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Depth related trends in proximate composition of demersal fishes in the eastern North Pacific

J.C. Drazen*

University of Hawaii, Department of Oceanography, 1000 Pope Road, Honolulu, HI 96822, USA

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Abstract

The proximate chemistry of the white muscle and liver of 18 species of demersal fish from the eastern North Pacific was studied to determine trends with depth, locomotory mode and buoyancy mechanism, foraging strategy and to elucidate energetic strategies. Data for 24 species from shallow water were taken from the literature and included for analysis of muscle water content. Benthopelagic species, primarily gadiforms, have significantly larger lipid-rich livers than benthic species. The benthopelagic species may use this lipid to add buoyancy, but it is also used as energy storage. Buoyancy mechanism was directly related to proximate composition. Fishes using gasbladders had normal muscle composition. The two species of benthopelagic fishes without gasbladders have either very high muscle lipid content (*Anoplopoma fimbria*) or gelatinous muscle (*Alepocephalus tenobrosus*) to aid in achieving neutral buoyancy. The macrourid, *Albatrossia pectoralis*, has a very small gasbladder and also has gelatinous muscle. Both of these benthopelagic fishes with gelatinous muscle feed on pelagic organisms. Gelatinous muscle was also found in two flatfishes that inhabit the oxygen minimum zone. For these fishes, high water content may serve to lower metabolic costs while maintaining large body size. Scavengers such as *Coryphaenoides armatus* and *Coryphaenoides acrolepis* have lipid rich livers and others such as *A. fimbria* and *Pachycara* sp. have high and variable muscle lipid content. Thus foraging mode also acts to influence proximate composition. Several depth-related trends in proximate composition were found. White muscle water content increased significantly with depth, and all four gelatinous species occurred at bathyal depths. This adds evidence in support of the hypothesis that decreasing light levels shorten reactive distances and relax the selective pressure for high locomotory capacity. In addition significant declines in liver protein content were observed, suggesting that the rates of metabolism in this organ also decline with depth. There was little evidence for food availability affecting proximate composition. There were no significant changes in either muscle or liver lipid or caloric density with depth. Total lipid stores actually increased significantly, but they were driven primarily by the abyssal scavenger *C. armatus* suggesting that foraging strategy rather than depth may be the most important factor determining total lipid stores.

Keywords: Proximate composition; Chemical composition; Locomotion; Buoyancy; Energetics; Energy content

1. Introduction

The proximate composition (protein, lipid, carbohydrate, and water) of a fish can yield information

*Tel.: +1 808 956 6567; fax: +1 808 956 9516.
E-mail address: jdrazen@hawaii.edu.

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about its locomotory habits and energetic adaptations (Childress and Nygaard, 1973; Childress et al., 1990). Such an approach is useful in the deep sea, where direct observations of locomotion and metabolism are difficult to obtain. The proximate composition of pelagic fishes has been investigated (Bailey and Robison, 1986; Childress and Nygaard, 1973; Childress et al., 1990; Donnelly et al., 1990; Stickney and Torres, 1989). Generally water content increased and lipid and protein contents declined with increasing depth of occurrence (Bailey and Robison, 1986; Childress and Nygaard, 1973; Stickney and Torres, 1989). These trends have been hypothesized to reflect reduced musculature and hence reduced locomotory capacity, because declining light levels reduce reactive distances between predators and prey in taxa that rely primarily on vision. As a consequence the selective pressure for active swimming capacities to pursue prey or avoid predators is reduced (Childress, 1995; Seibel and Drazen, in press). Trends have also been found that relate a fish's buoyancy mode to its proximate composition (Bailey and Robison, 1986; Childress and Nygaard, 1973; Stickney and Torres, 1989).

Regional variations in proximate composition have also been found. Fish in temperate or eutrophic waters have higher lipid reserves than relatives in oligotrophic waters, probably due to the seasonal nature of food input in the eutrophic temperate and polar environments (Bailey and Robison, 1986; Childress et al., 1990; Donnelly et al., 1990; Stickney and Torres, 1989). The overall energy content of fish has been used to infer the energy demands of the fish and to reflect realized food availability (Bailey and Robison, 1986; Crabtree, 1995). In short, the few studies to date have shown that a great deal of information can be determined about a fish's locomotory and energetic adaptations from its proximate composition.

Rarely has the technique been applied to benthic and benthopelagic species. Crabtree (1995) analyzed the carbon, hydrogen and nitrogen (CHN) of demersal fishes from 100–5000 m depth in the Atlantic and found trends similar to those found for midwater fishes. Other results are primarily from the food science literature and typically provide data on filets only (Gordon and Roberts, 1977; Stansby, 1976). Despite the potential information to be gained, no similar studies have been conducted on deep-sea demersal fishes in the Pacific. In this study, the proximate composition of 519 specimens representing 18 species of demersal fishes from ~100–4000 m was determined to examine the relationship between depth, locomotory mode and buoyancy mechanism, general foraging mode and to elucidate energetic strategies.

2. Methods

Fishes were collected in several ways. Bathyal species were collected from 200–1400 m off northern California with a Nor'eastern bottom trawl with a 37.4 m footrope. This was a part of the National Marine Fisheries slope survey conducted in November 1996 (Lauth, 1997). Fishes were also collected with traps and longlines from 1200 m depth in the San Diego Trough (mostly *Coryphaenoides acrolepis*) and two species of macrourids from a 4100 m site ~200 km off Pt. Conception, California, on the abyssal plain (Drazen, 2002; Smith and Druffel, 1998). Finally, *Spectrunculus grandis* and *Pachycara* sp. were collected in traps from depths of ~3500 m off of Monterey Bay, California.

For correlations to depth, the minimum depth of occurrence (MDO), defined as the depth below which 90% of the population is found (Childress, 1995), was used. MDO was identified from various literature sources, which are given in Table 1, with a minimum value of 10 m to designate those species found in shallow nearshore waters. Many benthic and benthopelagic species exhibit ontogenetic vertical migration (Jacobson and Hunter, 1993; Jacobson and Vetter, 1996). Thus the MDOs used in this study reflect a depth that corresponds to the size range of the fish used. Generally large adult specimens were used, and a single MDO was adequate. However, for *C. armatus*, *Sebastolobus alascanus*, and *Microstomus pacificus*, the MDOs for the size ranges sampled differed enough to warrant splitting them into separate groups for analysis (Table 1).

Tissue samples for proximate chemical analyses were taken from the liver and white muscle of all fish and immediately frozen in a −70 °C freezer aboard ship or in liquid nitrogen. In addition, triplicate samples of both muscle and liver were placed in pre-weighed test tubes, sealed with parafilm and frozen at −20 °C for later freeze-drying and water content determination. Total length, weight, liver weight, and gonad weight of all fish were taken. Sex and reproductive state were noted. For macrourids pre-anal fin length (PAFL)

Table 1
Collection information for the 18 species (and size/MDO categories) in this study

