophyll-*a* measurements closely followed the feeding cycles, decreasing during feed deprivation and increasing during refeeding (Fig. 8). However, this pattern was observed only after week 3 as all ponds had an increase in chlorophyll-*a* during the first 3 weeks of the study, regardless of whether feed was offered. Statistical differences in chlorophyll-*a* were observed between the control and 3/3 treatment ponds at 15 and 18 weeks, and between controls and the 3/6 treatment ponds at 3 week. There were no other statistical differences in other water quality parameters observed, and no patterns could be determined from samples taken 1, 3 and 5 days during the refeeding periods.

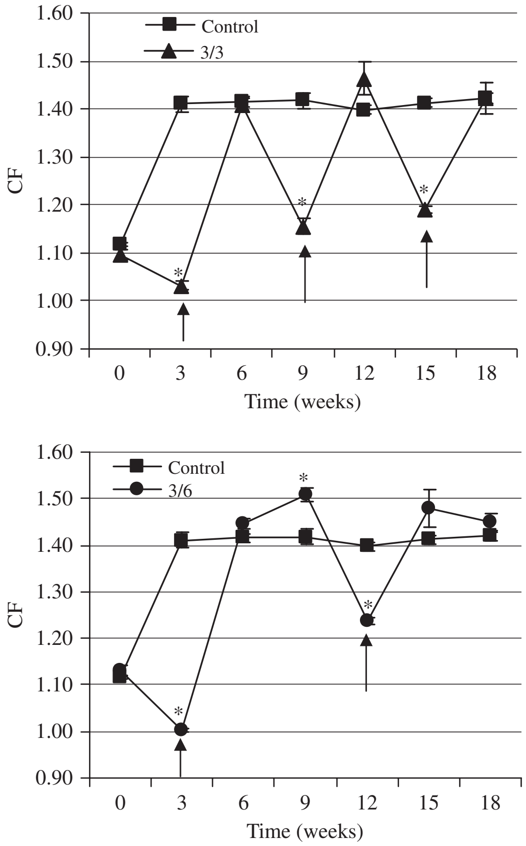

Figure 5 Condition factor [CF = (fish wt/length^3) × 10^5] of foodfish hybrid striped bass (*Morone chrysops* × *M. saxatilis*) fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively. Arrows indicate start of refeeding (* significant difference from controls, $P < 0.05$).

Discussion

Growth and body indices

All fish offered the cyclic feeding regime exhibited CG as defined by elevated SGR relative to control fish that were never exposed to feed deprivation. The CG response observed here is similar to that shown for other species grown in either tanks or ponds, including the catfish (Gaylord & Gatlin III 2000), hybrid sunfish *Lepomis cyanellus* × *Lepomis macrochirus* (Hayward, Noltie & Wang 1997; Hayward, Wang & Noltie 2000), yellow perch *Perca flavescens* (Hayward & Wang 2001), Atlantic salmon *Salmo salar* (Thorpe, Talbot, Miles & Keay 1990; Reimers, Kjorrefjord & Stavostrand 1993; Johansen, Ekli, Stagnes & Jobling 2001; Morgan & Metcalfe 2001), Artic char *Salvelinus*

Table 2 Mean (± SEM) overall pond water quality variables during an 18-week growth trial in which fish were fed twice daily to satiation (control), or cycles of 3 weeks of feed deprivation followed by twice daily feeding to satiation for 3 or 6 weeks, 3/3 and 3/6 respectively

