

Proximate composition and energy content of mesopelagic fishes from the eastern Gulf of Mexico

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Abstract

The proximate composition of 33 species of mesopelagic fishes collected from the eastern Gulf of Mexico during May–June 1984, July–November 1985 and January 1986 was determined. Water level increased and ash-free dry weight (% dry weight) and protein level (% wet weight) decreased with increasing species' minimum depth of occurrence (that depth below which 90% of a species' population lives). Lipid level (% wet weight or % ash-free dry weight), did not change with species' minimum depth of occurrence. Skeletal ash level (% wet weight) generally decreased with minimum depth of occurrence, whereas carbohydrate level did not change with depth. The variable water level, low lipid level, and high protein level in eastern Gulf of Mexico fishes resulted in a low energy content. These results are generally characteristic of fishes from warm, stable regions of low productivity, such as the eastern North Pacific Gyre. The constant food supply provided by a stable environment may obviate the need for large lipid reserves, in contrast to colder waters at higher latitudes where food availability is seasonal. In addition, the large energy requirements for diel excursions into high-temperature surface waters by the many vertically migrating fishes of this region may influence lipid deposition. The relatively high protein level found in migrators compared to that in non-migrators or weak migrators indicates that locomotory demands influence the percentage of protein found in Gulf fishes. The lack of a positive correlation between protein level and the food availability of a zoogeographic region, suggested in previous studies, is supported here.

Introduction

The major components of mesopelagic fishes are water, lipid, protein, ash and carbohydrate (Childress 1977). Water level tends to increase with increasing species' depth of occurrence, while lipid, protein, skeletal ash and caloric level,

decrease (Childress and Nygaard 1973, Bailey and Robison 1986). Carbohydrate levels are generally low in midwater fishes and do not show trends with depth of occurrence (Childress and Nygaard 1973).

In deeper living species, dilute fluids are substituted for organic matter (Childress and Nygaard 1973), allowing individuals to approach neutral buoyancy and thereby conserve metabolic energy. In addition, the high water levels of deeper living species allow for rapid growth with minimum caloric input, due to the low weight-specific caloric content of a watery body (Childress et al. 1980). Thus, the ecological advantages of larger size, larger prey spectrum, and fewer predators are obtained with a minimum energy investment. This strategy is clearly adaptive in the energy-poor deep sea.

The two primary organic components of mesopelagic fishes are lipid and protein. Lipids serve as an energy store and correlate positively with food availability, independent of depth-related factors (Bailey and Robison 1986). The decline in protein level with species' depth of occurrence is consistent with the reduction of muscle mass (Blaxter et al. 1971), metabolic rate (Torres et al. 1979) and tissue density observed in deeper living species (Childress and Nygaard 1973, Childress et al. 1980).

Species proximate composition also varies between regions. In midwater fish inhabiting the highly productive, cold waters of the California Current, water level increases while all other components decrease with depth (Childress and Nygaard 1973). Higher water and protein level were found in mesopelagic fishes from the warmer, low productivity waters of the eastern North Pacific Gyre than in species from the California Current or the transition region between them (Bailey and Robison 1986). In the Southern Ocean, total lipid levels for many organisms are similar to those of temperate species (Reinhardt and Van Vleet 1986). In general, regions of high productivity, such as the California Current, have mesopelagic species with high lipid and energy levels, whereas regions of low productivity are distinguished by species with low lipid and high protein levels (Childress and Nygaard 1973, Bailey and Robison 1986).

The eastern Gulf of Mexico is a stable, warm-water region of low productivity, with many vertically migrating mesopelagic fishes. Proximate composition of Gulf species would be expected to reflect the environmental influences of high temperature, with its associated high energy expenditure, and a low food supply that varies little throughout the year. This study examines the proximate composition of mesopelagic fishes from the eastern Gulf of Mexico.

Materials and methods

Collection of specimens

Specimens were collected in the eastern central Gulf of Mexico within a 10 nautical-mile radius of 27°N; 86°W during May–June 1984, July 1985, November 1985, and January 1986. Individuals were taken in the upper 1 000 m of the water column using a mouth-closing Tucker trawl with either a 3.2 m² or 6.5 m² mouth area. The body of the trawl was constructed of 1.1 cm stretch mesh with a 1.1 cm stretch mesh conical fish-catcher fitted anterior to the 505 µm mesh codend (Hopkins et al. 1973, Hopkins and Baird 1975). Towing speed was approximately 2 knots.

Following net retrieval, fishes selected for analysis were identified to species, measured to the nearest millimeter standard length (mm SL), blotted to remove excess moisture, and individually placed in polypropylene vials. Samples were kept frozen at –20°C until analyzed.

Proximate analyses

Individual specimens were allowed to partially thaw, remeasured to the nearest 0.1 mm SL, transferred to preweighed glass serum vials of appropriate sizes, and weighed to the nearest 0.01 g on a Mettler analytical balance. Any water inside the vials was considered to be part of the wet weight (WW) since all specimens were blotted before freezing. After wet weights had been obtained, specimens were refrozen until hard, and then lyophilized for a minimum of 8 h or until a constant weight was obtained. Specimens were then reweighed for dry weight (DW) in the same vial, and water content was calculated from the difference between WW and DW determinations. Lyophilized specimens were stored in a vacuum desiccator over silica gel. They were reweighed for exact DW in preparation for slurry volume determination.

Each fish was homogenized in a Brinkmann Polytron homogenizer using enough deionized water to make a 25 mg ml⁻¹ slurry. The slurry was transferred to a glass tissue-grinder for final homogenization. Individual samples were taken from the slurry for the various analyses. Proximate composition is expressed as percent of WW and percent ash-free dry weight (% AFDW).

Ash-free dry weight, total ash and skeletal ash

Two 0.4 ml samples (10 mg DW) were placed into individual, preweighed aluminum pans, and dried for 24 h at 60°C

to a constant weight. Dried samples were weighed, then combusted to ash in a low-temperature asher (International Plasma Corporation, Series 1 000). Samples were reweighed to determine the ash weight, which was subtracted from the dry weight to yield the ash-free dry weight. A low temperature asher combusts a sample at low temperature (110° to 150°C) in an atmosphere of pure oxygen; this insures complete combustion and minimizes volatilization of inorganics. The technique minimizes error in determining ash weights (Childress and Price 1983).

Skeletal ash was estimated by assuming the solute concentration of the body fluids to be 40% that of seawater and subtracting the estimated solute ash from total ash to obtain the skeletal ash (Childress and Nygaard 1973). An internal solute concentration of 40% seawater is a mid-range value typical of marine teleosts, e.g. Holmes and Donaldson (1969) reported a value of 435 ± 41 mM l⁻¹ ($\bar{x} \pm SD$) for six species of marine teleost, and a solute concentration of 1 070 mM l⁻¹ for seawater (41%). The technique assumes that all water evaporated-off to determine individual dry weights was part of the internal fluids of the individual, leaving behind the solute as ash. In addition, since the total ash is comprised of the inorganic components present in intracellular fluids, extracellular fluids, and the skeleton, it assumes that the intracellular and extracellular fluids are isosmotic (Prosser 1973). Differences in the concentration of inorganic solutes between intra- and extracellular fluids caused by organic compounds are assumed to be negligible.

Lipid

Lipids were extracted from two samples (0.2 ml, 5.0 mg DW each) of homogenate using 2:1 methanol-chloroform according to the method of Bligh and Dyer (1959). Extracts were evaporated under a flow of nitrogen at 30°C and analyzed for lipid using the charring method of Marsh and Weinstein (1966) with stearic acid (Kodak) as the standard.

