Serum Lipoproteins in Striped Bass (*Morone saxatilis*): Effects of Starvation

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Withholding food for 4 wk resulted in more extensive alterations within serum lipoprotein classes in striped bass (*Morone saxatilis*) than were evident in serum total lipids where only a decrease in triglycerides was significant. Total serum lipoprotein concentrations were about 3300 mg/dL in both fed and starved fish; however, high density lipoproteins (HDL) increased and very low density lipoproteins (VLDL) decreased significantly in the starved group. Quantitatively, the greatest changes in VLDL, the primary transporter of triglycerides, were declines in triglycerides and cholesterol esters. Within low density lipoproteins, triglycerides and phospholipids decreased. The HDL composition was affected least by starvation. Phospholipids were the dominant lipid in HDL and increased from 479.1 mg/dL in fed to 670.2 mg/dL in starved fish. The apoproteins of each lipoprotein class changed little qualitatively due to starvation. Our results reflect the importance of maintaining high levels of lipoproteins as a transport system for lipids from storage depots to depleted tissues permitting survival during prolonged periods of starvation that are often encountered by fish during colder months and during spawning migrations. Furthermore, during starvation HDL appears to assume increased significance as a vehicle for the transport of structural lipids to maintain tissue integrity.

La privation de nourriture pendant quatre semaines a produit des altérations plus importantes dans les classes de lipoprotéines sériques chez le Bar d'Amérique (*Morone saxatilis*) qu'il ne paraissait dans les lipides sériques totaux, ce qui n'avait révélé de baisse importante que dans la teneur en triglycérides. La concentration en lipoprotéines sériques totales était d'environ 3300 $mg \cdot dL^{-1}$ chez les sujets nourris ainsi que les sujets affamés. Cependant, la teneur en lipoprotéines de haute densité (HDL) a augmenté alors que celle des lipoprotéines de très basse densité (VLDL) a diminué significativement chez les sujets affamés. Sur le plan quantitatif, les plus importants changements en VLDL, le principal vecteur des triglycérides, a été la diminution en concentration des triglycérides et des esters du cholestérol. Quant aux lipides de basse densité (LDL), la teneur en triglycérides et en phospholipides a diminué. La composition en HDL a le moins varié par suite du traitement. Les phospholipides constituaient la principale forme de HDL et leur concentration est passée de 479,1 $mg \cdot dL^{-1}$ chez les sujets nourris à 670,2 $mg \cdot dL^{-1}$ chez les sujets affamés. Les apoprotéines de chaque classe de lipoprotéines ont peu varié qualitativement par suite de l'inanition. Nos résultats montrent l'importance de garder les lipoprotéines à un niveau élevé comme moyen de transport des lipides, des réserves aux tissus qui se sont appauvris, ce qui assure la survie durant les périodes prolongées de famine que les poissons doivent souvent affronter durant les mois d'hiver et au cours des migrations pour la reproduction. En outre, le HDL associé à l'inanition semble gagner en importance comme vecteur pour le transport des lipides structuraux en vue de conserver l'intégrité des tissus.

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Fish have an impressive ability to withstand long periods of starvation. This capacity is adaptive since many species of fish are subjected to natural periods of starvation or very low food intake during spawning or cold months of the year in temperate latitudes when prey abundance is low (Love 1970). Energetic demands are met primarily by lipid oxidation in fish (Cowey and Sargent 1979) and this is particularly true during starvation (Shul'man 1972).

Lipids are stored in substantial quantities in various tissues, including muscle, liver, and mesenteric depots, and, in addition

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to being a source of energy, provide components for membrane synthesis and precursors of steroid hormones. Many studies have shown that fish mobilize energetic lipids (e.g. triglycerides) from tissues preferentially to structural lipids (e.g. phospholipids) during starvation, but phospholipids are mobilized if starvation is prolonged (reviewed by Love 1980; Henderson and Tocher 1987). Since a basic minimum of energy and structural integrity of tissues must be maintained for survival, lipids must be supplied to depleted tissues from storage depots. Beyond these needs for maintenance, substantial quantities of energetic and structural lipids must be supplied to gonads, especially ovaries, during reproductive development. In anadromous species which undergo lengthy spawning migrations without feeding, gonadal development is dependent to a large extent on the transport of stored lipids (Henderson and Tocher 1987).