Treatment	pH	Turbidity (NTU)	TAN (mg L^{-1})	NO_2-N (mg L^{-1})	NO_3-N (mg L^{-1})	SRP (mg L^{-1})	Chlorophyll-*a* (ug L^{-1})	TN (mg L^{-1})	TP (mg L^{-1})
Control ($n = 3$)	8.78 ± 0.03	50.3 ± 3.30	0.08 ± 0.02	0.01 ± 0.00	0.02 ± 0.01	0.46 ± 0.08	138.21 ± 17.60	4.84 ± 0.23	0.72 ± 0.07^a
3/3 ($n = 4$)	8.77 ± 0.05	50.7 ± 5.51	0.16 ± 0.06	0.03 ± 0.01	0.09 ± 0.06	0.27 ± 0.04*	99.79 ± 16.49*	4.59 ± 0.16	0.44 ± 0.01^b
3/6 ($n = 4$)	8.82 ± 0.07	55.7 ± 8.60	0.13 ± 0.03	0.03 ± 0.01	0.05 ± 0.02	0.35 ± 0.06	122.22 ± 5.29	4.46 ± 0.19	0.54 ± 0.05^b
Pr > *F*	$P = 0.8166$	$P = 0.4766$	$P = 0.4972$	$P = 0.4316$	$P = 0.1563$	$P = 0.1563$	$P = 0.2083$	$P = 0.4457$	$P = 0.0079$

Means followed by different letters indicates a significant difference ($P < 0.10$).

*Significantly different from controls as indicated by pre-planned contrast ($P < 0.10$).

TAN, total ammonia nitrogen; NO_2-N, nitrite-nitrogen; NO_3-N, nitrate-nitrogen; SRP, soluble reactive phosphorus; TN, total nitrogen; TP, total phosphorus.

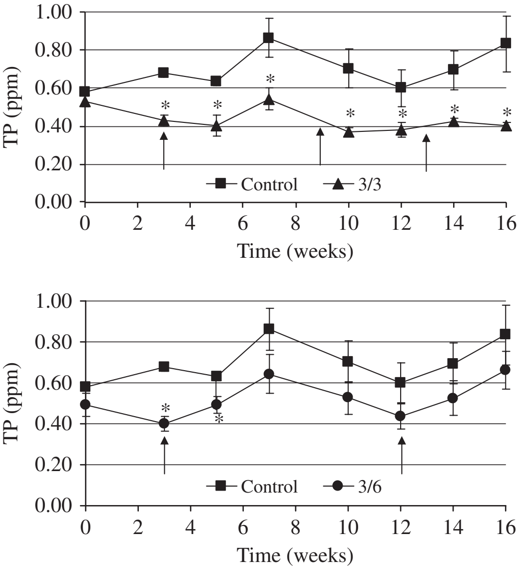

Figure 6 Mean total phosphorus (TP) levels of ponds during an 18-week hybrid striped bass growth trial in which fish were fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively. Arrows indicate start of refeeding (* significant difference from controls, $P < 0.10$).

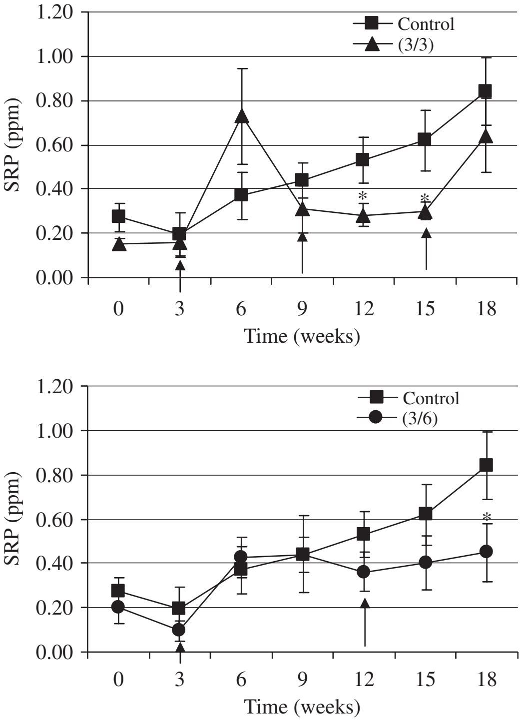

Figure 7 Mean soluble reactive phosphorus (SRP) levels in ponds during an 18-week hybrid striped bass growth trial in which fish were fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively. Arrows indicate start of refeeding (*significant difference from controls, $P < 0.10$).

alpinus (Jobling, Jorgensen & Siikavuopio 1993), rainbow trout *Oncorhynchus mykiss* (Quinton & Blake 1990) and HSB (Picha *et al.* 2006; Turano *et al.* 2007). Gaylord and Gatlin III (2000) suggested that 4 weeks of feed deprivation for channel catfish may have resulted in excessive catabolism and prevented complete growth compensation. Similarly, in a study with fingerling HSB that were substantially smaller than the fish used here, Turano *et al.* (2007) observed rapid increases in SGR following 2 and 4 weeks of complete feed deprivation, although the CG responses only resulted in partial compensation. Likewise, the feed deprivation periods of 3 weeks used in this study seem to have resulted in only partial catch-up growth.