Protein

One sample of homogenate per species (0.1 ml; 2.5 mg DW) was diluted 1:10 into deionized water, mixed, and 0.1 ml placed into each of three test tubes for protein analysis. Samples were increased to 0.2 ml volume using deionized water, with the standard (Sigma; human albumin and globulin) treated in an identical manner. Samples and standards were hydrolyzed by adding 0.3 ml of 0.1 N NaOH to each tube and then heating at 100°C for 10 min. The method of Lowry et al. (1951) was used for protein determination.

Carbohydrate

Two samples of 0.4 ml each (10 mg DW) were placed into preweighed 5 ml centrifuge tubes and dried in an oven at 60°C to constant weight. The samples were then washed

with acetone and ethyl ether to remove lipids and dried in a 60°C oven. Trichloroacetic acid (10%) was added and samples were heated at 100°C for 20 min to allow hydrolysis. The supernatant was removed and analyzed for carbohydrate using the method of Dubois et al. (1956), with D-glucose (Sigma) as the standard.

Energy content

Absolute caloric values were calculated using the conversion factors of Brett and Groves (1979): 8.7 kcal g⁻¹ lipid; 5.7 kcal g⁻¹ protein; 4.1 kcal g⁻¹ carbohydrate. These values were used to calculate the energetic density by assuming that 1 cal equals 4.19 J.

Vertical distributions

Assignment of migration categories correlated specific patterns of migration with minimum depth of occurrence (MDO), "that depth below which 90% of the population lives" (Childress and Nygaard 1973). Fishes were grouped into three categories based on vertical migration patterns: (1) migrators, those species whose peak abundances shifted by ≥200 m during a diel cycle; (2) weak migrators, species whose peak abundances shifted by <100 m during a diel cycle; (3) non-migrators. Twenty-four species were migrators, two were weak migrators, and six were non-migrators (migration/non-migration could not be determined for *Maurolicus muelleri*).

Depth ranges for the fishes were obtained from Hopkins and Baird (1985b) for Sternoptychidae, Gartner et al. (1987) for Myctophidae, Keene et al. (1987) for *Poromitra* sp. and *Scopeloberyx* sp., and from unpublished data from the University of South Florida Midwater Ecology Group for Anoplogasteridae, Bathylagidae and Gonostomatidae. Vertical migration patterns and depth distributions reported were for species size ranges given, with the exception of some non-migratory individuals included in the size ranges of the family Myctophidae. In this study, MDO refers to the shallowest depth at which any post-metamorphic member of a species has been found.

Swimbladders

The presence or absence of a functional swimbladder was determined using several sources including: Brooks (1977) for *Anoplogaster cornuta*, Sternoptychid Symbols 3, 4, 6, and Myctophid Symbols I, J, O, R, T, U, V, W, X, Y, Z (Table 1); J. V. Gartner, Jr. (personal communication) for *Bathylagus longirostris*; T. M. Lancraft (personal communication) for *Cyclothone pallida*; Denton and Marshall (1958) for *Gonostoma elongatum*; Marshall (1960) for *Maurolicus muelleri*; and Hopkins and Baird (1985b) for *Sternoptyx pseudobscura*. Information on swimbladder presence or absence was not available for other species.

Statistics

Regressions and the Mann-Whitney-Wilcoxon test were performed on the 21 species of fishes which had $n \geq 2$, and whose depth distributions were well established. The statistical tables of Rohlf and Sokal (1969) provided critical values for the correlation coefficients and the Student's *t*-distribution. Values for regressions are significant at $P < 0.05$ (unless noted otherwise), with slopes and all mean values $\pm 95\%$ confidence limits.

Results

Water level

The water level of fishes ranged from 64.5 to 88.3% WW (Table 1). Six of the thirty-three species had water levels >85.0% wet weight. Three of these were weak migrators or non-migrators. Weak migrators and non-migrators had a mean water level of 82.8% WW (± 5.9 ; $n=5$) while migrators had a mean water level of 77.6% WW (± 3.1 ; $n=16$). Water level in the two groups was not significantly different, although non-migrators had higher levels (Mann-Whitney-Wilcoxon-test: $z=1.73$, $0.05 < P < 0.09$). Water level (% WW) increased as a function of MDO (Fig. 1).

Ash-free dry weight, total ash weight, and skeletal ash

Ash-free dry weight (AFDW) ranged from 65.3 to 90.2% DW (Table 1), decreasing with increasing MDO (Fig. 2). Skeletal ash varied from 1.1 to 8.1% of the WW (Table 1). A non-significant decrease in skeletal ash (% WW) with

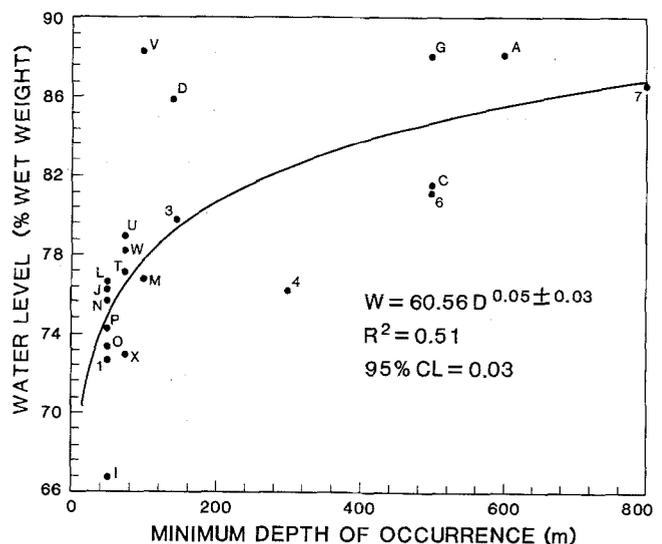


Fig. 1. Regression of water level (% wet weight) on minimum depth of occurrence in 21 species of mesopelagic fishes from the Gulf of Mexico (specific code designations as in Table 1). Equation for regression is $W = 60.56 D^{0.05 \pm 0.03}$, where W = water level and D = depth (significant at $P < 0.01$)

Table 1. Families, genus and species, code designations, migration, depth ranges (0=surface; ND=no data), minimum depth of occurrence (MDO), standard length (SL), wet weight (WW), water, ash-free dry weight (AFDW), and skeletal ash (SA) of 33 species of mesopelagic fishes from the Gulf of Mexico. Values in parentheses below water, AFDW, and SA values are (standard error of mean; number of individuals analyzed). Migration: M, migrator, WM, weak migrator; NM, non migrator; brackets [] indicate uncertain migration patterns. DW: dry weight