Species	Family	*N*	Habit	gb	Length (cm)	Mass (g)	Capture Depth (m)	MDO (m)	Ref.
Albatrossia pectoralis	Macrouridae	17	BP	Y	17–32	704–4456	853–1249	600	1
Alepocephalus tenobrosus	Alepocephalidae	17	BP	N	20–45	66–938	646–1200	550	1, 2
Anoplopoma fimbria	Anoplomatidae	20	BP	N	49–68	1092–3016	609–1200	200	3, 4
Antimora microlepis	Moridae	16	BP	Y	22–51	44–1010	750–1249	510	3, 5
Coryphaenoides acrolepis	Macrouridae	134	BP	Y	13–29	290–2321	924–1249	1000	1, 6, 7
Coryphaenoides armatus <1000 g	Macrouridae	85	BP	Y	15–22	299–960	4100	2200	7, 8
Coryphaenoides armatus	Macrouridae	17	BP	Y	21–28	1000–1969	4100	3000	7, 8
Coryphaenoides armatus >2000 g	Macrouridae	17	BP	Y	25–34	2120–3760	4100	3500	7, 8
Coryphaenoides cinereus	Macrouridae	26	BP	Y	9–16	101–484	844–1406	720	5
Coryphaenoides yaquinae	Macrouridae	44	BP	Y	13–24	179–1107	4100	3700	9, 10
Embassichthyes bathybius	Pleuronectidae	15	B	N	28–41	248–1044	1193–1224	730	1, 10
Glyptocephalus zachirus	Pleuronectidae	15	B	N	27–41	126–458	338–507	50	6, 11
Merluccius productus	Merluccidae	15	BP	Y	40–53	474–970	191–347	50	5
Microstomus pacificus	Pleuronectidae	7	B	N	32–40	302–656	511–691	200	12, 13
Microstomus pacificus >750 g	Pleuronectidae	8	B	N	43–53	790–1692	511–691	400	12, 13
Pachycara sp.	Zoarcidae	6	B	N	36–55	140–667	3300	1800	2, 14
Parophrys vetulus	Pleuronectidae	15	B	N	27–38	168–498	191–337	100	1, 11
Sebastes diploproa	Scorpaenidae	14	BP	N	16–34	72–692	215–352	215	6
Sebastolobus alascanus	Scorpaenidae	12	B	N	24–36	148–516	598–609	400	15
Sebastolobus alascanus >750	Scorpaenidae	3	B	N	41–54	834–2182	598–609	600	15
Sebastolobus altivelis	Scorpaenidae	15	B	N	18–34	60–410	750–853	400	15
Spectrunculus grandis	Ophidiidae	1	BP	Y	73	2911	3270	2000	2, 16

Length is standard length except for macrourids for which preanal fin length is reported. Habit is either benthic (B; resting on the bottom) or bent hopelagic (BP; swimming above the bottom most of the time), gb = gasbladder. References are given which were used to determine the MDO for each group.

1—Lauth (1997).
2—MBARI VARS database.
3—Eschmeyer et al. (1983).
4—Jacobson et al. (2001).
5—Cohen et al. (1990).
6—Miller and Lea (1972).
7—Stein and Pearcy (1982).
8—Merrett (1992).
9—Wilson and Waples (1983).
10—Pearcy et al. (1982).
11—Vetter et al. (1994).
12—Hunter et al. (1990).
13—Jacobson and Hunter (1993).
14—Anderson (1994).
15—Jacobsen and Vetter (1996).
16—Mauchline and Gordon (1984).

was used instead of total length as their long tail tips are often missing or damaged during capture.

Protein, carbohydrate, and lipid assays were performed on tissue homogenized in distilled water in triplicate. The bicinchoninic acid (BCA) protein assay (Smith et al., 1985) and the Dubois et al. (1956) carbohydrate assay were used with bovine serum albumin and D-glucose as standards. Lipids were extracted according to Bligh and Dyer (1959). For *S. grandis* and *Pachycara* sp. total lipids were measured by the charring method of Marsh and Weinstein (1966) as modified by Reisenbichler and Bailey (1991). For the rest of the species lipid composition was determined by the Iatroscan technique, which combines thin layer chromatography to separate lipid classes and flame ionization for detection and quantification (Fraser et al., 1985; Volkman and Nichols, 1991). Cholesteryl oleate, triolein, oleic acid, cholesterol, diolein, and phosphotidycholine were used as standards for steryl esters (SE), triglycerides (TAG), free fatty acids (FFA), sterols (ST), diglycerides (DAG) and phospholipids (PL), respectively. Wax esters (WE) may also have been present in some fishes. Waxes could not be separated from SE in the solvent system used in this study. Standards were run for each set of 10 SIII chromorods, and standard curves were best fit as either linear or power functions. Lipids were concentrated, resuspended in chloroform, and spotted (1 μl) in duplicate. Rods were developed in 85:15:0.01 (muscle lipids) or 90:10:0.01 (liver lipids) hexanes, diethyl ether, formic acid for 20–25 min. Rods were dried for 8–10 min in an oven at 110 °C prior to scanning on a Mark V Iatroscan. Each frame was scanned once to quantify the lipid classes and a second time to remove residual material.

Approximate caloric density of both muscle and liver were calculated assuming the following conversion factors: 5.7 kcal/g protein, 8.7 kcal/g lipid, 4.1 kcal/g carbohydrate (Childress et al., 1990). Fishes store energy primarily as lipids (Love, 1970). To estimate changes in energy storage with depth, each fish's total lipid was calculated from the total lipid stored in the liver and muscle assuming that the muscle was 50% of the wet mass of the fish (Bone, 1978). The relationships between each variable and fish mass were explored with linear and power regressions.

The focus of the collections for this study was at bathyal depths. To augment these data and provide a more robust analysis of depth-related trends, data from the literature were incorporated. Studies were chosen that presented data for fishes collected in the same region, namely off California and Oregon (Gordon and Roberts, 1977; Stansby, 1976; Sullivan and Somero, 1980). Each of these studies presented data on the fishes' muscle. No data for liver were available. When both literature sources and my data overlapped, my data were used. In cases where more than one literature source presented data for a species, the values were averaged. The techniques for protein and lipid determinations varied from those used in this study, which made comparisons difficult. Fortunately, the determination of the water content of a tissue is relatively simple and offers comparable results. Data for eight species were available from my analyses and those from the literature sources and they were not significantly different (M W U-test, $p > 0.05$).

A nonlinear regression analysis was used to determine changes in proximate composition with depth. Comparisons between groups of fishes were made with Mann-Whitney U-tests. Statistica 7.0 was used for all statistical procedures.

3. Results

Regression analysis between fish mass and proximate composition yielded few consistent trends for muscle tissue, so values were used for interspecific comparisons without correction for size (Table 2). Size influenced liver composition in some cases. However, correction to a common interspecific fish mass of 500 g changed the values negligibly, because this size was near the average (Table 1) for most of the species for which size scaling effects were evident. Therefore, the values were used without applying size standardizations. In two cases (*C. armatus* and *S. alascanus*) both MDO and liver composition varied with size (Table 3). Thus for intraspecific changes in composition it is difficult to dissect the competing influences of ontogeny and depth. In the case of *C. armatus,* all of the individuals examined in the present study were collected at the same depth. This suggests that at least in this species the influence of ontogeny is extremely important. Additional samples of this species at various sizes and across a broad depth range could more clearly determine the effects of both variables.

An examination of fish muscle composition revealed four gelatinous species and three high-lipid species (Table 2). *Albatrossia pectoralis*, *Alepocephalus tenebrosus*, *Embassichthyes bathybius* and *M. pacificus* had muscle water of 87–92% and a gelatinous appearance to the muscle tissue. *Anoplopoma fimbria* had very high muscle lipid and low water and was very unique in its muscle composition. *Alepocephalus tenebrosus* and *Pachycara* sp. also had relatively high lipid (Table 2), but it was still 3–7 times lower than that of *A. fimbria,* which had an average of 91.4 mg g^{-1}. The majority of the lipids in *A. fimbria* and *A. tenobrosus* were TAGs (Table 3). No lipid class analysis was performed on *Pachycara* sp., but it would follow that the lipid reserves were primarily TAG. Large (>750 g) *S. alascanus* also had large amounts of storage lipid (TAG) in their muscle, yet they did not have an unusually large amount of total lipids. The muscle lipids of the other species were primarily membrane bound PL, particularly for the gadiform fishes (families Merlucciidae, Macrouridae, Moridae). Only small amounts of SE/WE or FFA were present in the fishes. The proportion of muscle TAG was strongly correlated to total muscle lipids ($r = 0.90$; $p < 0.05$). Carbohydrate was a minor component of fish muscle with less than 2.25 mg g^{-1} in the fishes examined.

