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Dietary lipid level but not L-carnitine affects growth performance of hybrid striped bass (*Morone chrysops* ♀ × *M. saxatilis* ♂)

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Abstract

The objectives of this experiment were to determine if dietary lipid levels in excess of previously reported minima would increase performance of hybrid striped bass, and to determine if supplementation of L-carnitine would improve growth and/or body composition when feeding elevated dietary lipid. Therefore, a 2 × 4 factorial design was utilized to test the efficacy of dietary L-carnitine at 0 and 3000 mg/kg diet at each of four lipid levels (5%, 10%, 15% and 20%). Semipurified diets were formulated to contain 40% crude protein and dextrin was substituted for menhaden oil at a rate of 2.25 to 1 to maintain digestible energy at approximately 14.2 kJ/g. Juvenile reciprocal cross hybrid striped bass initially averaging 2.5 g/fish were cultured in a 5‰ brackish water recirculating system and fed twice daily at a rate approaching apparent satiation.

At the end of the 8-week feeding trial, L-carnitine supplementation did not influence weight gain, but dietary lipid level did, with the lowest value (1084% of initial weight) achieved by fish fed 5% lipid and the highest (1343%) by fish fed 15% lipid; fish fed 20% lipid had intermediate weight gain (1215%). Feed efficiency also was influenced by dietary lipid with fish fed the 10% and 20% lipid diets having higher feed efficiency values than those fed the 5% and 15% lipid diets. Body condition indices were only slightly altered by L-carnitine supplementation, but dietary lipid over 10% influenced body condition. Liver composition was altered by dietary lipid level but not L-carnitine supplementation. As dietary lipid level increased, liver lipid increased and liver glycogen decreased dramatically, especially in fish fed the diet with 20% lipid, which had no soluble carbohydrates. Muscle composition was unaltered by any dietary treatment. In conclusion,

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hybrid striped bass generally did not utilize dextrin as efficiently as lipid, and lipid levels between 10% and 15% of diet provided maximum growth with intermediate lipid deposition.

Keywords: L-Carnitine; Lipid; Hybrid striped bass; *Morone*; Nutrition

1. Introduction

Lipid nutrition of fish produced in aquaculture has attracted considerable interest both historically from the standpoint of satisfying essential fatty acid requirements (NRC, 1993) and more recently for its protein-sparing capability. Current salmonid diets may contain upwards of 30% lipid for enhancing feed efficiency as well as growth of these coldwater carnivorous species (Hardy, 1999). Most warmwater species are typically fed diets with less than 10% lipid due to their ability to utilize higher levels of carbohydrate for energy, the high cost of lipid relative to carbohydrate, and unwanted accretion of lipid depots. Various warmwater species also may differ in carbohydrate utilization according to natural feeding habits, with more carnivorous species typically having reduced ability to utilize dietary carbohydrate (Wilson, 1994). Hybrid striped bass are crosses of two carnivorous *Morone* species, which generally would not be expected to utilize carbohydrates for energy as efficiently as lipid. One previous study indicated hybrid striped bass were able to utilize dextrin as efficiently as lipid for energy based on weight gain and feed efficiency (Nematipour et al., 1992a). However, more recent studies have indicated these fish may use lipid more efficiently than carbohydrate for energy (Hutchinson et al., 1998; Gaylord and Gatlin, in press).

To improve utilization of dietary lipids by fish, L-carnitine has shown promise by improving growth and feed efficiency and reducing lipid deposition in some species

Table 1
Composition of the basal diets (g/100 g dry weight)[a]

	Dietary lipid (%)			
	5	10	15	20
Special Select™ menhaden fishmeal[b]	38.0	38.0	38.0	38.0
Casein[c]	15.0	15.0	15.0	15.0
Menhaden oil[b]	0.0	5.0	10.0	15.0
Dextrin[c]	33.75	22.5	11.25	0.0
Vitamin premix[d]	3.0	3.0	3.0	3.0
Mineral premix[d]	4.0	4.0	4.0	4.0
Carboxymethyl cellulose[c]	2.0	2.0	2.0	2.0
Cellulose[c]	4.25	10.5	16.75	23.0

[a] Diets were formulated to contain 40% crude protein and either 5%, 10%, 15% or 20% lipid with 14.2 kJ estimated digestible energy per g diet. Diets at each lipid level were supplemented with L-carnitine (US Biochemical, Cleveland, OH) at either 0 or 3000 mg/kg.

