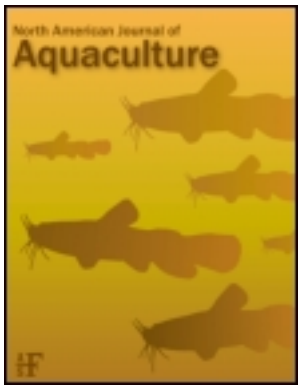

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Effect of Dietary Carbohydrate on Growth, Glucose Tolerance, and Liver Composition of Juvenile Striped Bass

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Abstract.—Dietary carbohydrate utilization by juvenile striped bass was evaluated in two studies. An incomplete factorial design was employed to determine the effect of carbohydrate complexity and dietary level on glucose tolerance. Five diets were formulated to contain 0, 12.5, or 25% of glucose or cornstarch, respectively. After 4 weeks, fish were fasted and administered an oral glucose challenge of 167 mg glucose/100 g body weight. Blood samples were collected at 0, 1, 2, 3, 4, 5, and 6 h after administration. Fasting plasma glucose concentrations (7.2 ± 0.8 mM/L) were similar among all treatments. Plasma glucose concentrations peaked higher at 4 and 5 h after administration in fish fed diets containing 25% glucose (23.9 ± 3.6 and 23.3 ± 3.2 mM/L, respectively) and 25% cornstarch (26.1 ± 2.0 and 23.9 ± 4.0 mM/L, respectively) when compared with plasma values for fish fed 0 and 12.5% carbohydrate ($P < 0.05$). There was neither a significant effect of carbohydrate type nor a significant interaction between type and level ($P > 0.05$). In the second study, five diets containing 0, 10, 15, 20, and 25% glucose were fed to juvenile striped bass. After 7 weeks, oral administration of glucose resulted in a persistent hyperglycemia. Weight gain and feed efficiency were significantly decreased ($P < 0.05$) in fish fed dietary glucose at concentrations above 15%. Inclusion of dietary glucose resulted in greater ($P < 0.05$) hepatosomatic index values and liver glycogen concentration. However there were no significant effects in liver proximate composition ($P > 0.05$). These data suggest that striped bass are able to most effectively utilize dietary carbohydrate at a maximal level between 15 and 20% of the diet.

Digestible carbohydrate is widely used in aquaculture feeds to provide dietary energy in place of costlier proteins and lipids. While many of the enzymes involved in carbohydrate metabolism have been demonstrated in fish (Shimeno 1974; Cowey and Walton 1989), the relative utilization of dietary carbohydrate varies greatly among piscine species as does the optimal dietary level of digestible carbohydrate. Carbohydrate complexity appears to be a significant factor in dietary utilization. Within certain limits, channel catfish *Ictalurus punctatus* (Garling and Wilson 1977), redbelly tilapia *Tilapia zillii* (El-Sayed and Garling 1988), and sunshine bass (female white bass *Morone chrysops* × male striped bass *M. saxatilis*) (Nematipour et al. 1992) have been shown to utilize dextrin as a dietary energy source as effectively as lipids and complex carbohydrates without a reduction in growth performance. Berger and Halver (1987) reported that striped bass fed a high-protein, high-fat diet could tolerate as much as 33% carbohydrate, in the form of dextrin, without a reduction in growth. Hutchins et al. (1998) found that sunshine bass fed a level of 20% soluble carbohydrate had significantly better growth than fish fed a 40% carbohydrate diet regardless of carbohydrate complexity.

There is a lack of data concerning the effects dietary carbohydrate levels below 25% on the growth performance and glucose metabolism of striped bass. Therefore, the objectives of these studies were to determine the effects of dietary carbohydrate source and level on juvenile striped bass growth, glucose tolerance, and liver composition.

Methods

Experimental system.—Juvenile striped bass were obtained from the University of Maryland Crane Aquaculture Facility, Baltimore, Maryland, as fingerlings and reared in circular fiberglass tanks to an average weight of 76 and 147 g for each study, respectively. Fish were then selected at random and stocked, 10 fish/tank, in 10 or 15 150-L tanks for the first or second study, respectively. All fish were fed a commercial hybrid striped bass feed (Southern States Cooperative, Inc., Richmond, Virginia) for 1 month before the start of each experiment.