Liver size and composition varied greatly between the fishes (Table 3). The scorpaenids (*Sebastolobus diploproa*, *Sebastolobus alascanus*, and *Sebastolobus altivelis*) and *E. bathybius* had relatively high carbohydrate concentrations of ~5%. All of the gadiformes had large livers (HSI = 3.2–16%) that were very lipid-rich and hence had high caloric densities. They had very high liver lipid storage as a percent of body mass (Table 4) except for the abyssal macrourid, *Coryphaenoides yaquinae*. The scorpaenids and *A. fimbria* had intermediate lipid, and the pleuronectids and *A. tenebrosus* had low lipid and small livers (HSI = 0.39–1.41%). *Parophrys vetulus* had the lowest lipid levels and the

Table 2
Muscle proximate composition and caloric density

Species	% Water	Protein (mg/g)	Carbohydrate (mg/g)	Lipid (mg/g)	Caloric Density (kcal/g)
A. fimbria	70.29±4.12	89.08±8.29	2.05±0.93	91.4±21.74	1.31±0.2
A. microlepis	82.82±0.71	95.6±9.87	1.2±0.35	3.85±0.34	0.51±0.19
A. pectoralis	91.86±0.91	47.15±6.65	0.86±0.33	2.17±0.26	0.29±0.04
A. tenobrosus	89.94±3.52	55.32±7.41	0.81±0.38	12.72±11.07	0.43±0.12
C. acrolepis	83.39±1.1	107±7.88	1.33±0.31	3.82±0.44	0.65±0.04
C. armatus <1000 g	82.71±1.05	107.68±13.23	1.28±0.6	4.27±0.98	0.68±0.05
C. armatus	83.46±0.93	112.21±3.66	1.59±0.37	4.78±0.39	0.69±0.02
C. armatus >2000	83.24±0.85	113.33±12.43	1.76±0.7	4.34±0.84	0.71±0.06
C. cinereus	83.01±0.66	87.61±8.54	0.9±0.21	3.3±0.47	0.5±0.02
C. yaquinae	83.45±1.63	94.46±20.33	1.04±0.37	3.44±1.23	0.55±0.15
E. bathybius	89.11±2.48	60.9±17.28	1.48±0.49	4.54±2.17	0.39±0.1
G. zachirus	83.12±2.66	92.65±6.26	1.21±0.3	4.82±1.15	0.58±0.04
M. pacificus	87.02±2.38	63.57±17.42	1.21±0.44	3.8±0.79	0.34±0.18
M. pacificus >750	88.16±1.71	68.19±8.11	1.26±0.18	5.19±1.61	0.33±0.21
M. productus	82.16±0.51	99.13±7.72	1.33±0.46	5.95±1.12	0.62±0.05
P. vetulus	82.53±0.96	97.22±4.81	1.14±0.43	5.97±1.46	0.61±0.03
Pachycara sp.	80.43±3.49	105.17±9.87		27.69±32.87	0.84±0.25
S. alascanus	81.87±0.24	99.95±7.3	1.5±0.4	5.06±1.15	0.62±0.04
S. alascanus >750	80.38±2.42	100.27±0.66	2.24±0.41	8.49±3.29	0.65±0.03
S. altivelis	83.07±0.8	94.89±8.49	1.19±0.35	4.77±2.46	0.59±0.06
S. diploproa	79.32±2.25	111.14±5.11	1.79±0.74	6.45±1.04	0.7±0.03
S. grandis	85.74	82.63		2.88	0.5

Total muscle lipid is given as a percentage of body mass (% bm).

lowest TAG (11.60%) of any of the fishes (Table 5). The majority of the lipids in the fishes were TAGs, but *A. tenebrosus* and the pleuronectids had a considerable amount of PL (Table 5). Similar to muscle, liver TAG was strongly correlated to total liver lipid concentration ($r = 0.86$; $p<0.05$). Some diglyceride (DAG) was present in the liver lipids of *A. fimbria*, *Antimora microlepis*, *Merluccius productus* and *S. altivelis,* but not in the other species. SE was present in larger proportions than in the muscle tissue for all the fishes.

Comparisons between fishes with either benthic or benthopelagic habits and gasbladder presence or absence were performed to examine how locomotory mode and buoyancy (Tables 1 and 6) might be related to proximate chemistry. There were no significant differences in muscle composition or caloric density between benthic and benthopelagic species (MW *U*-tests, $p>0.05$). Only the data collected directly in this study were available to compare liver composition. These results indicated that benthopelagic fishes had significantly larger livers with more lipid, less water, and less protein than benthic fishes (MW *U*-tests, $p<0.05$). The percentage of liver TAG's was significantly higher in the benthopelagic fishes (MW *U*-test, $p<0.05$). Comparison between fish with and without gasbladders is not independent of the above tests because all but two benthopelagic fishes had gasbladders and only one benthic fish, *Paralabrax nebulifer* (water content data only), had a gasbladder (Tables 1 and 6). Therefore, comparisons were made between benthopelagic fish with and without gasbladders. HSI was significantly larger in those species with gasbladders (MW *U*-tests, $p<0.05$). Muscle lipid (Table 2) and %TAG (Table 4) were significantly higher in the two species without gasbladders, *A. fimbria* and *A. tenebrosus*.

As stated in the methods section, it was difficult to compare protein and lipid data acquired with different techniques in other studies to the present values. The water contents of muscle were available for a variety of shallow living fishes (Table 6). Muscle water and protein content are strongly correlated in most fish (Childress and Nygaard, 1973; Love, 1970) and they certainly were for the data used in this study (Fig. 1). The protein concentrations reported from the present analysis