[b] Omega Protein, Reedville, VA.

[c] US Biochemical, Cleveland, OH.

[d] Same as Moon and Gatlin (1991).

(Santulli and D'Amelio, 1986; Torreele et al., 1993; Chatzifotis et al., 1995; Ji et al., 1996). Previous research in this laboratory, however, did not find any benefits of dietary L-carnitine supplementation at relatively low lipid levels for hybrid striped bass (Gaylord and Gatlin, in press). Therefore, the purpose of the present study was to determine if hybrid striped bass could utilize elevated levels of dietary lipid, and if supplemental L-carnitine could enhance utilization of dietary lipid.

2. Materials and methods

Diets were formulated to contain 40% crude protein and were maintained isocaloric at an estimated digestible energy level of 14.2 kJ/g (Nematipour et al., 1992b) by adjusting dextrin and menhaden oil levels (Table 1). All other known nutritional requirements of hybrid striped bass were satisfied by these diets (Gatlin, 1997). A factorial design was utilized in which diets containing lipid at either 5%, 10%, 15% and 20% were supplemented with L-carnitine at 0 and 3000 mg/kg diet. Lipid levels were chosen to meet (5% or 10%) or exceed (15% and 20%) previously reported optima for hybrid striped bass (Nematipour et al., 1992a). The rather high L-carnitine level was

Table 2
Weight gain, feed efficiency and muscle L-carnitine concentration of hybrid striped bass fed diets containing four levels of lipid at two L-carnitine levels

Dietary treatment		Weight gain (% of initial weight)[a,b]	Feed efficiency (g gain/g dry feed)[a]	Muscle L-carnitine (mg/g)[c]
Lipid (%)	L-Carnitine (mg/kg)			
5	0	1092a	0.60a	6.64a
5	3000	1076a	0.55A	11.60A
10	0	1363bc	0.73b	6.82a
10	3000	1263bc	0.56AB	20.50B
15	0	1300c	0.61a	13.50b
15	3000	1386c	0.59B	30.90C
20	0	1296b	0.70b	16.20b
20	3000	1134b	0.57AB	61.20D
ANOVA, Pr > F[d]				
Lipid		0.0002	0.0002	0.0001
L-Carnitine		0.1718	0.0001 (0 > 3000)	0.0001 (0 < 3000)
Lipid × L-Carnitine		0.0897	0.0002	0.0001
Pooled S.E.		47.53	0.01	3.31

[a] Values are means of three replicate groups.
[b] Average initial fish weight was 2.5 g.
[c] Means of three fish from each of three replicate groups expressed on a fresh-weight basis.
[d] Significance probability associated with the *F*-statistic. If a significant ($P < 0.05$) main effect occurred with significant interaction, lipid levels within an L-carnitine level followed by different letters (0 L-carnitine = lower case; 3000 L-carnitine = upper case) are significantly different as determined by Duncan's multiple range test; whereas, a significant main effect without interaction allowed data to be pooled by lipid level prior to means separation.

chosen because levels up to 1000 mg/kg did not affect growth or body composition of hybrid striped bass in a previous study (Gaylord and Gatlin, in press). L-Carnitine was added to each diet by dissolving in water and mixing prior to pressure pelleting, ensuring this hygroscopic compound was evenly distributed in the diets. Other procedures for diet preparation and storage were as previously described (Moon and Gatlin, 1991).

Juvenile reciprocal cross hybrid striped bass (*Morone chrysops* ♀ × *M. saxatilis* ♂) were obtained from a commercial producer (Keo Fish Farm, Keo, AR) and were maintained in freshwater earthen ponds. Prior to the experiment, fish were moved indoors into a brackish water (5‰) recirculating system containing 24, 38-l aquaria maintained at 27 ± 2°C and on a 12:12 h diurnal cycle. Water flow into the aquaria was restricted to 1 l/min. The fish were conditioned to the system and fed the basal diet with 5% lipid for 2 weeks prior to the start of the experiment. Ten hybrid striped bass initially averaging 2.5 g/fish at the start of the 8-week experiment were stocked into each aquarium (triplicate aquaria per dietary treatment) and fed their respective diets twice daily a percentage of their body weight to a level approaching apparent satiation. Feeding rates were adjusted weekly to ensure limited feed waste as well as supplying