The use of feed deprivation to induce CG involves a trade-off between lost growth and the degree to which fish can compensate upon refeeding. In all CG studies, feed deprivation periods represent lost growth opportunity. Additionally, if feed deprivation also results in weight loss, the increase in SGR upon refeeding may not be sufficient to overcome both, as observed in this trial. Feeding regimes that do not cause weight loss, but rather maintain weight during feed deprivation periods, and are still long enough in duration to elicit a CG response may have the best potential for eliciting complete growth compensation. For example, Tian and Qin (2004) demonstrated that Barramundi (*Lates calcarifer*) subjected to feed rations of 50% and 75% of satiation for 2 weeks, followed by feeding to satiation for 5 weeks, fully compensated for growth. Barramundi did not lose weight during the feed deprivation period. Similar results were achieved with the use of short-term feed deprivation periods in catfish. Channel catfish fed every third day to satiation for 3 weeks fully compensated for the decrease in weight gain after 6 weeks of daily feeding to satiation (Kim & Lovell 1995). Again, no weight loss was observed during feed deprivation. Hence, it is possible to induce full catch-up growth without complete feed deprivation.

Of interest between the two cyclic feeding regimes in this study is the similarity in timing and severity of weight loss. The greatest weight loss (12–13% body weight) occurred when feed deprivation periods were

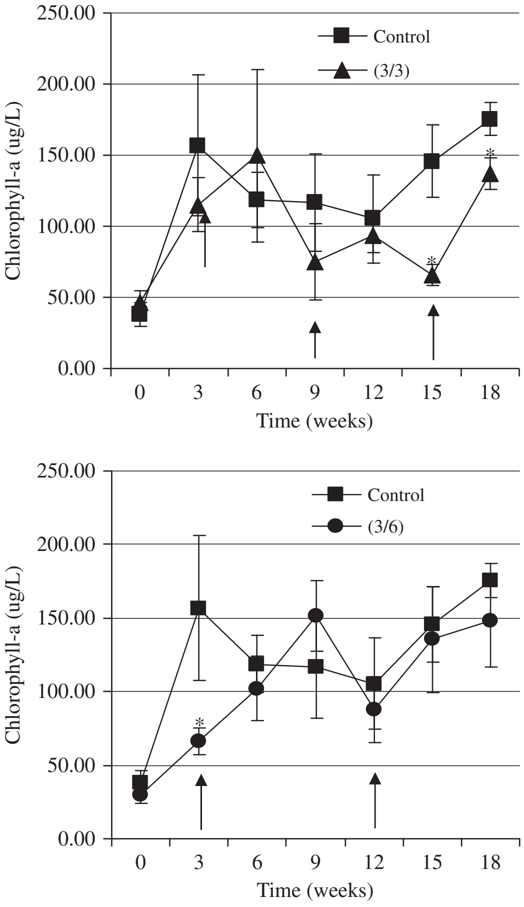

Figure 8 Mean chlorophyll-*a* levels in ponds during an 18-week hybrid striped bass growth trial in which fish were fed twice daily to satiation (control) or consecutive cycles of 3 weeks feed deprivation followed by 3 or 6 weeks of twice daily feeding to satiation, 3/3 and 3/6 respectively. Arrows indicate start of refeeding (*significant difference from controls, $P < 0.10$).