Family, genus, species	Code	Migra- tion	Day/night range (m)	MDO (m)	Mean (range) SL (mm)	Mean (range) WW (g)	Water (%WW)	AFDW (%DW)	SA (%WW)
Anoplogasteridae									
<i>Anoplogaster cornuta</i>	A	[NM]	600–950 ^a /ND	600	86.5 (72.0–101.0)	32.8 (20.7–45.0)	88.1 (1.9; 2)	77.1 (3.9; 2)	1.1 (0.3; 2)
Bathylagidae									
<i>Bathylagus longirostris</i>	B	[WM]	ND/180–200 ^a	200	90.8 (42.0–117.0)	6.8 (0.5–11.3)	86.7 (0.1; 6)	76.5 (1.8; 6)	1.9 (0.3; 6)
Gonostomatidae									
<i>Cyclothone pallida</i>	C	[NM]	430–690 ^a /430–690	500	42.2 (36.5–49.0)	0.5 (0.4–0.7)	81.6 (1.5; 4)	67.6 (4.4; 4)	4.7 (1.2; 4)
<i>Gonostoma elongatum</i> ^b	D	M	425–725/25–325	140	107.9 (85.0–121.0)	4.1 (0.9–12.7)	85.9 (1.0; 14)	67.9 (0.9; 13)	3.0 (0.2; 13)
Melamphaidae									
<i>Melamphaes longivelis</i>	E	[M]	800 ^a /130 ^a	150	20.0	0.2	78.7	65.6	5.9
<i>Poromitra</i> sp.	F	[M]	800–1 100 ^e /150–550 ^c	150	15.0	0.1	84.6	70.6	2.8
<i>Scopelegadus mizolepis mizolepis</i>	G	[M]	800–1 000/400–600	500	47.6 (31.0–64.0)	3.6 (0.5–6.9)	88.0 (1.9; 6)	67.7 (2.2; 6)	3.0 (0.1; 6)
<i>Scopeloberyx</i> sp.	H	[NM]	700–1 000 ^a /700–1 000	700	22.0	0.2	77.3	90.2	1.1
Myctophidae									
<i>Benthosema suborbitale</i>	I	M	400–600/50–105	50	20.6 (18.7–22.5)	0.4 (0.3–0.5)	66.7 (3.7; 2)	80.4 (3.0; 2)	5.4 (1.6; 2)
<i>Bolinichthys photothorax</i>	J	M	550–700/50–250	50	36.8 (21.0–49.0)	1.0 (0.4–1.8)	76.2 (1.4; 4)	75.9 (1.9; 4)	4.0 (0.5; 4)
<i>Centrobranchus nigroocellatus</i>	K	M	400–550/0–150	O	24.0	0.2	73.7	69.5	5.5
<i>Diaphus dumerilii</i>	L	M	300–600/50–155	50	36.1 (23.5–48.0)	0.9 (0.3–1.7)	76.7 (1.3; 6)	76.7 (1.4; 6)	4.9 (0.4; 6)
<i>D. effulgens</i>	M	M	300–500/100–330	≥100	39.6 (24.0–57.0)	1.7 (0.2–3.9)	76.8 (0.7; 5)	75.2 (4.1; 5)	3.4 (0.9; 5)
<i>D. lucidus</i>	N	M	450–1 000/50–300	50	50.5 (45.0–55.0)	2.1 (1.5–2.7)	75.6 (1.6; 6)	81.4 (1.9; 6)	3.7 (0.6; 6)
<i>D. mollis</i>	O	M	300–1 000/50–225	50	31.4 (18.0–39.0)	0.6 (0.3–0.9)	73.3 (1.6; 5)	76.0 (4.5; 4)	5.7 (1.5; 5)
<i>D. splendidus</i>	P	M	300–600/50–250	50	42.5 (28.0–57.0)	1.3 (0.2–2.4)	74.2 (1.2; 2)	72.7 (8.3; 2)	6.5 (2.8; 2)
<i>Gonichthys cocco</i>	Q	M	ND/0	O	34.7 (23.0–43.0)	0.4 (0.1–0.6)	70.0 (0.1; 3)	69.8 (3.3; 2)	8.1 (1.6; 2)
<i>Hygophum benoiti</i>	R	M	300–700/0–250	O	18.0	0.1	64.5	75.5	6.0
<i>H. reinhardtii</i>	S	M	550–700/0–250	O	31.0	0.3	70.7	86.2	2.9
<i>Lampadena luminosa</i>	T	M	500–>1 000/65–350	75	43.6 (22.3–67.0)	1.8 (0.3–4.2)	77.1 (1.0; 4)	70.9 (2.1; 4)	5.7 (0.9; 4)
<i>Lampanyctus alatus</i>	U	M	550–700/80–200	75	36.0 (21.7–46.0)	0.6 (0.3–1.1)	78.9 (0.6; 8)	77.3 (1.0; 7)	4.2 (0.4; 7)
<i>L. lineatus</i>	V	M	400–1 000/80–1 000	>100	58.5 (48.0–70.0)	1.5 (0.7–1.6)	88.3 (0.9; 4)	65.3 (2.7; 4)	2.4 (0.6; 4)
<i>Lepidophanes guentheri</i>	W	M	400–900/75–155	75	38.4 (28.0–51.0)	0.8 (0.3–2.4)	78.2 (1.1; 10)	72.6 (2.1; 11)	5.0 (0.6; 11)
<i>Lobianchia gemellarii</i>	X	M	300–450/75–210	75	20.5 (19.5–21.5)	0.5 (0.4–0.6)	72.9 (3.4; 3)	68.8 (0.6; 3)	7.4 (1.0; 3)
<i>Myctophum nitidulum</i>	Y	M	ND/0–50	O	53.0 (35.0–65.0)	2.7 (0.6–4.6)	74.9 (1.4; 3)	79.4 (2.9; 3)	4.1 (1.0; 3)
<i>Notoscopelus resplendens</i>	Z	M	ND/50–250	50	49.1 (40.0–56.0)	2.0 (0.1–2.3)	73.5 (0.5; 7)	79.5 (2.2; 7)	4.6 (0.5; 7)
<i>Notolychnus valdiviae</i> ^b	1	M	400–500/50–155	50	18.0 (17.5–18.5)	0.1 (0.1)	72.7 (2.7; 2)	88.0 (2.6; 2)	2.6 (1.0; 2)
<i>Taaningichthys bathyphilus</i>	2	NM	600–>1 000/900	600	54.0	1.5	79.1	88.5	2.0
Sternoptychidae									
<i>Argyropelecus aculeatus</i>	3	M	160–500/145–300	145	33.1 (13.0–55.0)	1.9 (0.2–4.8)	79.8 (0.5; 21)	70.2 (1.0; 19)	4.9 (0.3; 19)
<i>A. hemigymnus</i>	4	WM	350–600/300–500	300	26.1 (17.5–25.0)	0.7 (0.3–1.2)	76.2 (1.0; 4)	68.9 (1.6; 4)	6.2 (0.5; 3)

Table 1 (continued)

Family, genus, species	Code	Migra- tion	Day/night range (m)	MDO (m)	Mean (range) SL (mm)	Mean (range) WW (g)	Water (%WW)	AFDW (%DW)	SA (%WW)
<i>Maurolicus muelleri</i>	5		ND	ND	30.5 (29.0–32.0)	0.3 (0.3–0.4)	71.2 (1.0; 2)	68.8 (2.4; 2)	8.0 (1.0; 2)
<i>Sternoptyx diaphana</i>	6	NM	500–800/500–900	500	25.3 (16.0–37.0)	1.7 (0.4–3.6)	81.2 (0.5; 8)	70.9 (3.5; 7)	5.2 (0.3; 8)
<i>S. pseudobscura</i>	7	NM	800–1 000/800–1 000	800	33.4 (27.0–39.0)	3.5 (1.6–5.5)	86.7 (1.6; 5)	72.6 (3.3; 5)	2.7 (0.8; 4)

^a Depth distributions uncertain

^b Data suggests all members are migratory

^c Data from Keene et al. (1987)