Table 3
Body condition indices of hybrid striped bass fed diets containing four levels of lipid at two L-carnitine levels[a]

Dietary treatment		HSI[b]	IPF ratio[c]	MR[d]
Lipid (%)	L-Carnitine (mg/kg)			
5	0	2.32bc	2.24a	43.5b
5	3000	2.09bc	2.64A	44.6b
10	0	2.30c	4.10b	44.4b
10	3000	2.30c	4.41BC	43.7b
15	0	1.89b	5.13bc	40.6a
15	3000	2.16b	5.13C	41.6a
20	0	1.21a	5.55c	41.3a
20	3000	1.11a	4.50B	41.1a
ANOVA, Pr > F[e]				
Lipid		0.0001	0.0001	0.0006
L-Carnitine		0.8050	0.7889	0.6701
Lipid × L-Carnitine		0.0865	0.0073	0.7153
Pooled S.E.		0.17	0.39	1.61

[a] Values are means of three fish from each of three replicate groups.
[b] Hepatosomatic index (HSI) = liver weight × 100/body weight.
[c] Intraperitoneal fat (IPF) ratio = IPF weight × 100/body weight.
[d] Muscle ratio (MR) = fillet weight × 100/body weight.
[e] Significance probability associated with the *F*-statistic. If a significant ($P < 0.05$) main effect occurred with significant interaction, lipid levels within an L-carnitine level followed by different letters (0 L-carnitine = lower case; 3000 L-carnitine = upper case) are significantly different as determined by Duncan's multiple range test; whereas, a significant main effect without interaction allowed data to be pooled by lipid level prior to means separation.

ample food for maximized growth. At the termination of the trial, three fish per aquarium were randomly removed, euthanized, and hepatosomatic index (HSI = liver weight × 100/fish weight), intraperitoneal fat (IPF) ratio (IPF weight × 100/fish weight) and muscle ratio (MR = fillet weight × 100/fish weight) were determined. Muscle and liver samples from these three fish per aquarium also were removed and stored at −20°C prior to proximate analysis that followed standard procedures (AOAC, 1990). Muscle and liver total lipid was determined by chloroform/methanol extraction (Folch et al., 1957). Analysis of free L-carnitine in muscle and diets was performed according to the method of Wieland et al. (1983). Muscle and liver lipid class analysis was performed using the Iatroscan TLC-FID system (Bioscan, Washington, DC) according to the procedures of Tocher et al. (1985) with modifications of the solvent system (Craig and Gatlin, 1997). Glycogen was determined in the liver according to the method of Hassid and Abraham (1957).

Statistical analysis of the data was performed using factorial analysis of variance (SAS, 1985). Differences were considered significant at $P \leq 0.05$. If interactions occurred between main effects then differences among treatments were determined by Duncan's multiple-range test (Duncan, 1955).

Table 4
Liver and muscle composition of hybrid striped bass fed diets containing four levels of lipid at two L-carnitine levels[a]

Dietary treatment		Liver lipid (%)[b]	Liver glycogen (%)[b]	Muscle lipid (%)[b]
Lipid (%)	L-Carnitine (mg/kg)			
5	0	3.90a	15.04c	2.18
5	3000	5.96a	15.63c	3.87
10	0	4.94a	15.33c	5.89
10	3000	5.87a	13.53c	1.96
15	0	10.80b	12.50b	3.25
15	3000	8.24b	12.71b	6.38
20	0	19.70c	2.94a	2.81
20	3000	17.70c	4.43a	4.31
ANOVA, Pr > F[c]				
Lipid		0.0001	0.0001	0.7553
L-Carnitine		0.5846	0.8388	0.6243
Lipid × L-Carnitine		0.0964	0.2880	0.2085
Pooled S.E.		1.00	0.84	1.69

[a] Values are means of three fish from each of the three replicate groups.
[b] Expressed on a fresh-weight basis.
[c] Significance probability associated with the *F*-statistic. If a significant ($P < 0.05$) main effect occurred with significant interaction, lipid levels within an L-carnitine level followed by different letters (0 L-carnitine = lower case; 3000 L-carnitine = upper case) are significantly different as determined by Duncan's multiple range test; whereas, a significant main effect without interaction allowed data to be pooled by lipid level prior to means separation.