Fish were reared in tanks supplied with dechlorinated water in a flow-through system at a rate of two complete turnovers per day. Calcium chloride and sodium chloride (9:1), as a solution, were injected directly into the incoming water line at a

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continuous rate to achieve a minimum concentration of 36 mg calcium/L in the rearing tanks. A photoperiod of 12 h light : 12 h dark was maintained throughout the experiment. Water temperature was maintained at 23°C and recorded four times daily by a central computerized monitoring system (REES Scientific, Trenton, New Jersey). All other water quality characteristics were monitored weekly throughout the experiment to insure optimal levels of pH, dissolved oxygen (DO), ammonia, chlorine, and hardness (as Ca). Temperature and DO were measured with a YSI model 58 oxygen meter (Yellow Springs Instruments Corp., Yellow Springs, Ohio). The pH was monitored with a Corning model 250 ion analyzer (Corning Co., Corning, New York). Chlorine, both free and total, and ammonia were measured with a Hach DR/700 colorimeter (Hach Co., Loveland, Colorado). Calcium concentration in the culture systems was measured with a Hach model HA-4P hardness test kit and by atomic absorption spectrophotometry (Perkin-Elmer 5100 PC, Perkin-Elmer Corp., Norwalk, Connecticut). Throughout the experiments, environmental conditions within the culture systems were maintained as outlined by Nicholson et al. (1990).

Experimental design.—In the first study, a 3 × 3 incomplete factorial design was employed, in which a basal diet was formulated without soluble carbohydrate and four semipurified diets were formulated to contain 12.5% or 25% carbohydrate as glucose or as cornstarch (Table 1). Diets were maintained isonitrogenous (49% crude protein) and isoenergetic (3.6 kcal/g of diet) by adjusting lipid and fiber content. Diets were extruded through a 3-mm die with a laboratory extruder (C. W. Brabender Instruments Inc., Hackensack, New Jersey) after the addition of 20% moisture, and allowed to air dry following extrusion. Fish were fed their respective diets to satiation twice daily Monday through Friday and once daily Saturday and Sunday throughout the experiment.

After 4 weeks of feeding on experimental diets, fish were weighed, and individual weights were recorded according to passive integrated transponder identifications. Reagent grade D-glucose (Sigma Chemical Co., St. Louis, Missouri) was incorporated into gelatin capsules at a concentration of 167 mg/100 g body weight (Furuichi and Yone 1982) and orally administered 24 h postprandial. Fish were anaesthetized by immersion in a water bath containing tricaine methanesulfonate (MS-222) at 0.2 g/L. Blood samples were then collected in syringes via puncture of the caudal vein from one fish per tank (three per treatment) at 0, 1, 2, 3, 4, 5, and 6 h after glucose administration. Syringes were coated with heparin (1,000 units/mL) and sodium fluoride (4%) to prevent coagulation and glycolysis. Blood samples were immediately centrifuged, and plasma glucose was determined by the glucose hexokinase method (Procedure 16-UV, Sigma)

TABLE 1.—Percent composition of experimental diets used for determining the effect of carbohydrate type and level on glycemic response of juvenile striped bass to a glucose challenge.

Ingredient	Diet carbohydrate level and type				
		12.5%		25%	
	0% control	Glucose	Cornstarch	Glucose	Cornstarch
Menhaden fish meal[a]	25.0	25.0	25.0	25.0	25.0
Isolated soy protein[b]	30.0	30.0	30.0	30.0	30.0
Blood meal	9.2	9.2	9.2	9.2	9.2
Menhaden fish oil[a]	13.5	10.0	10.0	6.0	6.0
Vitamin premix[c]	1.2	1.2	1.2	1.2	1.2
Mineral premix[d]	2.0	2.0	2.0	2.0	2.0
Stay C[e]	0.1	0.1	0.1	0.1	0.1
Lignin sulfonate	1.5	1.5	1.5	1.5	1.5
Cellulose	17.5	8.5	8.5	0	0
D-glucose	0	12.5	0	25	0
Cornstarch	0	0	12.5	0	25