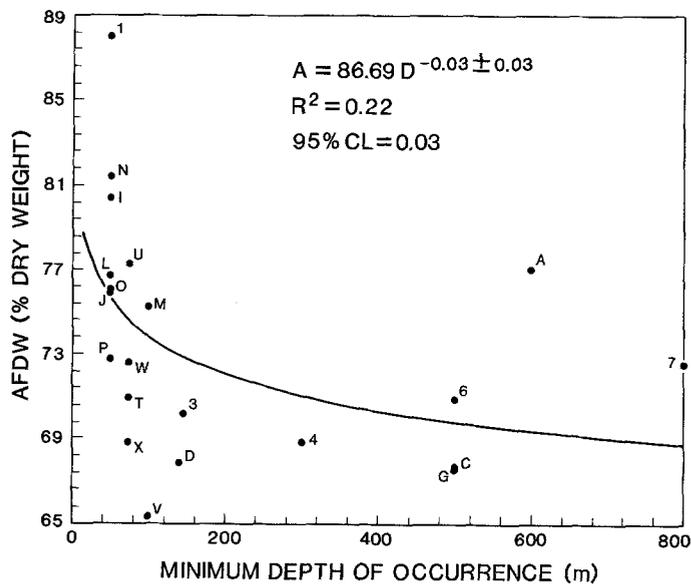


Fig. 2. Regression of ash-free dry weight (% dry weight) on minimum depth of occurrence in 21 species of mesopelagic fishes from the Gulf of Mexico (specific code designations as in Table 1). Equation for regression is $A = 86.69 D^{-0.03 \pm 0.03}$, where A = ash-free dry weight and D = depth (significant at $P < 0.05$).

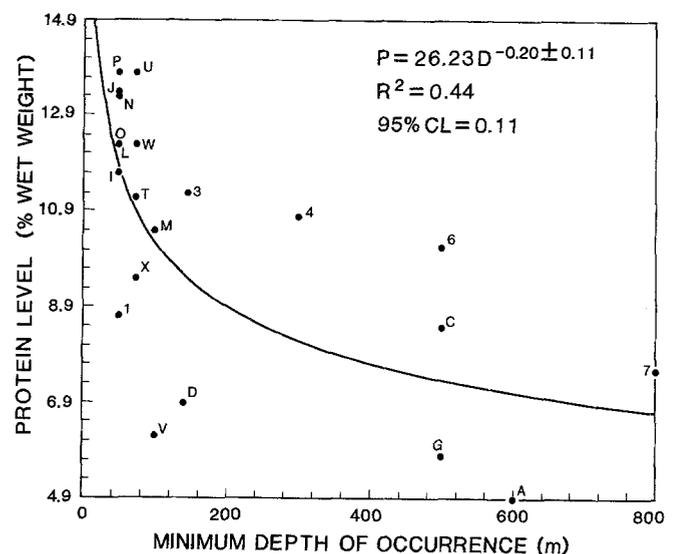


Fig. 3. Regression of protein level (% wet weight) on minimum depth of occurrence in 21 species of mesopelagic fishes from the Gulf of Mexico (specific code designations as in Table 1). Equation for regression is $P = 26.23 D^{-0.20 \pm 0.11}$, where P = protein and D = depth (significant at $P < 0.01$).

increasing MDO was found (equation for the regression is $S = 9.44 D^{-0.18 \pm 0.19}$, where S = skeletal ash and D = depth; $P > 0.05$). Those species known to have functional swimbladders (Table 1: Code designations I–J, O, R, T–Z, and 1–8) showed a mean skeletal ash level of $4.8 \pm 0.4\%$ WW ($n = 18$). Those without swimbladders (Table 1: Codes A–D) had a skeletal ash value of $2.7 \pm 2.5\%$ WW ($n = 4$). Differences between the two groups were not significant.

Lipid

Lipid level varied from 4.3 to 43.3% AFDW and from 0.6 to 10.7% WW (Table 2). An exception to the low lipid level in most species was *Notolychnus valdiviae* which had a high lipid level (43.3% AFDW ± 6.7 and 10.7% WW ± 1.3 ; $n = 2$). Lipid level (expressed as % AFDW or as % WW) was not correlated with MDO. The lipid level of migrators was not

significantly different from that of weak migrators and non-migrators, whether expressed as % AFDW or % WW. Fishes with swimbladders had a mean lipid level of 10.0% AFDW (± 4.2 ; $n = 18$), while fishes without swimbladders had a mean lipid level of 10.7% AFDW (± 4.6 ; $n = 4$). Lipid level (% AFDW) in two groups was not significantly different, although probability levels were sufficiently low to suggest a trend towards lower lipid levels in fishes with swimbladders (Mann-Whitney-Wilcoxon-test: $z = 1.92$, $0.05 < P < 0.06$).

Protein

Protein level varied from 4.9 to 14.9% WW (Table 2), decreasing with increasing MDO (Fig. 3). Vertical migrators had a mean protein level of 11.0% WW (± 1.1 ; $n = 23$) while weak migrators and non-migrators had a mean protein level

Table 2. Family, genus and species, lipid level, protein level carbohydrate (Carb.) content and energy level (kJ 100 g⁻¹ WW) of 32 species of mesopelagic fishes from the Gulf of Mexico (no data for *Poromitra* sp. due to insufficient sample for determination of chemical composition). Values in parentheses are (standard error of mean; number of individuals analyzed). Corrected energy level assumes that difference between percent recovered organic matter and 100% is due to refractory protein, and is calculated accordingly. Lipid, protein, and carbohydrate data are presented as % AFDW (first line) and [%WW] (second line)