3. Results

Diets not supplemented with L-carnitine were analyzed to contain undetectable levels of free L-carnitine while 85%, 98%, 92% and 93% of the targeted level of 3000 mg L-carnitine/kg was analyzed in the diets containing 5%, 10%, 15% and 20% lipid, respectively. Muscle L-carnitine levels were readily modified by dietary supplementation of L-carnitine and were also affected by dietary lipid concentrations (Table 2). A notable interaction occurred with high levels of dietary lipid augmenting L-carnitine supplementation in elevating muscle free L-carnitine levels.

Dietary factors had dramatic effects on weight gain and feed efficiency (Table 2). Fish fed diets containing 5% lipid grew less than the fish fed the other lipid levels; however, L-carnitine had no effect on weight gain at any level of dietary lipid. Feed efficiency was generally improved by increasing dietary lipid. L-Carnitine supplementation also affected feed efficiency of hybrid striped bass with fish fed the L-carnitine-supplemented diets having reduced feed efficiency compared to fish fed the same level of dietary lipid without L-carnitine supplementation.

Body condition indices were influenced by dietary L-carnitine supplementation and lipid level (Table 3). Increasing dietary lipid up to 20% reduced HSI values but elevated

Table 5
Liver and muscle lipid classes of hybrid striped bass fed diets containing four levels of lipid at two L-carnitine levels

Dietary treatment		Liver lipid classes (%)[a,b]				Muscle lipid classes (%)[a,b]			
Lipid (%)	L-Carnitine (mg/kg)	TG	FFA	CE	PL	TG	FFA	CE	PL
5	0	32.7ab	39.5	5.03a	19.6	45.36	13.45	3.17	34.47
5	3000	36.2ab	37.5	4.49a	18.9	56.98	11.24	1.86	27.34
10	0	38.1a	39.6	3.36b	16.5	58.96	8.35	0.98	29.31
10	3000	41.2a	36.1	2.89b	17.6	32.79	9.83	1.77	53.41
15	0	41.7a	37.6	2.63b	15.7	68.84	7.53	0.90	20.76
15	3000	39.1a	45.0	3.10b	9.6	68.55	5.53	1.24	18.73
20	0	28.4b	43.5	1.95b	22.1	58.01	11.57	2.50	25.41
20	3000	26.4b	52.4	2.79b	15.3	41.05	14.48	3.07	39.13
ANOVA, Pr > F[c]									
Lipid		0.0140	0.0993	0.0015	0.5452	0.1871	0.0859	0.1414	0.1019
L-Carnitine		0.8640	0.3671	0.8396	0.3822	0.3091	0.9814	0.8676	0.2243
Lipid × L-Carnitine		0.7854	0.3554	0.4595	0.8057	0.3268	0.7073	0.5802	0.2276
Pooled S.E.		3.85	4.16	0.51	4.94	10.69	2.63	0.82	8.02

[a] Values are means of three fish from each of the three replicate groups.

[b] Relative percentages of total identified lipid classes: triglycerides (TG), free fatty acids (FFA), cholesterol esters (CE), phospholipids (PL).

[c] Significance probability associated with the *F*-statistic. If a significant ($P < 0.05$) main effect occurred with significant interaction, lipid levels within an L-carnitine level followed by different letters (0 L-carnitine = lower case; 3000 L-carnitine = upper case) are significantly different as determined by Duncan's multiple range test; whereas, a significant main effect without interaction allowed data to be pooled by lipid level prior to means separation.

IPF ratio values. The IPF ratio was reduced by L-carnitine supplementation in fish fed 20% lipid. MR was unaltered by L-carnitine supplementation but was significantly reduced at lipid levels in excess of 10% of diet.

Liver lipid was increased in response to dietary lipid supplementation (Table 4). A moderate elevation in liver lipid occurred in fish fed diets with 15% lipid, although the greatest elevation in liver lipid occurred in fish fed diets with 20% lipid. Liver glycogen concentrations were inversely related to liver lipid (Table 4). As dietary lipid increased above 10%, glycogen concentrations in the liver decreased, most dramatically when dietary lipid was elevated from 15% to 20%. Muscle lipid was not affected by either dietary lipid or L-carnitine supplementation (Table 4). The relative amounts of triglycerides, free fatty acids, cholesterol and cholesterol esters in muscle lipids were not significantly affected by either of the dietary factors (Table 5). Liver lipid classes were not affected by dietary L-carnitine supplementation; however, liver triglycerides were depressed at an inclusion level of 20% dietary lipid (Table 5). Cholesterol esters in liver lipid were reduced as dietary lipid increased above 5%. Relative amounts of free fatty acids and phospholipid in liver were not altered by either of the dietary factors.