Lipids are transported in blood serum complexed with specific proteins (apolipoproteins) as particles known as lipoproteins. Serum lipoproteins are routinely characterized by size, density, and their chemical composition. In ascending order of density, they are chylomicrons, very low density (VLDL), low density (LDL), and high density (HDL) lipoproteins. Although studied rather extensively in birds and mammals, serum lipoproteins have been described in only a few species of fish (Chapman 1980), most notably rainbow trout (Chapman et al. 1978; Skinner and Rogie 1978; Fremont et al. 1981). A common feature of serum lipoproteins in teleost species studied to date is that they are found in very high concentrations relative to birds and mammals (Chapman 1980). Moreover, during the prespawning period HDL appears to become elevated in rainbow trout (Fremont and Marion 1982) and pink salmon (Nelson and Shore 1974).

From the above observations, assessing changes in serum lipoproteins during starvation may reveal which components are most significant for maintenance of tissue integrity and synthesis. Black and Skinner (1986) found that starvation produced changes in cholesterol concentrations in serum lipoproteins of rainbow trout. However, there are no published reports on the effects of fasting on the lipid and protein compositions of serum lipoproteins in fishes. To investigate this, a study was conducted to determine the changes in the composition and concentration of serum lipoprotein classes of starved striped bass (*Morone saxatilis*), an anadromous species that experiences periods of starvation during winter months and during spawning (Woodhull 1947; Stevens 1966; Jones and Sidell 1982).

Materials and Methods

Adult striped bass (4-yr-old, mean FL 47 ± 15 cm) were collected in June 1983, after the spawning period, from the San Francisco Bay estuary by gill net and transported to a 20 000-L raceway using an aerated mobile fish transporter. They were acclimatized in the raceway to ambient, filtered bay water (approximately 17°C and 25 ‰ salinity) for 2 wk prior to randomized placement in the experimental tanks. All fish were fed anchovies on alternate days while in the raceway. Each circular 3200-L fiberglass experimental tank contained six fish and received flow-through ambient filtered bay water (approximately 18.5°C and 27 ‰ salinity) under the natural photoperiod. During the 4-wk experimental period, fish in one of the tanks were fed anchovies daily until satiated whereas no food was provided to fish in the other tank.

Blood was obtained by cardiac puncture using sterile Vacutainers[3] without anticoagulant and allowed to clot prior to centrifugation and serum withdrawal. After separation, each serum sample received antibacterial agents (0.001% sodium merthiolate and 0.01% sodium azide) and 1 mg/mL EDTA. Samples were stored at −80°C under nitrogen until analyzed.

Isolation of Lipoproteins

Serum lipoproteins were separated by sequential ultracentrifugation into density classes routinely used for human lipoprotein isolation for comparative purposes with studies of fishes and other animals. The density intervals employed were; $d<1.0063$ g/mL for VLDL, $1.0063<d<1.063$ g/mL for LDL, and $1.063<d<1.21$ g/mL for HDL. Appropriate density salt solutions for ultracentrifugal isolation of lipoprotein classes were prepared with NaCl and NaBr in deionized water and checked by pycnometry according to Lindgren (1975). All salt solutions contained antibacterial and antioxidation agents at the same concentrations as in serum samples. Since the nonprotein density of striped bass serum was unknown, it was adjusted to 1.0063 g/mL by exhaustive dialysis with a NaCl solution of $d = 1.0063$ g/mL prior to lipoprotein fractionation.

Lipoprotein fractions were isolated by the sequential ultracentrifugation techniques described in detail by Lindgren (1975) using a Beckman L5-75 with a 50-Ti rotor at 10°C. Briefly, 2.0 mL of dialyzed serum was added to a polycarbonate centrifuge tube and mixed with 4.0 mL of d 1.0063 g/mL NaCl solution and spun at 45 000 rpm (135 000 × g) for 18 h. The top 1.0 mL containing VLDL and the next 1.0 mL background fraction were removed. The remaining solution's density was raised to 1.063 g/mL with 2.0 mL of the appropriate density NaCl–NaBr solution and centrifuged for 20 h at 45 000 rpm (135 000 × g). The top 1.0 mL containing LDL and the next 1.0 mL for background assessment were removed. The remaining infranatant was increased in density to 1.21 g/mL with 2.0 mL of a NaCl–NaBr solution and spun at 45 000 rpm (135 000 × g) for 40 h at 10°C. As before, the top 1.0 mL containing HDL was removed as well as the next 0.5 mL for background.