Table 3
Liver composition, caloric density and total fish lipid

Species	HIS (%bm)	% Water	Protein (mg/g)	Carbo. (mg/g)	Lipid (mg/g)	Caloric Density (kcal/g)	Total Liver Lipid (%bm)	Total Fish Lipid (%bm)
A. fimbria	2.23±0.52	55.2±6.00	82.7±10.7	26.8±15.9	238.8±57.15	2.66±0.46	0.52±0.14	5.09±1.15
A. microlepis	5.85±2.97	38.2±13.0	60.6±20.3	13.7±5.93	334.9±69.51	3.32±0.51	2.11±1.26	2.27±1.30
A. pectoralis	3.29±1.36	29.5±3.77	33.6±4.74	14.4±7.60	424.7±59.65	3.95±0.52	1.42±0.66	1.53±0.66
A. tenobrosus	0.54±0.29	77.1±4.06	73.4±6.08	16.0±9.93	74.41±32.03	1.13±0.29	0.04±0.03	0.68±0.57
C. acrolepis	3.47±1.34	46.7±9.42	71.3±13.3	15.9±7.35	304.3±79.21	3.12±0.63	1.13±0.64	1.31±0.64
C. armatus <1000 g	6.11±5.18	43.7±14.9	60.7±16.8	10.7±4.14	301.8±119.8	2.99±1.00	2.23±2.53	2.46±2.53
C. armatus	9.10±4.04	26.3±7.66	48.3±7.53	12.6±5.00	455.8±54.91	4.29±0.47	4.18±2.29	4.42±2.30
C. armatus >2000	15.8±2.44	20.3±6.77	38.1±2.59	12.8±3.61	456.8±47.20	4.24±0.42	7.03±1.43	7.27±1.43
C. cinereus	5.56±3.30	41.7±14.4	52.7±17.7	9.13±3.65	354.2±51.96	3.42±0.40	1.30±1.01	1.47±1.01
C. yaquinae	3.23±2.00	58.7±17.5	71.9±19.7	12.4±11.0	126.2±111.1	1.56±0.86	0.66±0.80	0.88±0.81
E. bathybius	0.50±0.19	72.4±5.65	78.6±9.35	46.2±12.9	85.01±49.72	1.38±0.43	0.05±0.04	0.28±0.12
G. zachirus	0.61±0.20	70.3±4.87	95.1±6.99	25.5±9.52	101.7±51.97	1.53±0.44	0.07±0.05	0.31±0.10
M. pacificus	0.39±0.14	75.4±2.99	91.5±4.96	17.3±9.17	65.23±30.81	1.16±0.25	0.03±0.01	0.19±0.09
M. pacificus >750	0.67±0.29	76.1±3.09	93.4±7.06	18.8±10.9	55.10±23.45	1.09±0.19	0.04±0.03	0.23±0.13
M. productus	4.87±0.75	36.2±5.41	62.8±8.81	19.9±6.99	372.8±39.91	3.68±0.33	1.82±0.34	2.11±0.36
P. vetulus	1.41±0.51	76.7±2.82	104.6±7.47	17.7±7.88	39.50±14.19	1.01±0.15	0.06±0.04	0.36±0.10
Pachycara sp.	3.26±0.38	68.7±7.19	92.8±5.07		64.17±37.89	1.09±0.31	0.20±0.11	1.59±1.67
S. alascanus	1.32±0.58	58.0±6.29	70.8±23.0	54.1±15.5	160.6±39.72	2.02±0.32	0.22±0.12	0.48±0.17
S. alascanus >750	2.97±0.95	47.9±5.20	64.9±6.13	43.9±17.3	242.8±80.92	2.66±0.62	0.69±0.25	1.12±0.41
S. altivelis	1.22±0.74	57.5±6.42	77.9±8.92	54.7±17.7	170.5±81.21	2.15±0.62	0.21±0.14	0.45±0.20
S. diploproa	2.45±0.88	58.0±7.56	87.2±13.5	57.8±27.6	175.5±65.69	2.26±0.48	0.49±0.33	0.81±0.36
S. grandis	3.66	53.9	71.7		140.7	1.63	0.51	0.66

Total liver lipid and total fish lipid are given as a percentage of body mass (% bm). Carbo. = carbohydrate.

Table 4
Muscle lipid composition as a percentage of total lipid

Species	SE	TAG	FFA	ST	PL
A. fimbria	0.00±0.00	92.7±2.40	0.00±0.00	0.30±0.06	6.97±2.36
A. microlepis	0.28±0.14	1.89±2.26	0.44±0.14	5.43±1.11	92.0±2.87
A. pectoralis	0.25±0.15	0.86±0.44	0.40±0.11	6.99±0.82	91.5±0.92
A. tenobrosus	0.25±0.18	52.9±33.1	0.50±0.43	2.05±1.44	44.3±31.2
C. acrolepis	0.21±0.09	1.43±1.35	0.57±0.16	7.14±0.81	90.7±1.57
C. armatus <1000 g	0.36±0.35	0.61±0.59	0.66±0.24	4.64±0.82	93.7±1.46
C. armatus	0.18±0.05	0.91±1.75	0.53±0.15	4.37±0.43	94.0±1.47
C. armatus >2000	0.24±0.13	0.41±0.33	0.53±0.25	4.21±0.42	94.6±0.73
C. cinereus	0.17±0.12	1.69±1.98	4.62±7.17	6.51±0.61	87.0±8.86
C. yaquinae	0.65±0.51	0.88±1.37	0.87±0.33	4.74±0.95	92.9±1.73
E. bathybius	1.05±1.42	22.8±20.5	0.25±0.16	5.98±1.78	70.0±18.6
G. zachirus	0.98±0.32	3.21±2.95	0.63±0.31	6.57±0.57	88.6±2.92
M. pacificus	0.58±0.10	9.75±7.91	0.60±0.42	7.27±1.02	81.8±6.85
M. pacificus >750	0.67±0.24	19.6±21.8	0.66±0.51	6.52±2.64	72.6±19.7
M. productus	0.19±0.05	10.32±9.49	0.32±0.08	4.59±0.75	84.6±9.57
P. vetulus	1.34±0.94	11.3±12.7	0.43±0.12	5.85±0.88	81.1±11.9
S. alascanus	0.33±0.09	7.68±10.4	0.27±0.14	5.61±0.93	86.1±9.72
S. alascanus >750	0.26±0.12	43.5±22.0	0.35±0.25	3.69±1.66	52.2±20.3
S. altivelis	0.25±0.15	14.3±20.5	0.36±0.29	4.96±1.38	80.1±19.3
S. diploproa	0.65±0.32	5.85±5.01	0.34±0.19	5.03±0.62	88.1±5.07

Abbreviations for lipid classes are SE-Steryl esters, TAG-triglycerides, FFA-free fatty acids, ST-sterols, and PL- phospholipids.

Table 5
Liver lipid composition as a percentage of total lipid

Species	SE	TAG	FFA	ST	DAG	PL
A. fimbria	3.78±1.37	87.6±3.01	0.16±0.06	0.31±0.14	0.05±0.14	8.10±3.27
A. microlepis	1.17±0.65	94.2±4.88	0.11±0.18	0.20±0.16	0.03±0.06	4.33±4.02
A. pectoralis	0.30±0.17	98.3±0.65	0.08±0.04	0.11±0.03	nd	1.23±0.51
A. tenobrosus	1.19±0.61	53.0±17.6	0.67±0.33	1.24±0.51	nd	43.6±17.3
C. acrolepis	0.30±0.21	94.1±4.33	0.26±0.16	0.26±0.14	nd	5.12±3.96
C. armatus <1000 g	0.60±0.21	97.6±0.64	0.15±0.06	0.21±0.05	nd	1.24±0.40
C. armatus	0.65±0.73	93.0±14.4	0.36±0.97	0.49±1.01	nd	5.25±11.4
C. armatus >2000	0.54±0.15	98.0±0.22	0.10±0.04	0.16±0.02	nd	1.03±0.21
C. cinereus	0.14±0.17	95.7±2.37	0.26±0.23	0.16±0.09	nd	3.72±2.06
C. yaquinae	0.67±1.86	70.6±31.8	1.84±2.52	1.76±2.13	nd	25.1±26.3
E. bathybius	3.49±3.25	61.3±18.0	0.83±0.78	1.02±0.57	nd	33.4±17.1
G. zachirus	5.94±3.27	64.3±15.5	0.44±0.23	0.94±0.43	nd	28.4±12.9
M. pacificus	2.42±1.43	42.5±22.0	0.81±0.43	2.00±0.77	nd	52.3±21.6
M. pacificus >750	4.41±2.77	36.2±17.5	1.11±0.66	1.89±0.74	nd	56.4±15.2
M. productus	0.46±0.31	96.0±1.54	0.07±0.04	0.18±0.07	0.06±0.15	3.19±1.36
P. vetulus	10.3±9.29	11.6±12.1	0.78±0.41	2.97±1.14	nd	74.3±16.8
S. alascanus	3.32±1.56	83.7±6.36	0.24±0.15	0.37±0.16	nd	12.4±5.30
S. alascanus >750	2.73±0.97	90.4±3.99	0.20±0.13	0.22±0.12	nd	6.43±2.97
S. altivelis	7.31±5.80	78.4±9.12	0.25±0.22	0.42±0.24	0.18±0.32	13.4±7.50
S. diploproa	4.83±5.22	82.5±7.77	0.28±0.19	0.53±0.24	nd	11.9±4.98

Abbreviations for lipid classes are SE-steryl esters, TAG-triglycerides, FFA-free fatty acids, ST-sterols, DAG—diglycerides, and PL-phospholipids. nd = not detectable.

were generally lower than those reported in the three literature sources (Fig. 1; Gordon and Roberts, 1977; Stansby, 1976; Sullivan and Somero, 1980). The BCA assay used in this study is known to yield concentrations lower than for the total nitrogen determinations or the Bradford assays (P. Yancey, personal communication) used by those authors. However tempting it is to use this relationship to calculate protein content from water content for the data in the literature, this would simply yield an analysis ultimately based on water content. Thus for analysis of depth related trends only the water content data was considered from the literature.