initiated at high water temperatures (> 28 °C). It is hypothesized that metabolic rate was also elevated as a result of the increased temperatures, leading to the greatest weight loss. Because metabolic rate increases with temperature, energy stores (as observed by HSI levels) will likely decrease more rapidly during periods of higher temperatures. During the summer months, a shorter feed deprivation period may result in a similar weight loss and CG response pattern to that of a longer feed deprivation period during the cooler season. In this study, a reduction in HSI levels to at least 1.9 resulted in an increased SGR in cyclic fed fish, which is close to the HSI threshold required for inducing a CG response in tank raised HSB (Picha *et al.* 2006). Feed deprivation during periods of increased temperatures resulted in further declines in HSI, however the subsequent CG response did not increase beyond the initial response during the cooler months. Unfortunately, the sampling regime (every 3 weeks) prevented the determination of HSI levels earlier in the feed deprivation period, not allowing for an accurate assessment. More specifically, it would be beneficial to determine if HSI is reduced to a basal level before 3 weeks of feed deprivation. Based on the results reported here, we hypothesize that cyclic feeding regimes will need to be shortened at higher temperatures, as excessive periods of feed deprivation during warmer temperatures could lead to more rapid weight loss that cannot be regained even with a strong CG response.

The responsiveness of HSI to cyclic feeding indicates that it is useful in predicting a CG response. Both IPF and CF were also measured as possible predictors of a CG response, and in the case of IPF, as a means of following energy distribution through feed restriction. Intraperitoneal fat was deposited early in the study, and only varied during the first 9 weeks. Hence, IPF was not proven useful in predicting a CG response. Alternatively, CF closely followed feeding cycle, decreasing below controls during feed deprivation, and returning to, or above controls during CG. Therefore, CF could be useful in identifying improved cyclic feeding regimes to result in the best CG response. Further, CF is a non-lethal measurement, allowing for repetitive sampling on individuals.

Water quality

Feed deprivation periods used in cyclic feeding effectively reduced nutrient inputs that led to phytoplankton abundance. Because phosphorus is a limiting nutrient to phytoplankton growth, the fate of phosphorus from feed is important in the management of water quality. Further, because phytoplankton have the capacity to store and use phosphorus, a process termed luxury consumption (Boyd 1990), the use of cyclic feeding to mitigate water quality must include feed deprivation periods sufficient in length to allow phosphorus to be depleted and phytoplankton abundance to decrease. In this study, TP, SRP, and chlorophyll-*a* were lower in the 3/3 and 3/6 treatments compared with the controls. Mean overall TP was 38% and 25% lower in 3/3 and 3/6 ponds, respectively, than in control ponds. The reduction in TP may be caused, in part, by the decreased levels of feed offered to the treatment ponds during the 18-week study. However, ponds subjected to the 3/6 feeding regime had significantly less TP, and did not statistically differ in the total amount of feed offered from control fish fed continuously throughout the study. Hence, we speculate that the reduction in phosphorus in the 3/6 treatment ponds was caused, in part, by improved P uptake by fish during the refeeding period. Clearly, further studies evaluating phosphorus budgets and uptake in fish during CG is warranted. Nevertheless, these findings could have significant implications for water quality and effluent management. Specifically, if phytoplankton store less phosphorus with pulsatile feeding regimes, excessive phytoplankton growth could be impeded, and this in conjunction with overall reductions in pond phosphorus levels, could lead to overall improvements in water quality, limiting potential impacts of discharged nutrients to the environment.

Summary

We show that cyclic feeding protocols have the potential to improve FE and water quality in pond raised HSB. The extent to which HSB display a CG response depends on two characteristics of the feed deprivation period: overall duration and water temperature. In this study, a 3-week period of deprivation led to different degrees of growth compensation when applied at low or high water temperatures. Based on these results, we recommend that future studies on HSB foodfish aimed at inducing full catch-up growth should employ a single 3-week period of feed deprivation applied when water temperatures are <28 °C.

Acknowledgments

The authors extend their thanks to those who have taken the time to critically review this manuscript as well as students and staff who help support research at North Carolina State University and the Tidewater Research Center. This research was supported in part by USDA-CSREES grant number MZ2003-06020 and North Carolina Sea Grant (02-EGS-01).

References

Ali M., Nicieza A. & Wootton R.J. (2003) Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries* **4**, 147–190.

APHA (American Public Health Association) (1995) American Water Works Association, and Water Pollution Control Federation. *Standard Methods for The Analysis of Water and Wastewater*, 19th edn. APHA, Washington, DC, USA.