Family, genus, species	Code	Lipid (%AFDW) [(%WW)]	Protein (%AFDW) [(%WW)]	Carb (%AFDW) [(%WW)]	Energy level		
					kJ 100 g ⁻¹ WW	kcal 100 g ⁻¹ WW	kJ 100 g ⁻¹ WW corrected
Anoplogasteridae							
<i>Anoplogaster cornuta</i>	A	15.0 (7.0; 2) [1.5 (0.9; 2)]	52.3 (0.3; 2) [4.9 (1.0; 2)]	0.9 (0.5; 2) [0.1 (0.0; 2)]	173.3	41.4	243.1
Bathylagidae							
<i>Bathylagus longirostris</i>	B	9.1 (2.0; 6) [0.9 (0.2; 6)]	64.6 (1.5; 6) [6.4 (0.4; 6)]	1.0 (0.1; 6) [0.1 (0.0; 6)]	187.1	44.7	248.8
Gonostomatidae							
<i>Cyclothone pallida</i>	C	8.9 (1.4; 3) [1.0 (0.2; 3)]	75.3 (11.4; 3) [8.5 (1.2; 3)]	0.8 (0.2; 3) [0.1 (0.0; 3)]	241.1	57.6	285.9
<i>Gonostoma elongatum</i>	D	9.9 (1.6; 10) [1.6 (0.8; 10)]	70.0 (2.3; 13) [6.9 (0.7; 13)]	1.0 (0.0; 12) [0.1 (0.1; 12)]	224.7	53.7	268.7
Melamphaidae							
<i>Melamphaes longivelis</i>	E	10.4 [1.4]	71.3 [9.5]	0.7 [0.1]	279.1	66.7	338.2
<i>Scopelegadus mizolepis</i>	G	8.5 (0.4; 6) [1.4 (0.3; 6)]	71.1 (3.8; 6) [5.8 (0.9; 6)]	1.0 (0.2; 6) [0.1 (0.0; 6)]	191.3	45.7	229.1
<i>Scopeloberyx</i> sp.	H	11.8 [2.5]	72.3 [14.8]	0.3 [0.1]	445.7	106.5	522.5
Myctophidae							
<i>Benthosema suborbitale</i>	I	6.0 (1.3; 2) [1.6 (0.1; 2)]	46.1 (4.2; 2) [11.7 (0.3; 2)]	0.6 (0.2; 2) [0.2 (0.1; 2)]	340.7	81.4	643.5
<i>Bolinichthys photothorax</i>	J	7.0 (0.2; 4) [1.0 (0.5; 4)]	73.2 (3.1; 4) [13.4 (0.4; 3)]	1.0 (0.3; 4) [0.2 (0.1; 4)]	359.5	85.9	441.0
<i>Centrobranchus nigroocellatus</i>	K	4.3 [0.8]	43.1 [7.9]	1.0 [0.2]	221.0	52.8	446.5
<i>Diaphus dumerilii</i>	L	8.4 (0.6; 6) [1.6 (0.1; 6)]	64.9 (2.9; 6) [12.3 (0.3; 5)]	1.1 (0.2; 6) [0.2 (0.0; 6)]	355.3	84.9	465.0
<i>D. effulgens</i>	M	9.7 (1.2; 4) [1.6 (0.1; 4)]	60.3 (5.6; 5) [10.5 (1.1; 5)]	0.8 (0.1; 5) [0.1 (0.0; 5)]	310.5	74.2	432.6
<i>D. lucidus</i>	N	11.9 (1.3; 6) [2.4 (0.3; 6)]	66.3 (5.6; 6) [13.3 (0.8; 6)]	0.9 (0.1; 6) [0.2 (0.0; 6)]	408.1	97.5	507.7
<i>D. mollis</i>	O	9.5 (2.2; 5) [2.0 (0.5; 5)]	59.8 (3.6; 5) [12.3 (0.9; 5)]	0.9 (0.1; 5) [0.2 (0.0; 5)]	369.5	88.3	514.4
<i>D. splendidus</i>	P	6.3 (0.4; 2) [1.2 (0.1; 2)]	71.6 (2.0; 2) [13.8 (0.1; 2)]	0.8 (0.1; 2) [0.2 (0.0; 2)]	376.2	89.9	472.1
<i>Gonichthys cocco</i>	Q	5.7 (0.5; 3) [1.3 (0.1; 3)]	66.4 (7.8; 2) [13.9 (1.2; 2)]	0.6 (0.2; 2) [0.1 (0.0; 2)]	380.8	91.0	517.8
<i>Hygophum benoitii</i>	R	13.4 [3.6]	40.8 [10.9]	1.5 [0.4]	398.0	95.1	682.0
<i>H. reinhardtii</i>	S	10.0 [2.5]	59.3 [14.5]	0.9 [0.2]	440.3	105.2	620.5
<i>Lampadena luminosa</i>	T	6.7 (0.3; 3) [1.0 (0.02; 3)]	69.2 (7.0; 4) [11.2 (1.2; 4)]	1.0 (0.1; 4) [0.2 (0.0; 4)]	307.2	73.4	397.1
<i>Lampanyctus alatus</i>	U	7.8 (0.5; 7) [1.4 (0.1; 7)]	77.3 (2.7; 7) [13.8 (0.9; 7)]	1.0 (0.0; 7) [0.2 (0.1; 7)]	383.8	91.7	438.4
<i>L. lineatus</i>	V	6.6 (0.4; 4) [0.6 (0.3; 4)]	77.9 (6.9; 4) [6.2 (0.7; 4)]	1.0 (0.1; 4) [0.1 (0.0; 4)]	171.6	41.0	198.2
<i>Lepidophanes guentheri</i>	W	7.3 (0.6; 10) [1.3 (0.1; 10)]	74.0 (2.6; 11) [12.3 (0.8; 11)]	0.7 (0.1; 10) [0.1 (0.0; 10)]	342.3	81.8	410.8
<i>Lobianchia gemellarii</i>	X	8.3 (1.7; 2) [1.6 (0.6; 2)]	62.1 (5.2; 2) [9.5 (1.0; 2)]	1.0 (0.1; 3) [0.2 (0.2; 3)]	288.3	68.9	416.0
<i>Myctophum nitidulum</i>	Y	7.2 (1.2; 3) [1.4 (0.3; 3)]	63.4 (5.4; 3) [11.1 (2.9; 3)]	0.7 (0.1; 3) [0.1 (0.0; 3)]	317.6	75.9	454.6
<i>Notoscopelus resplendens</i>	Z	7.8 (0.5; 7) [1.6 (0.1; 7)]	62.5 (3.0; 7) [13.2 (0.7; 7)]	0.8 (0.1; 6) [0.2 (0.0; 6)]	376.7	90.0	522.6
<i>Notolychnus valdiviae</i>	1	43.3 (6.7; 2) [10.7 (1.3; 2)]	32.8 (3.3; 2) [8.7 (1.0; 2)]		597.2	142.7	735.0
<i>Taaningichthys bathyphilus</i>	2	9.9 [1.8]	52.2 [9.6]	1.1 [0.2]	298.0	71.2	460.9

Table 2 (continued)

Family, genus, species	Code	Lipid (%AFDW) [(%WW)]	Protein (%AFDW) [(%WW)]	Carb (%AFDW) [(%WW)]	Energy level		
					kJ 100 g ⁻¹ WW	kcal 100 g ⁻¹ WW	kJ 100 g ⁻¹ WW corrected
Sternoptychidae							
<i>Argyropelecus aculeatus</i>	3	8.4 (0.9; 18) [1.0 (0.2; 17)]	80.6 (2.5; 21) [11.3 (0.4; 21)]	1.2 (0.1; 19) [0.2 (0.0; 19)]	309.3	73.9	342.8
<i>A. hemigymnus</i>	4	6.5 (0.7; 3) [1.1 (0.1; 3)]	66.1 (9.0; 3) [10.8 (2.0; 3)]	1.2 (0.1; 3) [0.2 (0.0; 3)]	301.3	72.0	404.3
<i>Mauroliticus muelleri</i>	5	6.9 (1.8; 2) [1.4 (0.4; 2)]	75.2 (10.0; 2) [14.9 (2.0; 2)]	0.9 (0.0; 2) [0.2 (0.0; 2)]	409.7	97.9	490.6
<i>Sternoptyx diaphana</i>	6	8.4 (0.7; 8) [1.1 (0.1; 8)]	73.2 (2.7; 7) [10.2 (0.5; 8)]	1.3 (0.1; 8) [0.2 (0.0; 8)]	286.7	68.5	341.5
<i>S. pseudobscura</i>	7	9.0 (0.4; 4) [1.0 (0.1; 4)]	67.5 (4.3; 4) [7.6 (0.8; 4)]	1.4 (0.2; 4) [0.2 (0.0; 4)]	221.0	52.8	272.2

of 9.1% WW (± 2.5 ; $n=8$). Migrators had a higher protein level (% WW) than weak or non-migrating species, but the difference was not significant at the 0.05 level (Mann-Whitney-Wilcoxon-test: $z=-1.86$; $0.05 < P < 0.07$). Protein constituted the highest percentage of AFDW, ranging from 32.8 to 80.6% AFDW (Table 2), but was not correlated with MDO. The protein level (% AFDW) of migrators was not significantly different from that of weak migrators and non-migrators. The protein level (% AFDW) showed a weak but significant correlation with water content (equation for the regression is $P=0.29$ W 1.24 ± 1.19 ; $n=21$). Lipid and protein levels (% AFDW) were not correlated.

Carbohydrate

Levels of carbohydrate varied from 0.3 to 1.5% AFDW and 0.1 to 0.4% WW (Table 2) and showed no relation to MDO.

Energy content

Recovery of organic matter was in all cases less than 100% of the AFDW ($x=72.3 \pm 5.7$), and this is reflected in the energy levels (Table 2, Fig. 4). To be consistent with previous studies (Childress and Nygaard 1973, Bailey and Robison 1986), all comparisons are made on the basis of recovered organic matter only. However, energy levels for all species are also provided (Table 2) based on the assumption that the difference between total organic matter recovered and 100% is due to refractory protein (Sibuet and Lawrence 1981).