[a] Source: Omega Protein Corp., Reedville, Virginia.
[b] Source: Archer Daniels Midland Co., Decantur, Illinois.
[c] Contains (as mg/kg diet unless otherwise noted): choline chloride, 3,465; inositol, 396; niacin, 153; α-tocopheryl acetate, 45; calcium pantothenate, 50.4; riboflavin, 20.7; menadione sodium bisulfate, 9.9; thiamin, 12.6; pyridoxine-HCl, 12.6; cyanocobalamin (3,000 μg/g), 5.8; folic acid, 5.4; retinyl acetate, 3.9; biotin, 4.5; cholecalciferol, 5 μg/kg; ethoxyquin (antioxidant), 125.
[d] Contains (as mg/kg diet): KCl, 5,200; NaCl, 3,600; $MgSO_4$, 1,640; $FeC_6H_5O_7$, 92; $MnSO_4$, 80; $ZnCO_3$, 100; $CuSO_4$, 3.2; KI, 0.4; Na_2Se_{O3}, 0.328.
[e] Calcium ascorbate-2-monophosphate; from Hoffmann-La Roche, Inc., Nutley, New Jersey.

In the second study, five semipurified diets were formulated to contain 0, 10, 15, 20, or 25% carbohydrate as glucose (Table 2). Diets were maintained isonitrogenous and isoenergetic and were extruded as described for the first study. Similarly, fish were fed their respective diets to satiation twice daily Monday through Friday and once daily Saturday and Sunday.

After 7 weeks of feeding on experimental diets, all 10 fish per tank were weighed, and individual weights were recorded according to passive integrated transponder identifications. Glycemic response to an oral glucose challenge was measured in the same manner as in the first study; however, blood was collected at 0, 4, 8, 12, and 24 h after

TABLE 2.—Percent composition of experimental diets used for determining the effect of increasing dietary glucose concentrations on growth, liver variables, and glucose tolerance.

Ingredients[a]	Diet glucose level				
	0%	10%	15%	20%	25%
Menhaden fish meal	25.0	25.0	25.0	25.0	25.0
Isolated soy protein	23.0	23.0	23.0	23.0	23.0
Blood meal	6.2	6.2	6.2	6.2	6.2
Gelatin	9.0	9.0	9.0	9.0	9.0
Menhaden fish oil	14.3	11	9.3	7.7	6.0
Vitamin premix	1.5	1.5	1.5	1.5	1.5
Mineral premix	2.5	2.5	2.5	2.5	2.5
Stay C	0.1	0.1	0.1	0.1	0.1
Lignin sulfonate	1.4	1.4	1.4	1.4	1.4
Cellulose	16.7	10.0	6.7	3.3	0
D-glucose	0	10.0	15.0	20.0	25.0

[a] See Table 1 for ingredient sources and premix compositions.

glucose administration. Before the glucose challenge, one fish per tank was sacrificed for liver analysis. Livers were quickly dissected, weighed, and stored at −80°C until proximate analysis could be conducted. Dry matter, crude protein, lipid, and ash were determined according to established methods (AOAC 1984). Liver glycogen was assayed according to Hassid and Abraham (1957). Hepatosomatic index (HSI) was calculated with the following formula: HSI = 100 × liver weight (g)/body weight (g).

Statistical analysis.—Plasma glucose concentrations at each sampling time in the first study were subjected to incomplete factorial analysis of variance mixed-model procedures (SAS Institute 1992). Pairwise contrasts were used to identify significant differences at $\alpha = 0.05$ among carbohydrate types and levels. Growth and liver composition in the second study were subjected to analysis of variance mixed-model procedures, and differences among carbohydrate levels were identified by pairwise contrasts at $\alpha = 0.05$. Significant differences in periodic plasma glucose concentrations in the second study were identified at $\alpha = 0.10$ (SAS Institute 1992).

Results

In the first study, fish fed diets containing different levels of carbohydrate from one of two sources exhibited an apparent hyperglycemic response over a 6-h period when challenged with oral glucose administered at 167 mg /100 g body weight (Figure 1). Basal plasma glucose concen-