Lipid Composition Analysis

Lipids were extracted from aliquots of serum and lipoprotein fractions with 2 × 15 volume of ethanol–ether (3:1). Precipitated protein was removed by centrifugation and the supernatant was evaporated under a stream of nitrogen. The dried lipid residue was reconstituted with chloroform–methanol (1:1) and analyzed for total lipid (Harvey and Patton 1981) and lipid class composition in triplicate using an Iatroscan TH-10 analyzer (Iatron Laboratories, Inc., Tokyo, Japan). The S-II Chromarods were developed in a solvent system of hexane–ethyl ether–acetic acid (95:5:0.2) which resolves triglycerides, alkyl esters/glyceryl ethers, free cholesterol, cholesterol esters, and phospholipids. Triglycerides were also determined in lipoprotein fractions and background fractions by the enzymatic method of Bucolo and David (1973).. Lipid-containing solutions were always stored in Teflon-lined screw-capped culture tubes under nitrogen in the dark at −20°C between procedural manipulations.

[3]References to trade names does not imply endorsement by the National Marine Fisheries Service.

TABLE 1. Total concentrations of lipid components and protein in serum of striped bass fed or starved for 4 wk. Values represent mean ± SE of six fish expressed as mg/dL. * = significantly different from fed ($P<0.05$).

Component	Treatment	
	Fed	Starved
Triglycerides	618 ± 132	252 ± 53*
Glyceryl ethers/alkyl esters	150 ± 60	189 ± 88
Cholesterol esters	240 ± 46	231 ± 48
Free cholesterol	201 ± 28	202 ± 29
Phospholipids	961 ± 118	859 ± 163
Total lipids	2169 ± 215	1733 ± 298
Protein	4067 ± 228	4433 ± 208

Apoprotein Analysis

Total protein concentrations in serum, lipoprotein fractions, and background fractions were determined by a modified Lowry method for lipoprotein samples, which incorporated sodium dodecyl sulphate into the alkali reagent, allowing direct assay without delipidation (Markwell et al. 1981). Bovine serum albumin standards were employed.

Apoproteins within each lipoprotein fraction were separated and characterized by molecular weight according to the sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) method of Laemmli (1970). Samples of apo-VLDL, apo-LDL, and apo-HDL were applied to separate gels to resolve high and low molecular weight apoproteins. High molecular weight apoproteins were separated using a 3.0% monomer stacking gel atop a 5.0% separation gel and low molecular weight proteins were resolved with a 5.0% monomer stacking gel and a 10.5% separation gel. Proteins were fixed and stained in a 0.1% Coomassie Brilliant Blue solution in 50% acetic acid, prepared fresh daily. Gels were destained by repeated washings in 7% acetic acid, dried, and scanned in a Helena "Fluor-vis" densitometer (Helena Laboratories, Inc., Beaumont, TX) equipped with a 560-nm filter. The molecular weight of each electrophoretic band was determined by comparing its mobility with that of a series of SDS-PAGE protein standards purchased from Bio-Rad Laboratories, Richmond, CA, according to the formula of Weber and Osborn (1969). Apoprotein electrophoretic bands were not quantified for reasons discussed extensively by Chapman et al. (1975).

Statistical Analysis

Differences in the lipid compositon of lipoprotein fractions and serum from fed and starved striped bass were analyzed using the paired *t*-test.

Results

Each treatment group of striped bass contained four females and two males. Statistical analysis of the data revealed no differences in lipid composition attributable to sex. Therefore, data from both sexes were combined.

Withholding food for 4 wk resulted in a 20% decrease in serum total lipids, but only the decline in triglycerides was statistically significant (Table 1). Serum triglyceride levels decreased by about 60%. Essentially no changes occurred in the concentrations of free cholesterol, cholesterol esters, and unknown compounds referred to here as glyceryl ethers/alkyl esters due to their similar mobilities on the Chromarods. The glyceryl ethers/alkyl esters fraction may contain 1-0-alkyl-diacylglycerides which have been found in other fish species (Mori et al. 1972; Kayama 1975; Mills and Taylaur 1977). Serum phospholipids were decreased by 11% and total serum protein increased by 9% in fish subjected to starvation, but neither change was statistically significant.