4. Discussion

The findings in this study are consistent with those of Hutchinson et al. (1998) and Gaylord and Gatlin (in press) in which hybrid striped bass had improved weight gain and feed efficiency when dietary lipid was elevated from 2% or 5%, respectively, to levels of 11% and 10%, respectively. In these studies diets were estimated to be isocaloric by substituting dextrin for lipid at a rate of 2.25 to 1 by weight. An earlier study (Nematipour et al., 1992a) reported such a substitution rate resulted in similar growth performance of hybrid striped bass fed diets with lipid levels ranging from 2% to 10%. However, the more limited energy efficacy of dietary carbohydrates relative to lipid for hybrid striped bass also is supported by the study of Rawles and Gatlin (1998). In that study hybrid striped bass were not able to digest soluble carbohydrates as effectively as lipid. In the current study, lipid also appeared to provide more energy for metabolism of hybrid striped bass, resulting in increased growth rates as well as enhanced feed efficiency. At least 10% dietary lipid should be present to support the most rapid weight gain of hybrid striped bass. A dietary lipid level of 15% appeared to provide slightly excessive energy as determined by increased deposition of lipid in the liver and peritoneal cavity as well as depressed muscle yield. Similar results have been demonstrated with red drum, a carnivorous marine sciaenid, showing a preferential use of lipid rather than dextrin for energy when dietary lipid was increased from 3% to 10% with a concomitant decrease in dextrin (Serrano et al., 1992). The increase in dietary lipid improved weight gain, feed efficiency, as well as protein efficiency of red drum across three different dietary protein levels.

Relative changes in growth and feed utilization as well as lipid deposition in the body should give a reasonable indication of when dietary energy is adequate or excessive. Although no energy determinations were performed on whole fish from the present

experiment, a fatty fish of greater or equal size has stored more energy than smaller, leaner fish. This, taken along with a slight improvement in feed efficiency appears to indicate improved utilization of dietary lipid for net energy stores by hybrid striped bass compared to the soluble carbohydrate, which was used to keep diets isocaloric. Therefore, the maximal dietary lipid energy that can be utilized by hybrid striped bass for lean mass accretion can be roughly extrapolated from the current study. It appears that the composition of growth was not altered greatly until the diet provided between 10% and 15% lipid. A dietary energy supply of up to 3760 kJ/kg diet from lipid was beneficial for hybrid striped bass growth when they were fed a 40% crude protein diet. However, when dietary lipid energy was elevated to 5648 kJ/kg diet, lipid accretion increased relative to weight gain.

A minimum level of soluble carbohydrate in the diet does appear to be beneficial to hybrid striped bass as the diet that was devoid of soluble carbohydrate (20% lipid) showed slightly depressed weight gain. Similar trends have been shown with other carnivorous fish species. Rainbow trout have been shown to require low levels of soluble carbohydrate to maximize growth through minimizing protein degradation rates (Peragon et al., 1999). McGoogan (1998) also observed depressed weight gain of red drum fed an isocaloric diet devoid of soluble carbohydrate. Thus, a minimum level of soluble carbohydrate in the diet appears necessary to maximize growth and feed efficiency of carnivorous fish, but the current study was not designed to address a minimum level of soluble carbohydrate for maintaining maximal growth.

The limited influence of L-carnitine on hybrid striped bass growth and feed efficiency has been noted in another study from this laboratory (Gaylord and Gatlin, in press) as well as with other species of fish (Rodehutscord, 1995; Chatzifotis et al., 1997). A similar outcome occurred in the present study even with L-carnitine supplementation at three times the level fed to hybrid striped bass in the previous study. The only notable benefit of L-carnitine supplementation came in the reduction of IPF deposition in fish fed the diets with 20% lipid, though the reduction was relatively small. There appeared to be a slight ($P = 0.10$) decrease in liver lipid deposition with L-carnitine supplementation in fish fed diets with 15% and 20% lipid.