Energy levels (expressed as kJ 100 g⁻¹ WW) decreased significantly with MDO (Fig. 4). Migratory species had significantly higher energy levels (mean = 333.9 kJ 100 g⁻¹ WW ± 52.4) than weak migrators and non-migrators (mean = 245.1 kJ 100 g⁻¹ WW ± 64.1 ; Mann-Whitney-Wilcoxon-test: $z=-2.19$, $P < 0.05$). Depth-related changes in energy level followed changes in protein as % WW. The

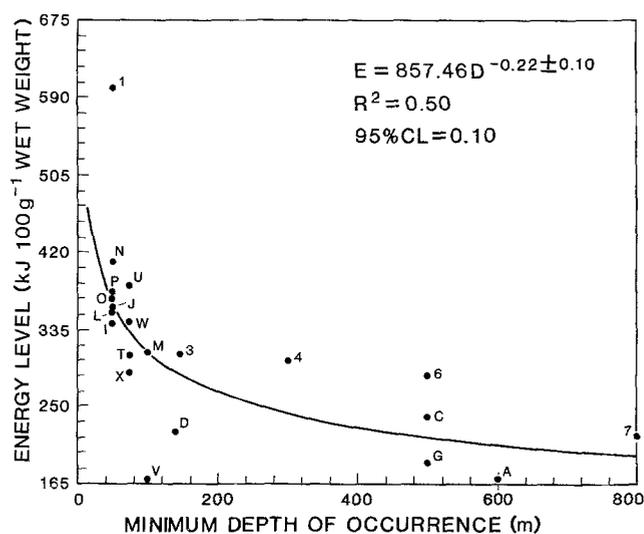


Fig. 4. Regression of energy level (kJ 100 g⁻¹ WW) on minimum depth of occurrence (MDO) in 21 species of mesopelagic fishes from the Gulf of Mexico (specific code designations as in Table 1). Equation for regression is $E = 204.89 D^{-0.22 \pm 0.10}$, where E = energy level and D = depth (significant at $P < 0.01$)

decrease in energy level (as represented by lipid and protein) with depth occurred in fishes with and without well developed swimbladders.

Discussion

Differences in the hydrography, productivity, and faunal composition of midwater systems are central to understanding compositional differences among species of different regions. The eastern Gulf of Mexico and other areas from which mesopelagic species have been taken for proximate analysis, e.g. the California Current, the eastern North Pacific Gyre, and the transition region between them, differ

greatly. The eastern Gulf of Mexico and North Pacific Gyre are stable, warm-water areas with high faunal diversity, low standing stocks, and a primary productivity of approximately $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ that varies by less than a factor of 1.5 seasonally (McGowan and Williams 1973, McGowan 1974, Cullen and Eppley 1981, Hopkins 1982, Hayward 1986, Gartner et al. 1987). The California Current is a colder, more variable system than either the Gyre or the Gulf, with a mean primary productivity ($\sim 150 \text{ g C m}^{-2} \text{ yr}^{-1}$) approximately three times that of the eastern North Pacific Gyre (McGowan and Williams 1973, McGowan 1974, Cullen and Eppley 1981, Bailey and Robison 1986). Primary production ranges from $0.226 \text{ g C m}^{-2} \text{ d}^{-1}$ in winter to $0.603 \text{ g C m}^{-2} \text{ d}^{-1}$ in late spring in the California Current, a seasonal variability of about three-fold (Smith and Eppley 1982, Hayward 1986). Despite these differences, species composition of the California Current and eastern North Pacific Gyre are similar, with greater diversity in the Gyre and higher standing stocks in the California Current (Barnett 1983, Bailey and Robison 1986).

The increased water level of deeper-living species in the eastern Gulf of Mexico is similar to that observed in deeper-living species from the California Current and from the transition water between the California Current and the eastern North Pacific Gyre. It differs from the species from the Gyre, where water level is not related to depth (Childress and Nygaard 1973, Bailey and Robison 1986). Regressions of water level on MDO for fishes from the eastern Gulf of Mexico ($W = 60.56 D^{0.054}$) and eastern North Pacific transition water ($W = 58.89 D^{0.055}$; Bailey and Robison 1986) have similar slopes. Substitution of dilute body fluids for organic matter is a means of achieving neutral buoyancy, of reducing energy required per unit growth, or a result of low food availability (Childress and Nygaard 1973, Bailey and Robison 1986).

As concluded by Childress (1977), AFDW (% DW) represented partitioning of organic matter, and was therefore useful in conceptualizing adaptive strategies in energy utilization. Wet weight was superior in its representation of the ecological and physiological state since it was the "live state" and accounted for the entire body weight (Childress 1977). Data as % WW and % AFDW allowed for comparisons with other proximate-analysis investigations.

The decline in AFDW (% DW) with MDO in Gulf of Mexico species contrasts with the absence of a decline in California Current species (Childress and Nygaard 1973). Mean AFDW for Gulf of Mexico species ($74.4\% \text{ DW} \pm 2.4$; $n = 33$) is lower than that of California Current species ($82.8\% \text{ DW} \pm 2.0$; $n = 29$; Childress and Nygaard 1973) and eastern North Pacific Gyre species (87.2 ± 2.0 ; $n = 12$; Bailey and Robison 1986). The highest values for AFDW (% DW) are similar in Gulf of Mexico, California Current, and Gyre species, while lowest values are lower in Gulf of Mexico species than in Current or Gyre fishes (65.3 to 90.2% AFDW in Gulf of Mexico species, 73.8 to 92.1% AFDW in California Current species; 81.3 to 93.7% AFDW in Gyre species; Childress and Nygaard 1973, Bailey and Robison 1986).

Table 3. Comparison of chemical composition of mesopelagic fishes recorded in present study with data from other investigators on congeneric fishes. Abbreviations as in Table 1

Species, area	MDO (m)	Mean (range) WW (g)	Water (%WW)	AFDW (%AFDW)	Lipid (%AFDW)	Protein		kJ 100 g ⁻¹ WW	kcal 100 g ⁻¹ WW	Source
						(%AFDW)	(%WW)			
<i>Anoplogaster cornuta</i> (Eastern Gulf of Mexico)	600	32.8 (20.7–45.0)	88.1 (1.9; 2)	77.1 (3.9; 2)	15.0 (7.0; 2)	52.3 (0.3; 2)	4.9 (1.0; 2)	173.3	41.4	Stickney and Torres (present study)
<i>Anoplogaster cornuta</i> (San Clemente Basin coast of Southern California)	550	ND (27.0–46.0)	85.0 (1.3; 2)	77.5 (3.2; 2)	24.1 (2.9; 2)	52.6 (0.9; 2)	ND	258.2	61.7	Childress and Nygaard (1978)
<i>Cyclothone pallida</i> (Eastern Gulf of Mexico)	500	0.5 (0.4–0.7)	81.6 (1.5; 4)	67.6 (4.4; 4)	8.9 (1.4; 3)	75.3 (11.4; 3)	8.5 (1.2; 3)	241.1	57.6	Stickney and Torres (present study)
<i>Cyclothone acclimens</i> (Eastern N. Pacific Gyre)	500	0.5 (0.1–1.1)	77.2 (1.2; 10)	88.8 (0.8; 10)	36.2 (1.1; 10)	43.9 (0.7; 10)	8.9 (0.6; 10)	481.3	115.0	Bailey and Robison (1986)
<i>Sternoptyx diaphana</i> (Eastern Gulf of Mexico)	500	1.7 (0.4–3.6)	81.2 (0.5; 8)	70.9 (3.5; 7)	8.4 (0.7; 8)	73.2 (2.7; 7)	10.2 (0.5; 8)	286.6	68.5	Stickney and Torres (present study)
<i>Sternoptyx diaphana</i> (Eastern N. Pacific Gyre)	500	0.3 (0.1–0.5)	83.4 (0.9; 18)	81.3 (0.9; 18)	10.9 (1.1; 18)	67.5 (2.2; 18)	9.0 (0.4; 18)	266.6	63.7	Bailey and Robison (1986)