Mean weight percentage composition of the major lipoprotein classes revealed that starvation altered the distributions of lipids and protein in all lipoprotein fractions (Table 2). The predominant lipid in striped bass VLDL was triglyceride, accounting for about half of the lipid present in fed fish and 39% in starved fish. Protein contributed, by weight, 9.8% of the VLDL in fed striped bass. The proportion of protein in VLDL increased during the starvation period of 18.1%. This was due to a much greater depletion of lipid relative to protein in VLDL of starved fish compared with fed; the mean absolute concentrations of protein in fed and starved striped bass VLDL were approximately the same, 62.7 mg/dL and 75.0 mg/dL, respectively. Within the lipids, the quantitative decrease in VLDL triglycerides, from 445.2 mg/dL in fed fish to 159.9 mg/dL, was the major change observed due to starvation and was largely responsible for the statistically significant decrease in total lipid (Table 2). Starvation produced a greater mean percent contribution of phospholipids in VLDL due to the decreased contribution of triglycerides, despite little change in concentration (125.7 mg/dL in fed fish, 114.1 mg/dL in starved fish). Cholesterol esters were diminished six-fold and lipids within the glyceryl ethers/alkyl esters fraction four-fold in percent composition in VLDL of starved fish. The percent contribution of cholesterol to VLDL particles remained essentially unchanged.

There was a greater proportion of cholesterol, in free and esterified forms, in striped bass LDL than in other lipoprotein classes; however, triglycerides predominated in the LDL of fed fish (Table 2). Protein contributed, on a mean weight basis, a greater proportion of the LDL mass than in VLDL. Consequently, there was less lipid in LDL particles than in VLDL. In fed fish, phospholipids comprised about the same proportion of LDL as for VLDL (14.1 and 18.6%, respectively) and also on a mean concentration basis (138.4 mg/dL in LDL and 125.7 mg/dL in VLDL). There was an inverse relationship between cholesterol esters and free cholesterol in LDL compared to VLDL, with cholesterol esters predominating in LDL.

Starvation resulted in significant decreases in the mean weight percentages of triglycerides, phospholipids, and total lipid in striped bass LDL (Table 2). The other lipid components and protein increased in starved fish LDL, although the changes were not statistically significant. Compounds with chromatographic mobilities similar to glyceryl ethers and alkyl esters accounted for a greater proportion of LDL in fed and starved striped bass than in the other two lipoprotein fractions.

Phospholipids dominated striped bass HDL lipids and accounted for about 33.5% of the weight of HDL in fed and starved fish (Table 2). In concentration, however, phospholipid increased from 479.1 mg/dL in fed fish to 670.2 mg/dL in starved fish. The composition of the HDL fraction appeared to be affected the least by starvation. The only significant change occurred in the triglycerides fraction which comprised a small proportion of HDL.

Summation of all lipid components and protein concentrations within each lipoprotein class provided an estimate of the concentration of individual lipoprotein classes within each fish.

TABLE 2. Mean weight percent composition of lipid components and protein in serum lipoprotein classes of striped bass fed or starved for 4 wk. Values represent mean (SE) of six fish. * = significantly different from fed ($P<0.05$); ** = significantly different from fed ($P<0.01$); *** = significantly different from fed ($P<0.001$).

	VLDL		LDL		HDL	
Component	Red	Starved	Fed	Starved	Red	Starved
Triglycerides	50.6	38.8	27.2	6.5**	4.6	1.2***
	(9.3)	(5.6)	(4.6)	(1.1)	(0.6)	(0.1)
Glyceryl ethers	4.9	1.2	9.1	15.1	0.1	0.8
/alkyl esters	(4.2)	(1.2)	(3.4)	(3.5)	(0.1)	(0.6)
Cholesterol	6.9	1.1*	12.2	15.6	4.3	3.2
esters	(2.5)	(0.8)	(2.9)	(0.9)	(1.0)	(1.0)
Free cholesterol	10.2	11.5	8.4	11.5	2.9	2.5
	(3.5)	(8.5)	(1.2)	(5.0)	(0.3)	(0.8)
Phospholipids	18.6	29.3*	14.1	9.1**	33.4	33.9
	(4.0)	(2.1)	(1.1)	(0.8)	(1.2)	(2.8)
Total lipids	91.2	81.9*	71.0	57.8*	45.3	41.6
	(2.0)	(3.4)	(4.0)	(3.5)	(1.3)	(4.0)
Protein	9.8	18.1*	29.0	42.2	54.7	58.4
	(2.5)	(3.3)	(4.9)	(3.7)	(1.3)	(4.0)

TABLE 3. Concentrations and mean weight percent of serum lipoprotein classes in striped bass fed or starved for 4 wk. Values represent mean (SE) of six fish. *significantly different from fed ($P<0.05$; **significantly different from fed ($P<0.01$); ***significantly different from fed ($P<0.001$).