Boyd C.E. (1990) *Water Quality in Ponds for Aquaculture*. Alabama Agricultural Experiment Station, Auburn University, Auburn, AL, USA.

Boyd C.E. & Tucker C.S. (1992) *Water Quality and Pond Soil Analysis for Aquaculture*. Alabama Agricultural Experimental Station, Auburn University, Auburn, AL, USA.

Gaylord T.G. & Gatlin D.M. 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**, 326–336.

Hayward R.S. & Wang N. (2001) Failure to induce overcompensation of growth in maturing yellow perch. *Journal of Fish Biology* **59**, 126–140.

Hayward R.S., Noltie D.B. & Wang N. (1997) Notes: Use of compensatory growth to double hybrid sunfish growth rates. *Transactions of the American Fisheries Society* **126**, 316–322.

Hayward R.S., Wang N. & Noltie D.B. (2000) Group holding impedes compensatory growth of hybrid sunfish. *Aquaculture* **183**, 299–305.

Hornick J.L., Van Eenaeme C., Gerard O., Dufranse I. & Istasse L. (2000) Mechanisms of reduced and compensatory growth. *Domestic Animal Endocrinology* **19**, 121–132.

Jobling M., Jorgensen E.H. & Siikavuopio S.I. (1993) The influence of previous feeding regime on compensatory growth response of maturing and immature Artic charr, *Salvelinus alpinus*. *Journal of Fish Biology* **43**, 409–419.

Johansen S.J.S., Ekli M., Stagnes B. & Jobling M. (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. & Lovell R.T. (1995) Effect of feeding regimes on compensatory weight gain and body tissue changes in channel catfish, *Ictalurus punctatus* in ponds. *Aquaculture* **135**, 285–293.

Li M.H., Robinson E.H. & Bosworth B.G. (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**, 444–453.

Morgan I.J. & Metcalfe N.B. (2001) Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. *Proceedings of the Royal Society of London B* **268**, 295–301.

Pechar L. (1987) Use of an acetone:methanol mixture for the extraction and spectrophotometric determination of chlorophyll-a in phytoplankton. *Archiv fuř Hydrobiologie* **78**(Suppl.), 99–117.

Picha M.E., Silverstein J.T. & Borski R.J. (2006) Discordant regulation of hepatic IGF-I mRNA and circulating IGF-I during compensatory growth in a teleost, the hybrid striped bass (*Morone chrysops* × M. *saxatilis*). *General and Comparative Endocrinology* **147**, 196–205.

Queiroz J.F. & Boyd C.E. (1998) Effects of a bacterial inoculum in channel catfish ponds. *Journal of the World Aquaculture Society* **29**, 67–73.

Quinton J.C. & Blake R.W. (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.

Reimers E., Kjorrefjord G. & Stavostrand M. (1993) Compensatory growth and reduced maturation in second sea winter farmed Atlantic salmon following starvation in February and March. *Journal of Fish Biology* **43**, 805–810.

Steel R.G.D., Torrie J.H. & Dickey D.A. (1997) *Principles and Procedures of Statistics. A Biometrical Approach*. McGraw-Hill, New York, NY, USA 666pp.

Thorpe J.E., Talbot C., Miles M.S. & Keay D.S. (1990) Control of maturation in cultured Atlantic salmon, *Salmo salar*, in pumped seawater tanks by restricted food intake. *Aquaculture* **86**, 315–326.

Tian X. & Qin J.G. (2004) Effects of previous ration restriction on compensatory growth in barramundi *Lates calcarifer*. *Aquaculture* **235**, 273–283.

Turano M.J., Borski R.J. & Daniels H.V. (2007) Compensatory growth of pond-reared hybrid striped bass, *Morone chrysops* × *M. saxatilis*, fingerlings. *Journal of the World Aquaculture Society* **38**, 250–261.

Van Dijk P.L.M., Hardewig I. & Holker F. (2005) Energy reserves during food deprivation and compensatory growth in juvenile roach: the importance of season and temperature. *Journal of Fish Biology* **66**, 167–181.