No pattern was apparent in the AFDW (% DW) of the same species or congeners from different systems (Table 3). The AFDW of the deep-dwelling, non-migratory fish *Anoplogaster cornuta* is the same in the eastern Gulf of Mexico (77.1% DW) and California Current specimens (77.5% DW; Childress and Nygaard 1973). However, AFDW of the non-migrator *Sternoptyx diaphana* from the eastern Gulf of Mexico (70.9% DW) differed from that of the same species from the eastern North Pacific Gyre (81.3% DW; Bailey and Robison 1986). The AFDW values of non-migrating *Cyclothone* congeners, *C. pallida* (67.6% DW) from the Gulf of Mexico and *C. acclinidens* (88.8% DW) from the eastern North Pacific Gyre, also differed.

Part of the difference in AFDW between species of the different systems may be methodological in origin. Ash-free dry weights were determined in Gulf species in a low-temperature ash, as opposed to ashing in a high temperature (500°C) muffle furnace. Childress and Price (1983) showed that a low-temperature ash underestimates the ash-free weight by 1.8% DW, while high temperature overestimates by 8.5% DW.

Skeletal ash (% WW) did not differ significantly in eastern Gulf of Mexico species with or without functional swimbladders. In contrast, skeletal ash values (% WW) for the two groups differed significantly in fishes from the California Current (Childress and Nygaard 1973). The mean values of skeletal ash (% WW) for eastern Gulf of Mexico species with functional swimbladders (4.8 ± 0.8 ; $n=18$) and without swimbladders ($2.7\% \pm 2.5$; $n=4$) are not significantly higher ($P < 0.01$) than values for the groups in species from the California Current (3.3 ± 1.03 , $n=4$; $1.8\% \pm 0.4$, $n=22$ respectively; Childress and Nygaard 1973).

An explanation for the relatively high skeletal ash in Gulf of Mexico species is not readily apparent, unless it is an indication of a more robust skeletal structure. Fishes that are shallow-living, or that migrate into shallow waters, have higher skeletal ash content (Childress and Nygaard 1973). The hatchetfishes *Argyropelecus aculeatus* and *A. hemigymnus* have a lower mean water content (78.0% WW) and higher mean skeletal ash content (5.5% WW) than their deeper living confamilials *Sternoptyx diaphana* and *S. pseudobscura* (84.0 and 4.0% WW, respectively). *A. aculeatus*, a migrator, has a higher protein content (11.3% WW; 80.6% AFDW) than the other three species which are weak migrators or non-migrators.

Mesopelagic fishes from the California borderland that achieve neutral buoyancy by means of a gas-filled swimbladder are low in mean water level (75.3% WW), high in skeletal ash (3.6% WW), low in mean lipid level (2.2% WW), and high in mean protein level (11% WW) (Childress and Nygaard 1973). Many of the Gulf migrators have similar values. A greater percentage of species examined from the eastern Gulf of Mexico have functional swimbladders than those examined from the California Current (Childress and Nygaard 1973). Species in the Gulf of Mexico may rely more heavily on swimbladders and dilute body fluids for achieving neutral buoyancy than species from other systems which have higher lipid contents. The decrease in skeletal ash (%

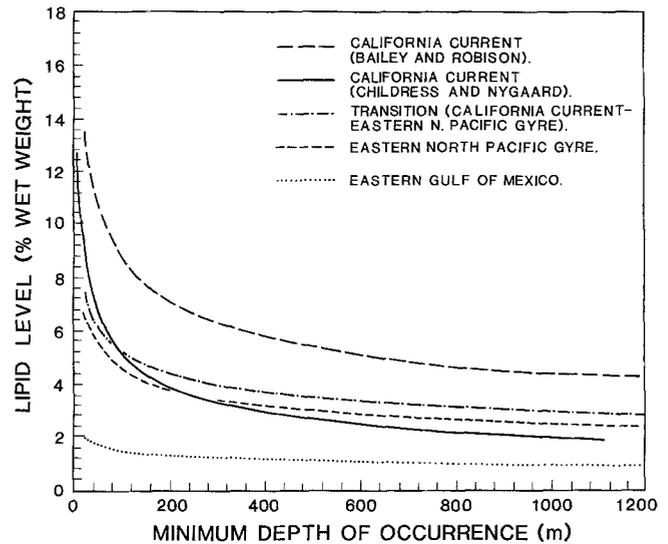


Fig. 5. Comparison of regression curves of lipid level (% wet weight) on minimum depth of occurrence (MDO) in mesopelagic fishes from California Current (Bailey and Robison 1986; significant at $P < 0.05$), California Current (Childress and Nygaard 1973; significance level for correlation coefficient not given); transition between California Current and eastern North Pacific Gyre [Bailey and Robison 1986; not significant ($P > 0.05$)], eastern North Pacific Gyre [Bailey and Robison 1986; not significant ($P > 0.05$)], and eastern Gulf of Mexico [present study; not significant ($P > 0.05$)]

WW) with depth suggests that this is a means for achieving neutral buoyancy in deeper-living fishes of the eastern Gulf of Mexico.

The lipid component of organic content is low in most eastern Gulf of Mexico species, particularly when compared with values in midwater fishes from cold waters (Table 3; Fig. 5). The differences in lipid level in three similar myctophid fishes (MDO = 50 to 75 m) from three markedly different systems, *Electrona antarctica* from the Southern Ocean (56.5% DW; Reinhardt and Van Vleet 1986), *Lampantyx ritteri* from the California Current (40.0% DW; Childress and Nygaard 1973), and *L. alatus* from the eastern Gulf of Mexico (6.6% DW; present study) emphasize this. High lipid deposition found in high-latitude species may be related to the long-term energy reserves necessary for overwintering (Reinhardt and Van Vleet 1986).

Diet may be important in determining the low lipid level in Gulf of Mexico species, since the lipid levels of predators may be similar to that of their prey (Love 1970, Reinhardt and Van Vleet 1986), and in some cases fatty acid composition of lipid reserves in predators reflects that of prey species (Sargent 1976). However, internally synthesized fatty acids also contribute to the pattern of fatty acids in depot lipids and a good correlation between dietary lipid and depot lipid generally cannot be made (Sargent 1976). An examination of lipid level and vertical distribution of principal prey items can be used to relate lipid levels of predators and prey.

The principal taxonomic components of the midwater fish community in the Gulf – the Gonostomatidae, Myctophidae, and Sternoptychidae – forage primarily on copepods and euphausiids (Hopkins 1982). The family containing the largest number of species examined, the Myctophi-

dae, occur primarily between 50 and 150 m at night (Gartner et al. 1987) where copepods, euphausiids, and ostracods dominate the biomass (Hopkins 1982, and personal communication).