	VLDL		LDL		HDL		Σ LP
Treatment	mg/dL	wt %	mg/dL	wt %	mg/dL	wt %	mg/dL
Fed	834	25.1	938	28.0	1436	46.9	3208
	(147)	(2.0)	(175)	2.1)	(65)	(3.8)	(378)
Starved	401*	11.7***	1063	30.9	1977**	57.4*	3441
	(35)	(0.9)	(98)	(2.8)	(101)	(2.4)	(91)

Although mean total lipoprotein concentrations changed little between fed and starved striped bass, significant differences occurred within lipoprotein classes (Table 3). The HDL was the most abundant lipoprotein in striped bass serum and was significantly elevated in starved fish. Inversely, the least abundant lipoprotein, VLDL, declined significantly in concentration subsequent to starvation. This was due, primarily, to the depletion of triglycerides, and to a lesser extent by lower levels of cholesterol esters and cholesterol. The LDL comprised about 30% of the lipoproteins and the concentration remained essentially unchanged by starvation.

The apoproteins of VLDL and LDL were resolved in sodium dodecyl sulphate polyacrylamide gels of 5% monomer concentration and those of HDL in gels of 10.5% monomer (Fig. 1). Apo-VLDL displayed four bands. The predominant component remained near the origin of the separating gel and was a broad, intense band with a molecular weight greater than 250 000 daltons. The remaining bands were much narrower and fainter and contained proteins of approximately 207 000, 47 000, and 42 000 daltons. No apoproteins with molecular weights less than 42 000 were evident on any gels of apo-VLDL.

The apoproteins of LDL separated into five major bands and two bands containing trace amounts of dye-binding material. As with apo-VLDL the largest, darkest staining component had a molecular weight in excess of 250 000 daltons. Apo-LDL also contained a band at about 42 000 daltons with the same staining characteristics as seen for apo-VLDL. Other bands of similar size and intensity were observed with molecular weights of about 77 000, 60 000, and 51 000 daltons. Trace amounts of polypeptides occurred with apparent molecular weights of approximately 203 000 and 149 000 daltons.

Apo-HDL was distinctly different in composition relative to VLDL and LDL (Fig. 1). The largest and darkest staining component corresponded to a molecular weight of about 24 000 daltons. The next most prominent band had an apoprotein of 13 000 daltons. A substantial amount of material was observed with a molecular weight greater than 100 000 daltons. Other faint bands were identified with molecular weights of 76 000, 50 000, and 28 000 daltons.

Qualitatively, withholding food for 4 wk resulted in very little change in the apoprotein content of lipoproteins in striped bass. Within the resolution obtained by SDS-PAGE, all components observed on the gels for apo-HDL and apo-LDL from fed fish were present on those from starved fish. The only difference noted occurred in apo-VLDL, where the band with an estimated molecular weight of 207 000 daltons found in fed fish was absent in apo-VLDL of starved fish. Since analytical manipulations (e.g. repeated washings, dialysis, and ultracentrifugations of lipoprotein fractions) and variable chemical characteristics (e.g. differential chromogenicities to stains between electrophoresis bands) are known to compromise the validity of band quantification (Herbert et al. 1978), we did not assess apoprotein concentrations within lipoprotein fractions of fed or starved fish.

