

Chemical composition of midwater fishes as a function of depth of occurrence off the Hawaiian Islands: food availability as a selective factor?

J. J. Childress¹, M. H. Price¹, J. Favuzzi¹ and D. Cowles²

¹ Oceanic Biology Group, Marine Science Institute and Department of Biological Sciences, University of California at Santa Barbara, Santa Barbara, California 93106, USA

² Department of Biology, Loma Linda University, Riverside, California 92515, USA

Date of final manuscript acceptance: February 16, 1990. Communicated by J. M. Lawrence, Tampa

Abstract. The variation with depth in water, lipid, protein, carbon and nitrogen contents (% wet weight) of 42 species of midwater fishes, collected in November 1976 off the west coast of Oahu in the Hawaiian Archipelago, was measured. The Hawaiian fishes show significant relationships between these components and depth of occurrence. The slopes of these relationships are not significantly different from those reported for midwater fishes from off California, USA. However, the fishes from Hawaii have significantly lower lipid levels and higher protein levels than do the species from off California. The deep-living Hawaiian species (500 m and deeper) have significantly lower lipid (% wet weight), but there is no significant difference in protein (% wet weight). The difference in lipid contents at all depths appears to be an evolved characteristic, with the greater lipid levels off California being selected for by greater spatial and temporal variation in the food supply for these fishes off the California coast than off Hawaii. The higher protein contents in the shallow-living Hawaiian fishes appear to reflect greater muscle power selected for in these fishes by the greater water clarity, and therefore greater "reactive distances", in the surface layers off Hawaii. These conclusions support the general hypothesis that the lower protein contents of bathypelagic fishes are not directly selected by food limitation at depth, but rather result from the relaxation of selection for rapid-swimming abilities at greater depths due to the great reduction at greater depths in the distance over which visual predator-prey interactions can take place. The lower lipid levels in the deeper-living species are apparently made possible by the reduced metabolic rates of these species which reduces their need for energy stores.

Introduction

Deep-sea fishes have long been regarded as different from shallower-living fishes in many ways for a variety of reasons. In recent years, attention has focussed on their met-

abolic processes. Midwater fishes and crustaceans living at greater depths have much lower metabolic rates than shallower-living pelagic species (Childress 1971, 1975, Torres et al. 1979, Smith and Laver 1981, Donnelly and Torres 1988, Torres and Somero 1988). The difference in rates between surface-living species and those living at 1000 m is ca. 15-fold. The activities of enzymes of intermediary metabolism have a comparable decline with depth, indicating that these lower metabolic rates are determined at the subcellular level (Childress and Somero 1979, Somero and Childress 1980, Siebenaller and Yancey 1984, Torres and Somero 1988). The proximate composition of midwater fishes off California also changes as their habitat-depth increases (Childress and Nygaard 1973, Torres et al. 1979). In particular, lipid and protein concentration (% wet weight) both decline and as a result water concentration (% wet weight) increases with increasing depth of occurrence.

We have suggested that this combination of lower metabolic rates and lower energy-density allow deeper-living midwater fishes to allocate a greater fraction of their ingested food energy to growth than do shallower-living species (Childress and Nygaard 1973, Childress et al. 1980). However, because of the generally larger sizes of the deeper-living midwater species, the result of these adaptations is not an absolute lower energy usage, but only a relative one. This led us to reject the hypothesis that these characteristics of deeper-living species were selected primarily by lower food availability at greater depth (Childress et al. 1980). Instead we hypothesized that these energy-conserving adaptations (which appear to be of adaptive value at all depths) were allowed to be evolved by the relaxation of selection for robust bodies and powerful swimming abilities at greater depths. In particular, visual predator-prey interactions have been suggested as the selective factor which is relaxed at depth (Childress et al. 1980, Childress and Mickel 1985).

These hypotheses can be tested by comparing the characteristics of midwater fishes from regions which differ greatly in their characteristics. The original studies were all done with fishes from the Southern California

borderland region, which is characterized by high productivity. A central North Pacific site with low productivity is the obvious choice for comparison. One could predict that if energy limitation is the primary selective factor for a given trait, then that trait should be found in fishes living closer to the surface in lower-productivity regions if all other factors are equal (Bailey and Robison 1986). However, central North Pacific sites differ from California sites in many ways in addition to low productivity. We suggest that the most important of these are that primary and secondary production are much less variable (Hayward 1986), water clarity near the surface is greater (Kampa 1970, Young et al. 1980), and temperatures above 400 m are warmer at the central Pacific sites. The present study compares the proximate compositions of midwater fishes from the Hawaiian region with those reported for California fishes (Childress and Nygaard 1973, Torres et al. 1979).