Proximate composition changed with increasing depth. For analysis of muscle composition the unique, extremely high lipid fish *A. fimbria* was excluded. Muscle water significantly increased with depth (Fig. 2a). The most notable feature is the presence of the four species with gelatinous muscle. *M. pacificus* had gelatinous muscle regardless of size and depth in the size ranges examined. All of these species have an MDO of 200 m or greater. The relationship with depth is still significant if these species are removed from the regression (% water-77.89*MDO$^{0.0082\pm0.0017}$, $r^2 = 0.38$, $p<0.001$). Muscle protein content from the present analysis did not show any significant changes with depth (Fig. 2b). Neither carbohydrate nor lipid had a significant relationship to MDO (Fig. 2c,d). In addition to *A. fimbria*, *Pachycara sp.* had muscle lipid much higher than any of the other species in this study (Table 2). If these two species are excluded, then there is a general decline in muscle lipid with depth but it is statistically insignificant (% lipid = 0.779*MDO$^{-0.064\pm0.038}$, $r^2 = 0.08$, $p = 0.10$). No significant changes in muscle lipid composition were found with depth. Estimates of caloric density were made but no significant trends were found (Fig. 2e).

Liver composition exhibited different trends with MDO than muscle (Fig. 3). Water content did not change significantly with depth (Fig. 3a), but protein content exhibited a significant decline (Fig. 3b). The macrourids have exceptionally large lipid rich livers and represent the majority of the deeper living species, so a regression was performed without any of the gadiformes. This still yielded a significant decline in liver protein content with MDO (% protein = 13.08*MDO$^{-0.077\pm0.033}$, $r^2 = 0.31$, $p<0.05$). Carbohydrate, lipid and caloric density did not change with depth (Figs. 3c–e).

Table 6
Proximate composition of fish white muscle taken from the literature

Species	Family	Habit	gb	% Water	Ref.	MDO (m)	MDO Ref.
Atheresthes stomias	Pleuronectidae	B	N	79.5	2	20	4
Caulolatilus princeps	Malacanthidae	BP	Y	80.8	3	10	4
Chromis puntipennis	Pomocentridae	BP	Y	77.8	3	10	4
Eopsetta jordani	Pleuronectidae	B	N	79.7	1, 2	20	4
Gadus macrocephalus	Gadidae	BP	Y	81.5	1, 2	10	4
Hippoglossoides elassodon	Pleuronectidae	B	N	81.0	2	10	4
Hippoglossus stenolepis	Pleuronectidae	B	N	78.3	2	10	4
Lepidopsetta bilineata	Pleuronectidae	B	N	80.7	2	20	4
Ophiodon elongatus	Hexagrammidae	B	N	80.5	1, 2	10	4
Paralabrax clathratus	Serranidae	BP	Y	77.4	3	10	4
Paralabrax nebulifer	Serranidae	B	Y	75.6	3	10	4
Phanerodon furcatus	Embiotocidae	BP	Y	77.3	3	10	4
Platichthys stellatus	Pleuronectidae	B	N	80.3	2	10	4, 5
Psettichthys melanosticus	Pleuronectidae	B	N	83.4	2	10	4, 5
Rachochilus toxotes	Embiotocidae	BP	Y	78.5	3	10	4
Sebastes alutus	Scorpaenidae	BP	Y	79.2	2	90	4
Sebastes elongatus	Scorpaenidae	BP	Y	78.5	2	60	4
Sebastes entomelas	Scorpaenidae	BP	Y	78.7	2	20	4
Sebastes flavidus	Scorpaenidae	BP	Y	79.3	2	20	6
Sebastes goodei	Scorpaenidae	BP	Y	76.5	2	75	6
Sebastes melanops	Scorpaenidae	BP	Y	79.7	1, 2	10	6
Sebastes paucispinis	Scorpaenidae	BP	Y	80.0	2	20	6
Sebastes pinniger	Scorpaenidae	BP	Y	79.6	1	20	6
Theragra chalcogramma	Gadidae	BP	Y	81.5	2	10	4

Abbreviations and notation as for Table 1. Where more than one study presented data for a species the values were averaged.
1—Gordon and Roberts (1977).
2—Stansby (1976).
3—Sullivan and Somero (1980).
4—Miller and Lea (1972).
5—Vetter et al. (1994).
6—Love et al. (2002).

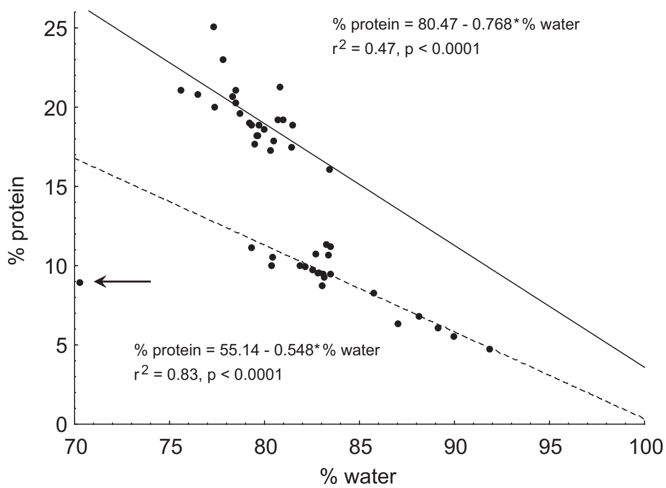

Fig. 1. Protein vs. water content in this study (dashed line) and from literature sources (solid line). Water content for *Anoplopoma fimbria* is indicated by the arrow and is not included in the regressions.