Discussion

Serum Lipids

A decrease in triglycerides concentration was the only statistically significant change observed in the serum of starved

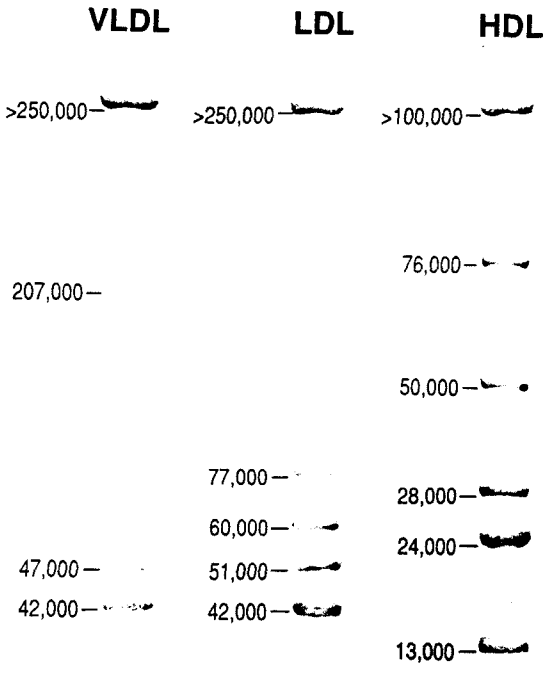

FIG. 1. Representations of sodium dodecyl sulphate-polyacrylamide gels of striped bass apolipoproteins. Apo-VLDL and apo-LDL were electrophoresed in 5% monomer gels and apo-HDL in 10.5% monomer gels. Gels were stained with Coomassie Briliant Blue and molecular weights were calculated from a series of molecular weight protein standards.

striped bass. This decline was not unexpected, however, since it is known that during the initial phases of starvation in fish triglycerides are catabolized while other lipids remain largely unchanged (Love 1980). Also, it has been shown in pink salmon (*Oncorhynchus gorbuscha*) that, during the nonfeeding spawning migration, the liver's triglyceride synthetic ability is lost and blood triglyceride levels fall (Phleger 1971). Decreased serum or plasma triglycerides have been observed in (*Oncorhynchus mykiss* (formerly *Salmo gairdnerii*; Takashima et al. 1971), *Salmo alpinus* (Dannevig and Norum 1983), and *Pleuronectes platessa* (White and Fletcher 1986) after periods of starvation.

Serum Lipoproteins

All the major lipid components were found to a variable extent in each serum lipoprotein class. Variability in the concentrations of lipid components between fish within each treatment group was high and has been noted in other fish species (Chapman et al. 1977; Fremont et al. 1981; Farrell and Munt 1983).

The lipid and protein composition of lipoprotein classes in the serum of fed striped bass was generally similar to that found in rainbow trout (Chapman et al. 1978; Skinner and Rogie 1978; Fremont et al. 1981). In comparison with rainbow trout, striped bass VLDL was somewhat richer in triglycerides and depleted in cholesterol esters. The LDL of striped bass contained the most total cholesterol (free + esterified) of all the lipoprotein classes; however, triglycerides were the predominant lipid in fed striped bass LDL. Phospholipids accounted for the greatest proportion of striped bass HDL lipid, consistent with other fish species studied (Chapman 1980). Otherwise, the HDL of fed striped bass was composed of similar proportions of triglycerides and cholesterol, lower cholesterol esters, and greater protein in relation to the composition of HDL in salmonids (Nelson and Shore 1974; Chapman et al. 1978; Skinner and Rogie 1978; Fremont et al. 1981).

The apoproteins of striped bass lipoprotein classes were characterized only by their molecular weights. This technique, by itself, does not constitute definite identity but is often used for comparative purposes between lipoprotein classes or with data from other species. In the SDS-PAGE of striped bass VLDL and LDL, the apoprotein band with a molecular weight >250 000 daltons was by far the largest and most intensely stained and may be analogous to mammalian apo-B (Eisenberg 1979; Steinberg 1979). Electrophoretic separations of VLDL and LDL from other fish species have found a similar apoprotein which, in combination with immunological and chemical analyses, has been determined to resemble apo-B (Mills et al. 1977; Chapman et al. 1978). Striped bass VLDL and LDL contained several other apoproteins of lower molecular weights in lesser amounts. This was also the case with rainbow trout (Chapman et al. 1978; Skinner and Rogie 1978). The HDL of striped bass differed from VLDL and LDL in that the primary apoproteins had molecular weights of about 24 000 and 13 000 daltons, and based on these weights may be similar to human apo-AI (27 000 daltons) and apo-AII (17 000 daltons) (Schaefer and Levy 1979). Rainbow trout HDL was found to contain predominantly apoproteins characteristic of apo-AI and apo-AII (Chapman et al. 1978; Skinner and Rogie 1978). The results of the present study and those from studies of fish, birds (Chapman et al. 1977), and mammals (Hollanders et al. 1986) would suggest that the apolipoprotein composition of higher vertebrates is generally similar.