Other researchers have noted more dramatic influences of dietary L-carnitine on composition of growth. For example, Ji et al. (1996) noted that Atlantic salmon fed diets supplemented with L-carnitine had reduced fillet lipid. Red sea bream also have been shown to be responsive to L-carnitine supplementation. Chatzifotis et al. (1995) reported increased growth rate and feed efficiency when L-carnitine was supplemented at a level of 1087 mg/kg diet. The lack of a strong L-carnitine effect on metabolism in the present study appears to be due to the ability of fish to synthesize adequate quantities of L-carnitine for lipid metabolism. The diets were not limiting in lysine or methionine, which are precursors for L-carnitine synthesis. If a limited precursor pool was available for metabolism, supplemental L-carnitine may have had more dramatic influences on growth and/or composition of gain.

Lipid supplementation also appeared to elevate L-carnitine synthesis by hybrid striped bass. An increase in dietary lipid above 10% dramatically increased levels of muscle free L-carnitine. The mechanism by which this occurs is not clear, though it is reasonable to postulate that more L-carnitine may be needed by the fish for metabolism

of dietary lipid. However, in the current study fish fed diets with and without L-carnitine supplementation had equal performance and composition.

Lipid class alterations in response to dietary L-carnitine supplementation were not observed in the current study. These findings are similar to those of a previous study in which carnitine supplementation up to 1000 mg/kg diet was ineffective in altering lipid utilization by hybrid striped bass (Gaylord and Gatlin, in press). In that study, there also was no influence of dietary lipid level on lipid class profile in the liver or muscle. In the current study, similar finding were observed with dietary lipid levels of up to 15%, but when dietary lipid was elevated to 20% a notable effect was observed in relative percentages of liver triglycerides and cholesterol esters. One might have expected an increase in triglycerides as dietary lipid increased because triglycerides are the primary storage form of lipid, but when dietary lipid was 20% liver triglycerides decreased. The decrease in liver triglycerides appeared to be due to lipolysis in that a small, but not quite significant ($P = 0.10$), elevation in free fatty acids occurred. The relative percentage of cholesterol esters in liver lipid also was modified by level of dietary lipid. Cholesterol esters appeared to be diluted out as dietary lipid increased above 5%. This would be reasonable because triglycerides and free fatty acids were the most prominent forms of lipid in the liver. Although limited effects were observed as dietary lipid levels increased, it appears that extremely high lipid diets may alter the metabolism of lipids in the liver. This may be detrimental to the fish as dietary lipid levels of 20% increased liver lipid and reduced growth.

In conclusion, data from the present study appear to indicate a limited benefit of L-carnitine supplementation to hybrid striped bass fed diets with lipid ranging from 5% to 20%. Dietary lipid appears to be more readily utilized as an energy source than carbohydrate by hybrid striped bass. However, lipid in excess of 10% of diet tended to increase deposition of lipid in the liver and peritoneal cavity.

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References

AOAC (Association of Official Analytical Chemists), 1990. Official Methods of Analysis. Arlington, VA, 1298 pp.

Chatzifotis, S., Takeuchi, T., Seikai, T., 1995. The effect of dietary L-carnitine on growth performance and lipid composition in red sea bream fingerlings. Fish. Sci. 61, 1004–1008.

Chatzifotis, S., Takeuchi, T., Watanabe, T., Satoh, S., 1997. The effect of dietary carnitine supplementation on growth of rainbow trout fingerlings. Fish. Sci. 63, 321–322.

Craig, S.R., Gatlin, D.M. III, 1997. Growth and body composition of juvenile red drum (*Sciaenops ocellatus*) fed diets containing lecithin and supplemental choline. Aquaculture 151, 259–267.

Duncan, D.B., 1955. Multiple range and multiple *F* tests. Biometrics 11, 1–42.

Folch, J., Lees, M., Sloane-Stanley, G.H., 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226, 497–509.

Gaylord, T.G., Gatlin, D.M. III, In press. Effects of dietary carnitine and lipid on growth and body composition of hybrid striped bass (*Morone chrysops* ♀ × *M. saxatilis* ♂). Fish Physiol. Biochem.

Gatlin, D.M. III, 1997. Nutrition and feeding of striped bass and hybrid striped bass. In: Harrell, R.M. (Ed.), Striped Bass and Other *Morone* Culture. Elsevier, Amsterdam, pp. 235–251.