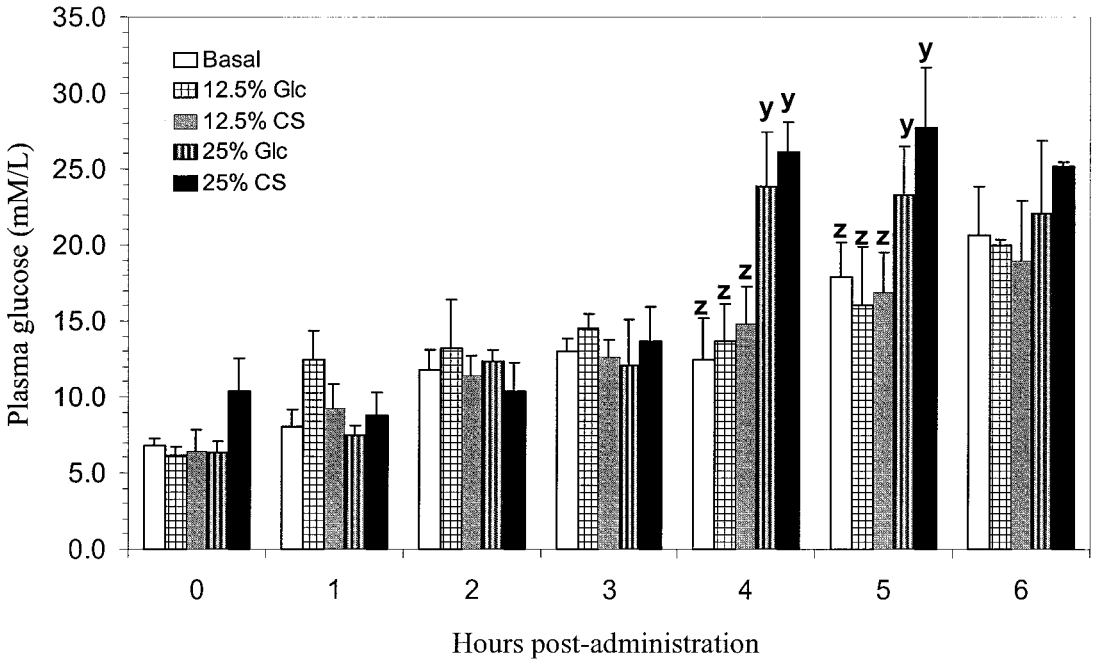

FIGURE 1.—Plasma glucose concentrations after administration of 167 mg glucose/100 g body weight to striped bass fed diets containing 0, 12.5, or 25% glucose (Glc) or cornstarch (CS), respectively. Values are means (+SE) of three fish from each dietary treatment. Means within the 4- or 5-h time group without a letter in common are significantly different ($P < 0.05$).

TABLE 3.—Growth performance and liver composition of juvenile striped bass fed diets containing increasing levels of glucose for 7 weeks. Means along a row without a letter in common are significantly different ($P < 0.05$).

Variable	Dietary glucose level					Pooled SE
	0%	10%	15%	20%	25%	
Weight gain (g)	88 Z	87 Z	92 z	68 Y	77 Y	3
FCR[a]	1.17 Z	1.13 Z	1.15 Z	1.33 Y	1.21 ZY	0.04
HSI[b] (%)	0.90 Z	1.35 Y	1.40 Y	1.24 Y	1.46 Y	0.10
Liver composition						
Glycogen (%)	2.1 Z	5.7 Y	7.4 Y	5.9 Y	7.3 Y	0.9
Moisture (%)	71.3 Z	69.0 Z	68.5 Z	70.5 Z	71.4 Z	1.5
Ash (%)	3.2 Z	2.9 Z	3.5 Z	3.0 Z	3.0 Z	0.4
Protein (%)	13.7 Z	12.6 Z	11.6 Z	11.4 Z	12.2 Z	0.7
Lipid (%)	9.3 Z	9.7 Z	8.7 Z	7.2 Z	6.1 Z	1.8

[a] Feed conversion ratio = weight of food fed/fish weight gained.
[b] Hepatosomatic index = 100 × liver weight/body weight.

trations (7.2 ± 0.8 mM/L) were relatively high in all fish sampled before the glucose challenge (0 h), with no significant differences among treatments. A gradual increase in plasma glucose concentration was noted in all treatments over the first 3 h. At 4 h after glucose administration, there was a substantial and statistically significant increase in plasma glucose concentrations in fish fed diets containing either 25% glucose or 25% cornstarch when compared with plasma glucose levels in fish fed diets containing less carbohydrate. Plasma glucose levels remained significantly higher at 5 h after glucose administration in fish fed diets containing 25% glucose or 25% cornstarch. Plasma glucose concentration was not significantly affected by carbohydrate source, nor was there a significant interaction between carbohydrate source and level. Plasma glucose concentrations did not return to basal (0 h) levels in any of the fish sampled during the 6 h after glucose administration.