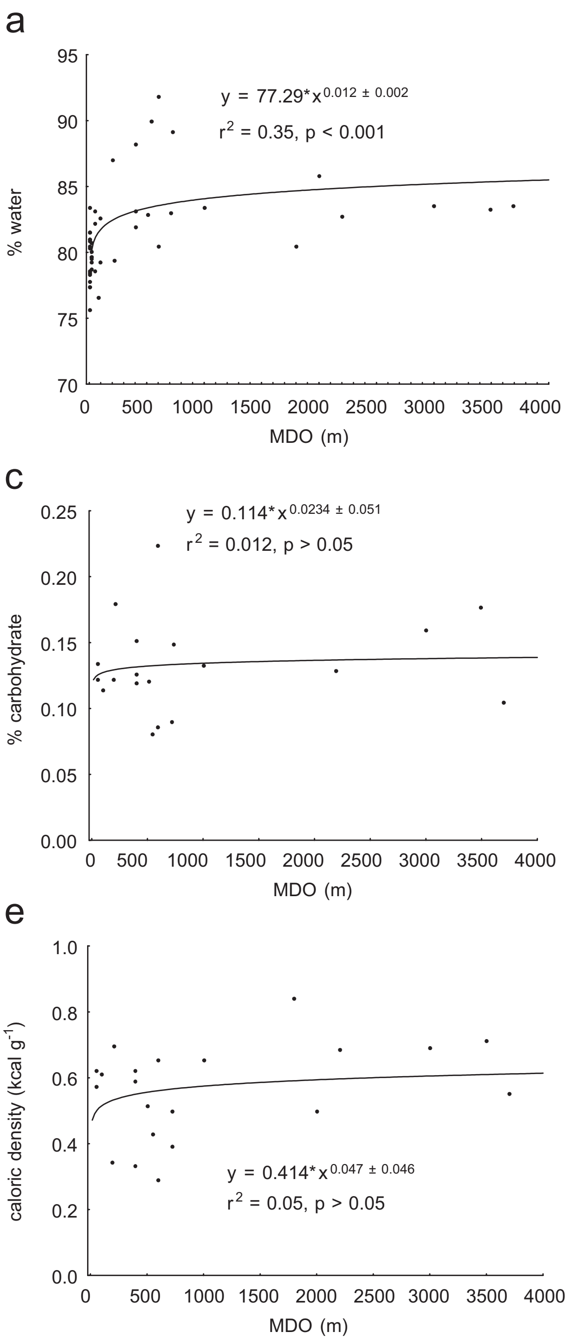

Fig. 2. a–e. Depth-related trends in white muscle proximate composition: (a) water, (b) protein, (c) carbohydrate, (d) lipid and (e) caloric density. Regression equations and correlation coefficients are given. Errors in estimates of b are standard error. Data for *Anoplopoma fimbria* are not plotted or included in the regressions (see text).

At the species level it is important to note the exceptionally strong size—(and hence MDO) related increases in liver size and lipid content and thus decreases in liver water content for *C. armatus* and *S. alascanus* (Table 3).

Changes in total fish lipid as a proportion of fish mass were explored as a proxy for energy storage. A significant increase in total lipid was found with MDO with *C. armatus* having the highest total lipid storage of any species.

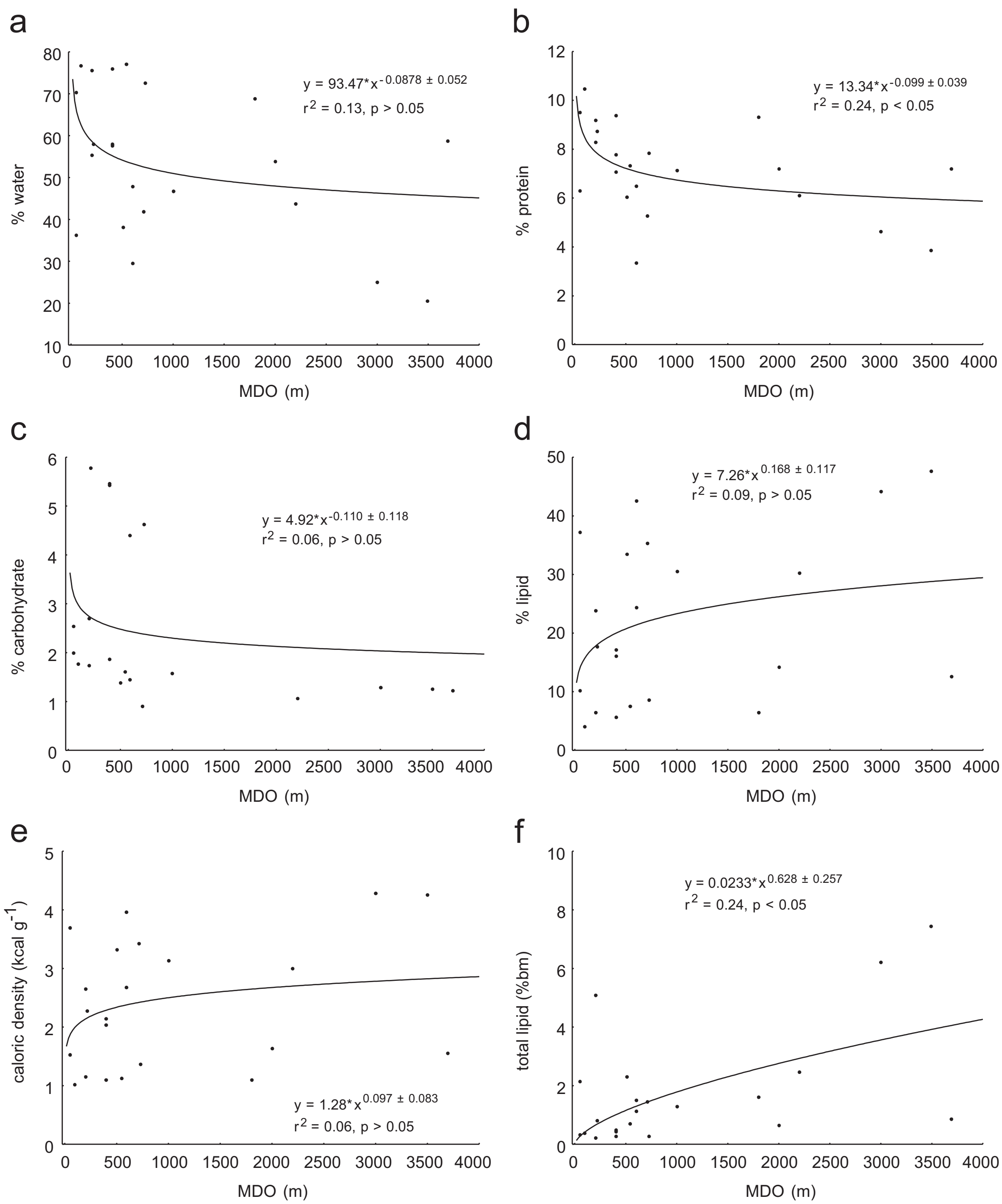

Fig. 3. a–f. Depth-related trends in liver proximate composition. (a) water, (b) protein, (c) carbohydrate, (d) lipid, (e) caloric density and (f) total fish lipid (see text) as a percent of total body mass. Regression equations and correlation coefficients are given.

4. Discussion

4.1. General trends in lipid composition

The lipid composition of muscle and liver tissue consisted primarily of storage lipid (TAG) and membrane bound PL. It was extremely variable among the fishes (Tables 4 and 5) but %TAG was significantly correlated with total lipid in both the liver and muscle. Fishes that had high lipid concentrations also had high %TAG. Variability in lipid composition simply reflected variability in total lipid content. Knowledge of the proportion of TAG did allow positive determination of the nature of the lipid content (storage vs. membrane bound), which was very useful (see below). Future studies could employ a simple total lipid assay, but care should be taken to determine the sensitivity of the analysis to different lipid classes, and appropriate standards must be chosen (Ohman, 1997).

4.2. Trends with locomotory mode, buoyancy mechanism and foraging strategy

Benthopelagic species differed from benthic species in having larger lipid-rich livers. However, much of this difference is attributable to phylogeny. Most of the benthopelagic species are gadiforms, such as cod, which are known for their lean muscle and lipid-rich livers (Stansby, 1976). In this study, only the scorpaenids have benthic and benthopelagic species represented. The benthopelagic species *S. diploproa* had an HSI almost twice that of the benthic scorpaenids (Table 3) and a HSI comparable to that of the largest *S. alascanus*. Why benthopelagic fishes should have large livers is not clear. Large lipid-rich livers may be important for buoyancy. It has been proposed that more active benthopelagic species use the liver instead of the muscle for fat storage because fat in the muscle could restrict motion (Sheridan, 1994). Certainly, relatively active fishes, such as *S. diploproa*, the macrourids, and the morid, have lower %TAG in their muscle indicating that this is not the site of storage (Table 4). However, *A. fimbria*, a very active fish (Sullivan and Smith, 1982), has extremely high levels of TAG in its muscle.