Hardy, R.W., 1999. Problems and opportunities in fish feed formulation. Aquaculture Magazine 25, 56–60.

Hassid, W.Z., Abraham, S., 1957. Chemical procedure for analysis of polysaccharides. In: Colowick, S.P., Kaplan, N.O. (Eds.), Methods of Enzymology vol. 3 Academic Press, New York, p. 37.

Hutchinson, C.G., Rawles, S.D., Gatlin, D.M. III, 1998. Effects of dietary carbohydrate kind and level on growth, body composition and glycemic response of juvenile sunshine bass (*Morone chrysops* ♀ × *M. saxatilis* ♂). Aquaculture 161, 187–199.

Ji, H., Bradley, T.M., Tremblay, G.C., 1996. Atlantic salmon (*Salmo salar*) fed L-carnitine exhibit altered intermediary metabolism and reduced tissue lipid, but no change in growth rate. J. Nutr. 126, 1937–1950.

McGoogan, B.B., 1998. Effects of dietary protein and energy manipulations on growth and aspects of nitrogen metabolism of red drum, *Sciaenops ocellatus*. PhD dissertation, Texas A&M University, College Station, TX, 135 pp.

Moon, H.Y., Gatlin, D.M. III, 1991. Total sulphur amino acid requirement of juvenile red drum, *Sciaenops ocellatus*. Aquaculture 95, 97–106.

Nematipour, G.R., Brown, M.L., Gatlin, D.M. III, 1992a. Effects of dietary carbohydrate:lipid ratio on growth and body composition of hybrid striped bass. J. World Aquacult. Soc. 23, 128–132.

Nematipour, G.R., Brown, M.L., Gatlin, D.M. III, 1992b. Effects of dietary energy:protein ratio on growth characteristics and body composition of hybrid striped bass, *Morone chrysops* ♀ × *M. saxatilis* ♂. Aquaculture 107, 359–368.

National Research Council (NRC), 1993. Nutrient Requirements of Fish. National Academy Press, Washington, DC, 112 pp.

Peragon, J., Barraso, J.B., Garcia-Salguero, L., de la Higuera, M., Lupianez, J.A., 1999. Carbohydrates affect protein-turnover rates, growth, and nucleic acid content in the white muscle of rainbow trout (*Oncorhynchus mykiss*). Aquaculture 179, 425–437.

Rawles, S.D., Gatlin, D.M. III, 1998. Carbohydrate utilization in striped bass (*Morone saxatilis*) and sunshine bass (*Morone chrysops* ♀ × *M. saxatilis* ♂). Aquaculture 161, 201–212.

Rodehutscord, M., 1995. Effects of supplemental dietary L-carnitine on growth and body composition of rainbow trout (*Oncorhynchus mykiss*) fed high fat diets. J. Anim. Physiol. Anim. Nutr. 73, 276–279.

Santulli, A., D'Amelio, V., 1986. Effects of supplemental dietary carnitine on growth and lipid metabolism of hatchery-reared sea bass (*Dicentrarchus labrax* L.). Aquaculture 59, 177–186.

SAS Institute, 1985. SAS User's Guide: Statistics, Version. 5th edn., Cary, NC 956 pp.

Serrano, J.A., Nematipour, G.R., Gatlin, D.M., 1992. Dietary protein requirement of the red drum (*Sciaenops ocellatus*) and relative use of dietary carbohydrate and lipid. Aquaculture 101, 283–291.

Tocher, D.R., Fraser, A.J., Sargent, J.R., Gambel, J.C., 1985. Lipid class composition during embryonic and larval development in Atlantic herring (*Clupea harengus* L.). Lipids 20, 84–89.

Torreele, E., Van Der Sluizen, A., Verreth, J., 1993. The effect of dietary L-carnitine on the growth performance in fingerlings of the African catfish (*Clarias gariepinus*) in relation to dietary lipid. Br. J. Nutr. 69, 289–299.

Wieland, O.H., Deufel, T., Paetzke-Brunner, I., 1983. Free and esterified carnitine: colorimetric method. 3rd edn. In: Bergmeyer, H.U. (Ed.), Methods of Enzymatic Analysis vol. VII Verlag Chemie, Deerfield Beach, FL, pp. 481–488.

Wilson, R.P., 1994. Utilization of dietary carbohydrate by fish. Aquaculture 124, 67–80.