In the second study, body weights of fish increased from an initial average weight of 147 g to a maximum average of 239 g after 7 weeks of adaptation to diets increasing in glucose concentration. Significantly greater weight gain and lower feed conversion ratios were observed in fish fed diets containing less than 20% glucose (Table 3). Hepatosomatic index values were significantly lower (0.90%) in fish fed the basal diet containing no soluble carbohydrate when compared with those fish fed diets with added glucose (1.24-1.46%).

Liver glycogen concentrations were also correlated to the incorporation of dietary glucose. Fish fed diets containing glucose had significantly more liver glycogen than those fed the basal diet. The percentages of moisture, crude protein, lipid, and ash in the liver were not significantly affected by dietary glucose concentration. There was a tendency, however, toward declining lipid concentrations as glycogen concentrations increased in the liver (Table 3).

A prolonged hyperglycemia was observed across all treatments in the second study, with significant differences ($P < 0.1$) observed in plasma glucose concentrations 0 h and 8 h after glucose administration (Figure 2). At 8 h after administration, plasma glucose levels of fish fed the 15, 20, and 25% glucose diets peaked at higher levels than in fish fed the basal diet. In each treatment, plasma levels peaked between 4 h and 8 h, with all treatments approximating 0-h levels 24 h after glucose administration.

Discussion

The results of the growth study indicate that juvenile striped bass are able to tolerate dietary carbohydrate in the form of glucose, but at levels below 20% of the diet. Weight gain in this study was comparable to other carbohydrate studies with striped bass, being equal to those reported by Rawles and Gatlin (1998) and somewhat greater than those reported by Woods et al. (1995) for similar-size fish. Hutchins et al. (1998) reported a significant depression in weight gain for sunshine bass fed diets containing 40% soluble carbohydrate when compared with fish fed diets containing 20% carbohydrate, regardless of type. Rawles and Gatlin (1998) found a negative correlation between weight gain and increasing molecular weight of dietary carbohydrate fed to hybrid striped bass and concluded that growth in the pure striped bass apparently was not related to carbohydrate complexity. Glucose tolerance in striped bass also appears to be unaffected by carbohydrate complexity.