A characteristic which does tie several of the high lipid fishes together is that they are scavengers. Baited cameras regularly record *A. fimbria* (Widder et al., 2005), *C. acrolepis* (Isaacs and Schwartzlose, 1975), *C. armatus* and *C. yaquinae* (these two species can not be distinguished from photographs; Priede et al., 1991), *A. microlepis* and *S. grandis* (Drazen, unpublished observations) feeding on bait in the eastern North Pacific. The zoarcid *Pachycara* sp., from this study, was captured using baited traps and a different *Pachycara* sp. has been documented as a primary scavenger in the Arabian sea (Janssen et al., 2000). Carrion is a regular part of the diet of several of these species (Buckley et al., 1999; Drazen et al., 2001). The capacity for large energy stores would allow for accumulation of energy after sporadic meals and for sustaining the animal between scavenging events (Ruxton and Bailey, 2005). *Coryphaenoides armatus* is a fish which is rapidly attracted to bait on abyssal plains the world over (Collins et al., 1999; Henriques et al., 2002; Isaacs and Schwartzlose, 1975; King et al., 2006; Priede and Bagley, 2000). The liver of *C. armatus* increases dramatically with size which is coincident with a shift towards fish and squid in the diet (Martin and Christiansen, 1997; Pearcy and Ambler, 1974) much of which could be carrion (Drazen et al., 2001). *Coryphaenoides yaquinae* has relatively low lipid content but it feeds primarily on infauna and epifauna in the eastern pacific where it co-occurs with *C. armatus* (Stein, 1985; Drazen, unpublished data). Larger *C. yaquinae* replace *C. armatus* in the central north Pacific (Wilson and Waples, 1983) where it is apparently the only abundant fish scavenger present (Wilson and Smith, 1984). The fact that *Pachycara* sp., the only benthic fish with high and variable lipid content (mostly in the muscle), is probably a scavenger (albeit not nearly as mobile as the others) strongly suggests that foraging mode influences the proximate composition of these animals.

Surprisingly, there were no significant differences in muscle water content between benthic and benthopelagic fishes that might reflect differing locomotory modes. Crabtree (1995) also did not find any significant differences in water content. There was considerable variability in muscle chemistry within benthic and benthopelagic groups (i.e. both groups contained species with gelatinous muscle) and this grouping scheme probably oversimplifies the spectrum of locomotory modes. It is also possible that, although structurally similar, the muscle of these two groups differs metabolically. Measurements of enzyme activities have shown that mobile benthopelagic deep-sea fishes such as *C. acrolepis* have much higher enzyme activities than benthic fishes like *S. altivelis* (Drazen, 2002; Siebenaller et al., 1982; Sullivan and Somero, 1980) even though these fish have nearly identical muscle proximate composition (Table 2).

The presence or absence of a gasbladder was correlated with proximate composition. Most of the fishes that possessed gasbladders had large lipid-rich livers that could also serve a buoyancy function. Only two benthopelagic species lacked gasbladders, *A. fimbria* and *A. tenebrosus*. Both of these species had high amounts of lipids, primarily low density TAGs, in their muscle tissue, which could help to achieve neutral buoyancy. *A. fimbria* also has lipid-filled bones which provide lift (Lee et al., 1975).

Unlike sharks, which use low-density squalene (0.86 g/ml; Phleger, 1998) in their livers to achieve neutral buoyancy, the major lipid class present in the gadiforms is TAG. TAG has a higher density (0.93 g/ml) than squalene, but it is a quickly metabolized lipid and could be used as energy during food shortages or during reproduction, making it a versatile storage compound. TAG is also the lipid present in the muscle tissue of *A. fimbria* and *A. tenebrosus*. Curiously, these fish do not use wax esters to increase buoyancy (see low SE/WE in Table 4). These lipids are ideal for adding buoyancy, because they are less dense than most other lipids including TAG, they are not easily metabolized and they can be stored extracellulary as in the orange roughy, *Hoplostethus atlanticus* (Phleger, 1998). It should be noted that although *A. fimbria* is generally considered a benthopelagic fish, it is often seen resting on the bottom and it is negatively buoyant (Sullivan and Smith, 1982; Wakefield, 1990). Muscle lipids of *A. fimbria* are depleted during starvation in the lab, so they are also used as energy reserves (Sullivan and Somero, 1983). Whether stored in the muscle or the liver, it is possible that TAG is used in cases when accessible energy storage and buoyancy are both required.

Four species of fish were found with 87–92% muscle water, giving their muscle a gelatinous appearance (Fig. 2a; Table 2). This has implications for both buoyancy and locomotion, which are clearly related to one another and have consequences for foraging behaviors. One consequence of watery muscle is that locomotory capacity is sacrificed. This may place constraints on these fishes' feeding behaviors and on their capacities to avoid mobile predators. For instance, Alepocephalids, including *A. tenebrosus* from this study, are gelatinous and primarily consume drifting gelatinous zooplankton (Gartner et al., 1997). The use of low density fluids and relatively high lipid content in place of heavy muscle mass or musculature probably is an adaptation for neutral buoyancy as has been seen in other demersal benthopelagic fishes without gasbladders (Crabtree, 1995). Interestingly, the macrourid *A. pectoralis* also has gelatinous muscle and a weakly ossified skull (Iwamoto and Stein, 1974), but feeds on active prey such as midwater fish and squid (Drazen et al., 2001). Perhaps *A. pectoralis* avoids aerobically active pursuit by ambushing its prey. It has a large liver that is rich in low density lipids and a gasbladder, albeit a relatively small one (Iwamoto and Stein, 1974), and its composition may be more related to buoyancy requirements than to locomotion. Certainly, species of mesopelagic vertical migrators are known to reduce their gasbladders and/or invest them with waxes to reduce volume changes during their rapid depth changes (Bone, 1973). It is conceivable that *A. pectoralis* has evolved a similar strategy in response to a foraging mode that is unique, at least amongst the macrourids examined here.

A gelatinous muscle composition has advantages other than as a buoyancy mechanism in demersal fishes. The other two fishes with gelatinous muscle are the flatfish *M. pacificus* and *E. bathybius* (Table 3). These benthic fish have no need of neutral buoyancy and feed primarily on sediment infauna and small epifauna such as polychaetes, ophiuroids, and small crustaceans (Buckley et al., 1999; Gabriel and Pearcy, 1981). Watery muscle reduces caloric density and should lead to less costly growth by reducing the energy input required to produce a given body size. Larger body size has the advantages of increasing prey size range and decreasing the number of potential predators (Childress and Nygaard, 1973; Crabtree, 1995). Consistent with this hypothesis, *A. pectoralis* is the only macrourid documented to have gelatinous muscle, and it is also the largest macrourid species, attaining lengths of 1.8 m and 8 kg (Iwamoto and Stein, 1974).

4.3. The influence of the oxygen minimum zone (OMZ)

Watery muscle may be an adaptation to low oxygen concentrations in addition to the possible adaptations described above. An OMZ is located between about 600 and 1000 m depth along the continental slope of the eastern Pacific (Levin, 2002; Vetter et al., 1994). Most adult *M. pacificus* and some *E. bathybius* live in this depth range (Hunter et al., 1990; Vetter et al., 1994; Wakefield, 1990), and the distribution of *A. tenobrosus* and *A. pectoralis* also intersect these depths (Lauth, 1997). Hunter et al. (1990) showed that the water content of *M. pacificus* increases with ontogenetic movement from the shelf to OMZ. No similar increase was noted with fish mass in this study, but only larger slope dwelling individuals were examined (Table 2). It was hypothesized that the gelatinous composition of *M. pacificus* is an adaptation for maintaining a low metabolism and low oxygen consumption (Hunter et al., 1990) and the same may be true for *E. bathybius.* However, a large proportion of the latter species' population lives below the OMZ to depths of at least 1400 m (Vetter et al., 1994). Measurement of enzyme activities of both *M. pacificus* and *E. bathybius* indicate very low metabolic activities and the increase in water content in *M. pacificus* accounted for ~50% of the reduction in enzyme activity with size (Vetter et al., 1994). Neither of these flatfishes requires high mobility, so the evolution of watery muscle and low oxygen demand at the expense of low locomotory abilities would be advantageous. The distribution of the two *Sebastolobus* spp. straddles the OMZ (Jacobson and Vetter, 1996). *Sebastolobus alascanus* maintains a relatively constant oxygen consumption rate even at low O_2 concentrations, has a high blood-O_2 affinity, and heart enzymes poised to deal with a hypoxic environment (Yang et al., 1992). Clearly this species is adapted physiologically to its low oxygen environment. However unlike the flatfishes described above its muscle water content is one of the lowest examined here and larger specimens (>750 g) which occupy greater depths, in the heart of the OMZ, actually have a lower muscle water content than smaller specimens (Table 2). In an examination of metabolic enzyme activities of both *Sebastolobus* spp. over their depth ranges, no significant change in aerobic or anaerobic poise was found in relation to the OMZ (Vetter and Lynn, 1997). Rather a significant decline in enzyme activities was found over the depth range of *S. altivelis*.