The concentration of total serum lipoproteins in both fed and starved striped bass was high, on the order of that found in salmonids (Nelson and Shore 1974; Chapman et al. 1978; Skinner and Rogie 1978), and reflects the importance of lipids in fish metabolism. Although the total serum lipoprotein concentration was unchanged by starvation, the relative contribution of lipoprotein classes was affected such that VLDL declined and HDL increased. Further, the changes in lipid distributions within serum lipoprotein classes of starved striped bass indicate that there were greater adjustments of lipid metabolism and transport produced by starvation than would be evident by simply assessing lipid changes in serum.

The largest change, on a mean weight percent basis, in the VLDL and LDL of starved striped bass was the depletion of triglycerides. Since VLDL is the principal transport vehicle for triglycerides (Eisenberg 1979) and LDL is formed from VLDL (Brown and Goldstein 1986), it may be expected that the combined influences of no ingestion, depletion of body reserves, and reduced triglyceride synthesis would result in decreased VLDL and LDL triglycerides.

In starved striped bass, HDL composition was the least affected of the serum lipoproteins. The HDL have been shown to be involved in "reverse" cholesterol transport, from peripheral tissues back to hepatocytes (Miller et al. 1985), and cholesterol and phospholipid exchanges between lipoproteins and

tissues (Glomset 1979). Cholesterol and cholesterol ester values were unaffected by starvation in striped bass HDL, both in mean weight percent and concentration. These results are similar to those of Black and Skinner (1986), using cholesterol concentration as an estimator of lipoprotein concentrations in rainbow trout. They found that 8 wk starvation produced no change in HDL cholesterol but diminished VLDL and LDL levels.

Phospholipids in the HDL of starved striped bass remained the same as in the HDL of fed fish on a weight percent basis, but the concentration increased significantly ($P<0.001$). The increased concentration of phospholipids, along with protein, was responsible for the increased HDL in starved striped bass compared with fed. In fact, phospholipids in HDL of starved striped bass accounted for 78% of the total serum phospholipid concentration, whereas phospholipid in fed fish HDL comprised about 50% of total serum levels.

Fish biomembranes contain 25 to 80 percent lipid, mainly phospholipids which are characteristically enriched in polyunsaturated fatty acids (PUFA), primarily 22:6($n-3$) (Henderson and Tocher 1987). The 22:6($n-3$) PUFA is an essential fatty acid in most fish species and is critical to growth and maintaining membrane fluidity in colder environments (Sargent et al. 1989). Striped bass are known to require 22:6($n-3$) for growth and membrane synthesis, and tissue levels of this essential fatty acid were selectively maintained during starvation (Martin et al. 1984). The results of the present study indicate that HDL assumes increased importance in the transport of phospholipids containing essential PUFA for maintenance of tissue integrity during starvation, and perhaps for the synthesis of gonadal tissue during annual reproductive development. The increased role of HDL during reproductive development has been suggested from the results of previous work on salmonids by Nelson and Shore (1974) and Fremont and Marion (1982). High levels of HDL were found in the serum of pink salmon (*Oncorhynchus gorbuscha*) just prior to spawning and after weeks to months of starvation; VLDL and LDL were undetected (Nelson and Shore 1974) but were evident in the early prespawning phase. In this study, phospholipid was about 50% of the lipid in HDL and contained 22:6($n-3$) and 20:5($n-3$) as the predominant PUFAs. Fremont and Marion (1982) found similar results in spermiating rainbow trout, where HDL accounted for greater than 50% of the serum lipoproteins with phospholipid comprising 70% of the lipid in HDL. Additionally, 22:6($n-3$) was the predominant PUFA in the phospholipids. Since phospholipids, enriched in 22:6($n-3$), predominate in egg yolk lipids of striped bass (Eldridge et al. 1983), it is reasonable that HDL functions as a primary vehicle for the transport of structural lipids and essential PUFA for gonadal maturation during the nonfeeding spawning period.

The findings of high serum levels of lipoproteins, and particularly HDL, in striped bass during starvation indicate their important role in permitting fish to withstand long periods without food by distributing lipids to tissues in order to maintain their integrity, whether or not starvation is accompanied by gonadal development. Furthermore, HDL appears to assume greater significance in facilitating the transport of structural lipids and essential PUFA during periods of starvation.

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