Lipid levels are low in the euphausiids ($7.66 \pm 1.98\%$ DW) and copepods ($9.71 \pm 3.28\%$ DW; Morris and Hopkins, 1983) in the eastern Gulf of Mexico. Only two zooplankton species with lipid levels $>27\%$ DW occur in the eastern Gulf of Mexico: *Eucalanus monachus* (56.3% DW), generally abundant below 550 m; and *Rhincalanus* spp., predominantly *R. cornutus*, abundant throughout the entire upper 1 000 m day and night (lipid level of 48.8% DW; Hopkins 1982, Morris and Hopkins 1983). The 50 to 150 m zone inhabited by most myctophids at night is not the zone of maximum energy density or maximum energy level per prey individual; that zone occurs shallower than 50 m (Hopkins 1982). Thus, the myctophids, which are reported to feed primarily at night (Hopkins 1982), apparently do not utilize the zooplankton with higher energy content.

Both *Gonostoma elongatum*, an abundant gonostomatid in the eastern Gulf of Mexico, and *Lampanyctus alatus*, a dominant subtropical myctophid (Gartner et al. 1987), selectively prey on the copepod genus *Pleuromamma* (Hopkins and Baird 1985a), which is low in lipid (Morris and Hopkins 1983). Other species from the present study with prey items low in lipid content are *Gonostoma elongatum*, *Benthoosema suborbitale*, *Diaphus dumerilii*, *Lepidophanes guentheri*, *Argyropelecus aculeatus*, *Sternoptyx diaphana*, and *S. pseudoscurea* (Hopkins and Baird 1977, Morris and Hopkins 1983).

Several species did not show correlations of low lipid level between predator and prey. *Notolychnus valdiviae* showed high lipid levels (43.4% AFDW; 10.7% WW) but feeds on prey [species of *Pleuromamma*, *Oncaea*, *Conchoecinae* (ostracod) and euphausiid larvae] with low lipid level (Hopkins 1982, Morris and Hopkins 1983). Another exception is the hatchetfish *Argyropelecus aculeatus*, which was low in lipid level but feeds heavily on the lipid-rich copepod *Eucalanus monachus* (Hopkins and Baird 1985b). Since most of the fishes examined were vertical migrators, similarity of lipid level between shallow and deep dwellers may reflect similar prey items, although most prey items also migrate (Hopkins 1982).

Notolychnus valdiviae is exceptional in that its lipid level was about four times that of any other myctophid examined in the study, and about three times that of its nearest rival in lipid level, *Anoplogaster cornuta*. *N. valdiviae* is the smallest myctophid species, reaching a maximum length of 16 to 18 mm (Nafpaktitis et al. 1977), and lives approximately one year, reproducing almost continuously after reaching sexual maturity (J. V. Gartner personal communication). It has a functional gas-filled swimbladder, eliminating buoyancy as a probable explanation for the high lipid levels. The short life of the species coupled with a prolonged intense reproductive effort probably requires a high lipid level. Even had all specimens analyzed in this study been ripe females, the expected increase in lipid would have been less than two times the baseline value of ca. 10% AFDW typical of the other myctophids (cf. Lasker 1970).

Low lipid values for most species suggest the possibility that reserves are unnecessary in a stable system. In a tropical-subtropical system, a constant food supply is available in the form of zooplankton (Hayward and McGowan 1979), lessening the need for lipid reserves. Large wax-ester reserves are typically seen in species from cold-water, high-latitude systems where food availability is strongly dependent on season (Sargent 1976). Herbivorous plankton do not abandon surface layers in tropical systems since seasonal changes are minimal, and therefore they serve as a more stable food supply (Vinogradov and Tseitlin 1983). Quarterly sampling in the top 200 m of the eastern Gulf of Mexico showed that zooplankton biomass ranges from 1 278 to 2 920 mg DW m⁻², with no clear seasonal trend (T. L. Hopkins personal communication).

Decreasing protein level (% WW) with increasing depth in Gulf of Mexico fishes supports previous studies (Childress and Nygaard 1973, Bailey and Robison 1986). Higher protein levels (% WW) occurred in migrators than in weak migrators and non-migrators in the eastern Gulf of Mexico. A correlation between protein level and the need for increased locomotory abilities is supported by the generally higher values found in migrators. Locomotory demands associated with vertical migration require more muscle. The differences in protein level, as muscle needed for locomotion, between migratory fishes and deep-dwelling non-migrators are independent of any enzymatic differences between the two groups (Childress and Somero 1979, Torres et al. 1979).

As reported in other studies (Childress and Nygaard 1973, Bailey and Robison 1986), protein (% AFDW) does not change with MDO in eastern Gulf of Mexico fishes. A small but significant increase in protein (% AFDW) occurs in species having higher water level. Since protein constitutes the major percentage of the AFDW (% DW), which decreases as water increases, the increase may be relative.

A reduction in energy required for growth in deeper living species, achieved by reducing energy level as suggested by Childress and Nygaard (1973), is supported by data for deeper living species from the eastern Gulf of Mexico. A majority of the eastern Gulf of Mexico species have a lower energy level than those found in colder waters (Fig. 6). The reduced energy level (primarily lipid and protein levels) is probably not a buoyancy mechanism, because it occurs in fishes with and without functional swimbladders (Childress and Nygaard 1973). The higher energy level in migrators than in weak migrators and non-migrators indicates the higher energy demands of the former group.

The high protein level of gulf migrators supports the idea that the protein level of mesopelagic fishes within an oceanic system does not correlate with the food availability or productivity of the system. It is a function of light penetration and the relative importance of visual predation at depth (Bailey and Robison 1986). Since light penetration is a function of water clarity, and therefore varies inversely with primary productivity (Isaacs et al. 1974), oligotrophic systems have consistently higher light levels throughout the top 1 000 m than do more productive areas such as the Califor-

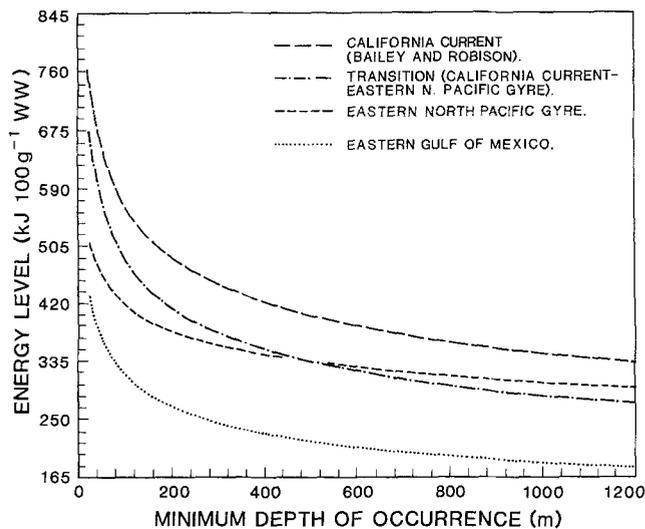


Fig. 6. Comparison of regression curves of energy level ($\text{kJ } 100 \text{ g}^{-1} \text{ WW}$) on minimum depth of occurrence (MDO) in mesopelagic fishes from California Current (Bailey and Robison 1986; significant at $P < 0.05$), transition between California Current and eastern North Pacific Gyre (Bailey and Robison 1986; significant at $P < 0.05$), eastern North Pacific Gyre (Bailey and Robison 1986; significant at $P < 0.05$), and eastern Gulf of Mexico (present study; significant at $P < 0.01$)

nia Current (Marshall 1979). The higher light levels in oligotrophic regions allow visual predation to be effective at greater depths, maintaining a selective pressure for competent locomotion in both predator and prey species and, concomitantly, the higher protein levels associated with a robust musculature.

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