While the OMZ probably affects the composition of several of the species in this study (i.e. the flatfishes), adaptation does not explain the depth related trends observed. If the gelatinous species are removed from the analysis there is still a significant increase in muscle water content. Furthermore, the increase in water content is not solely the result of the OMZ because species living below it (at higher O_2) still have significantly higher muscle water content than shallow living species (Fig. 2a).

4.4. Depth-related trends

It is clear that the specific ecology of these fishes can affect their proximate composition but by analyzing a large number of species, general trends with depth were also found. Food availability is often seen as a driving factor for depth related changes in composition and metabolic rate (Bailey and Robison, 1986; Collins et al., 1999; Dalhoff, 2004; Poulson, 2001). Previous studies have found a decline in lipid levels with depth and with decreasing regional productivity, indicating that food availability governs lipid content (Bailey and Robison, 1986; Childress et al., 1990). In contrast, I did not find declines in lipids or caloric density in muscle or liver tissues (Figs. 2 and 3). If lipids are indicative of food availability and energy storage, then overall lipid storage should decline with depth. Whole animals were not analyzed for this study because of their large size, but an estimate of whole body or total lipid content as a proportion of body mass was made. Surprisingly total lipid increased significantly with depth (Fig. 3f), although this was certainly driven by the abyssal scavenger *C. armatus,* which has extraordinarily large lipid rich livers for a teleost (HSI = 15.8%). It is possible that the lipids in shallower living fishes were underestimated because of lipid storage in tissues other than their muscle and liver. Fishes are known to store lipids in bone (Lee et al., 1975) and some scorpaenids can store lipids in mesenteric fat (MacFarlane et al., 1993). These alternate lipid stores would have to equal or surpass those already measured to bring whole-body storage up to the level of the macrourids, which does not seem probable. Additional data on shallow living species and abyssal non-scavengers is needed to assess the trend of increasing lipid content with depth.

The density of many prey organisms on the continental slope declines sharply with depth (Haedrich and Rowe, 1977; Haedrich et al., 1980; Lampitt et al., 1986; Rowe, 1983) and so do the population densities of demersal fishes (Haedrich and Rowe, 1977; Merrett and Haedrich, 1997). It is reasonable that long term food availability impacts population dynamics more strongly than it does physiological energetics. Thus perhaps it is not surprising that lipid levels are unrelated to depth within a single region. In benthic and benthopelagic fishes, lipid content inferred from CHN analyses is lower in oligotrophic regions compared to more eutrophic regions in the Atlantic (Crabtree, 1995); however, this may be attributable to the pulsed seasonal nature of organic inputs to eutrophic regions (Bailey and Robison, 1986; Childress et al., 1990; Donnelly et al., 1990; Stickney and Torres, 1989).

It has been hypothesized that the major factor affecting the protein and water content of midwater fishes is not food availability but locomotory requirements (Childress et al., 1990). Many studies show that protein concentrations decline and water content increases with increasing depth (Bailey and Robison, 1986; Childress and Nygaard, 1973; Childress et al., 1990; Stickney and Torres, 1989). These variables probably reflect the strength of the muscular architecture. With increasing depth, light levels decline, and the "reactive distances" of organisms are reduced. This results in a relaxation in the selective pressure for strong swimming capacity and developed musculature (Childress, 1995). Furthermore, protein concentrations are higher for midwater fishes in more oligotrophic regions, probably because light penetrates to much greater depths in the clear water (Childress et al., 1990). This hypothesis explains why fishes with gelatinous muscle are found primarily in the deep sea, where light levels are low to nil and reactive distances are small enough to allow them to capture prey and avoid predators despite poor locomotory capacity.

Deep-sea benthic and pelagic habitats are fundamentally different. In the open pelagic environment animals may hide by being transparent, but this is limited to small zooplankton and gelatinous animals because of the refraction and absorption of light through large robust bodies of the nekton (Hamner, 1995; Johnsen, 2001). As a result, when large pelagic animals encounter predator or prey they must swim. In the benthic realm the substrate affords many hiding places and the opportunity for camouflage, even for large organisms. In addition the presence of a substrate changes buoyancy requirements, possibly allowing normally sedentary fishes to retain large muscle masses for burst performance. Nevertheless, the trends in muscle composition with depth from this study support the hypothesis of Childress (1995), based primarily on data for pelagic animals. Muscle water content exhibited a significant decline with depth. Water content is rather steady below about 1000 m, a depth below which sunlight can no longer be detected by these organisms (Warrant and Locket, 2004). Protein content did not exhibit a significant decline with increasing depth, but there were not enough comparable data for shallow-water species. Protein content is strongly correlated with water content (Fig. 1), thus, I suspect that muscle protein content declines with increasing depth just as it does in pelagic fishes. Only one other study on the proximate chemistry of demersal fishes has been performed (Crabtree, 1995). This study reports similar increases in water content with depth in demersal fish from the North Atlantic.

An increase in water content could be the result of decreases in food availability or reduction in the need for locomotory capacity. If food availability were the only factor then overall lipid storage would probably decline before the fishes sacrificed locomotory capacity by increasing muscle water. However, overall lipid stores do not decline with depth and perhaps increase, so it is concluded that the increase in water content results from the relaxation of selective pressure for strong locomotory capacity. It could be argued that there are physiological limits to the depth related trends (Poulson, 2001) such that increases in water content reach a maximum (~85%) at 1000 m. However, the four gelatinous species in this study did have significantly higher water contents than the abyssal animals. If food availability were the important driver and food availability continues to decline downslope then the abyssal animals should have the highest muscle water content. It seems more likely that locomotory requirements dictate muscle composition. This conclusion is strengthened by the fact that the increasing water content is in the muscle and hence locomotion specific.

Interestingly, liver protein content declined with increased depth (Fig. 3b). The gadiforms include the macrourids, which make up the bulk of the species with the deepest MDOs. They also have the highest liver lipid content and low liver protein contents. However, the trend is apparent even if the gadiforms are removed from the regression analysis. Proteins in the liver could be either structural or metabolic. Most of the proteins are probably metabolic because the liver is not muscular, it does not provide any physical support for the fish, and its primary functions are metabolic: creation of bile, glycogen and lipid metabolism, and in some fish lipid storage (Bond, 1996; Love, 1970). Declines in metabolic rate with depth are well documented in deep-sea organisms (Seibel and Drazen, in press), and a significant reduction in liver protein content with depth suggests that liver metabolism declines. Declines in whole-animal metabolic rate and enzymatic activities of red and white muscle are well known, but these are the first data that suggest the possibility of liver-specific declines in metabolic activity. Further data from other regions are needed to assess the generality of this finding and its relationship to competing hypotheses of depth related changes in animal energetics.

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