Our results from the glucose tolerance test with

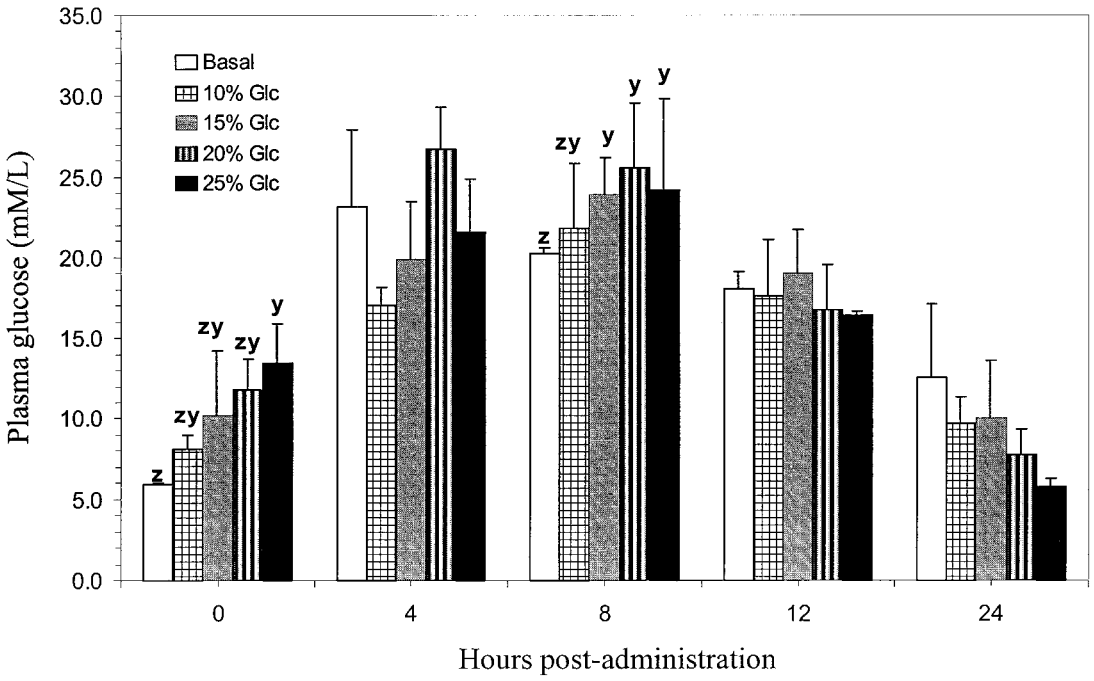

FIGURE 2.—Plasma glucose concentrations after administration of 167 mg glucose/100 g body weight to striped bass fed diets containing 0, 10, 15, 20, or 25% glucose (Glc). Values are means (+SE) of two fish from each dietary treatment. Means within the 0- or 8-hour time group without a letter in common are significantly different ($P < 0.05$).

striped bass fed increasing levels of glucose and cornstarch, respectively, indicated a significant effect of dietary carbohydrate level without an effect of carbohydrate type. Thus, it would appear that striped bass are better able to tolerate and perhaps utilize different forms of dietary soluble carbohydrate, such as glucose and cornstarch, than are sunshine bass.

In the second study, plasma glucose concentrations in striped bass measured over a 24-h period showed a prolonged hyperglycemia similar to that seen in diabetic mammals. A hyperglycemic response was also demonstrated with sunshine bass (Hutchins et al. 1998), rainbow trout *Oncorhynchus mykiss* (Brauge et al. 1994) and Atlantic salmon *Salmo salar* (Hemre et al. 1995). In each study, plasma glucose levels peaked between 4 and 8 h after carbohydrate administration. Physiological or handling stress has been shown to gradually increase plasma glucose levels in striped bass over a 24–48-h period (Reubush and Heath 1997). This could account for the overall increase in plasma glucose concentrations across all treatment levels observed in both experiments.

In the present studies, we have demonstrated results with striped bass similar to results published for other fish species in which an increase in plasma glucose concentration occurs as the level of carbohydrate in the diet increases (Fynn-Aikins et al. 1992; Brauge et al. 1994; Woods et al. 1995). Hutchins et al. (1998) also found that plasma glucose concentrations in sunshine bass increased with increasing dietary glucose; however, they reported an opposite effect when fish were fed increasing levels of maltose, a disaccharide, or dextrin, a polysaccharide.

Several postulations have been put forth regarding the apparent diabetic condition observed in piscine species. In some of the earlier glucose tolerance studies with fish, Furuichi and Yone (1982) and Wilson and Poe (1987) suggested that the observed prolonged hyperglycemia may be the result of low levels of endogenous insulin. However, with the development of radioimmunoassay methods for determination of insulin levels in fish, researchers have demonstrated that fish have insulin levels similar to and often higher than those observed in mammals (Wilson 1994). It has been suggested that the high sensitivity to glucose of pancreatic cells producing somatostatin may be a

possible cause for glucose intolerance in fish (Ronner and Scarpa 1987). Sheridan et al. (1987) demonstrated that somatostatin inhibits insulin release in fish, and observed no increase in plasma insulin concentration during the initial period following oral and intraperitoneal glucose administration (Sheridan et al. 1991).

The HSI values reported in this study are comparable to those published for both sunshine bass and striped bass (Rawles and Gatlin 1998). In both studies, bass fed diets containing no soluble carbohydrate had smaller livers than those fish fed diets containing soluble carbohydrate. Relative to the HSI values, liver glycogen concentrations were significantly greater in fish fed soluble carbohydrate than in fish fed the basal diet in both studies. Rawles and Gatlin (1998) also observed a decrease in liver protein and lipid concentrations with the addition of soluble carbohydrate to the diet. Increasing dietary carbohydrate resulted in increased nonlipid fluid in the hepatocytes of striped bass, which may have contributed to observed increases in HSI (Woods et al. 1995). From the data in the present study, a significant correlation could not be made between dietary carbohydrate inclusion and liver proximate composition. However, there was a tendency toward decreased liver fat concentration with increasing levels of dietary carbohydrate. Therefore, our results suggest that juvenile striped bass are able to tolerate dietary carbohydrate at a maximal level of between 15% and 20% of the diet.

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