We have examined our data and the similar data of Bailey and Robison (1986) in the light of previous studies on the composition of midwater and other animals. This analysis indicates that higher lipid contents are selected for not by higher levels of food availability, but by higher spatial and temporal variability in food availability. In contrast, the major selective factor for protein content is suggested to be visual predator-prey interactions as affected by such factors as water clarity, illumination and body size.

Materials and methods

Capture and proximate analysis of Hawaiian fishes

All specimens were collected with a 3.1 m Isaacs-Kidd midwater trawl 10 to 25 km off the west coast of Oahu, in the Hawaiian Archipelago, in the fall of 1976. Immediately after capture, they were identified, quickly blotted, sealed in preweighed plastic vials, and frozen. These frozen samples were brought to the University of California at Santa Barbara (UCSB) where they were thawed and then weighed while still sealed. The wet weight of each fish was taken as the additional weight in the sealed vial. The vials were opened after weighing, dried to constant weight (60°C) and reweighed.

The remainder of the analytical procedure was the same as that described in Childress and Nygaard (1974) and Childress and Price (1983). The dried fish were homogenized in distilled water and aliquots were taken for the analyses. The ash-free dry weight (AFDW) was measured by ashing to constant weight at low temperature in a plasma asher (Childress and Price 1983). Carbohydrate was measured spectrophotometrically according to the method of Dubois et al. (1956). Lipid was measured gravimetrically by a method derived from Folch et al. (1956). Protein was measured spectrophotometrically (Lowry et al. 1951), with bovine serum albumin as the standard. Carbon and nitrogen were analyzed by combustion, with measurement of resulting gases in a Perkin-Elmer 240B elemental analyzer. Energy values were calculated using the following factors: carbohydrate, 4.1 kcal g⁻¹; lipid, 8.7 kcal g⁻¹; protein, 5.7 kcal g⁻¹ (Brett and Groves 1979); and then converted to kJ g⁻¹ using the conversion factor of 0.23885 cal/J.

The depths at which the fish live were characterized as the "minimum depth of occurrence" (MDO) following Childress and Nygaard (1973), defined as "the depth below which 90% of the population of each species lives". This parameter emphasizes the shallow end of the depth range occupied by a species. The MDO for

each species was estimated from publications on the vertical distribution of midwater fishes off Hawaii (Clarke 1973, 1974, Clarke and Wagner 1976) and unpublished data of T. Clarke and J. Childress. Species which come to the surface or near it were assigned MDO values of 10 m to avoid distorting the regressions produced after log-transformation of the data.

Standing-stock measurements

Data on the abundance of major micronekton groups in the San Clemente basin off Southern California were obtained from 11 oblique trawls taken in July 1970, January 1971, October 1972 and January 1974. These trawls are described in Childress and Price (1978, their Table 1), where the catch of *Gnathopausia ingens* is described. The gear used was either a Tucker trawl with a 9.6 m² mouth or a 3.1 m Isaacs-Kidd midwater trawl, both with liners which had 6.4 mm mesh on each side. The 9.5 to 12 h-long trawls were done entirely in darkness. The trawl net was lowered quickly to the greatest depth and then slowly retrieved for the duration of the trawl. Succeeding trawls ran reciprocal courses. When the trawl was recovered, the catch was sorted to species for the major components of the micronekton and into larger groupings for the less abundant species. These groupings were then frozen and returned to the laboratory at UCSB, where they were weighed.

Statistical analysis

Because the proximate compositions varied with depth as well as between the two sites, a good deal of effort was devoted to the statistical analysis of the data. All data were initially viewed as scattergrams, including both the Hawaiian data from this report and the Californian data described below. The Californian midwater-fish data used for comparison consists of the data sets from Childress and Nygaard (1973) and Torres et al. (1979) augmented with the data for four additional deep-living species (*Kali normani*, *Chiasmodon niger*, *Tactostoma macropus*, and *Taaningichthys paurolychnus*) analyzed since the latter publication (Childress in preparation). All the California data were recalculated in terms of percent wet weight, and their energy contents were recalculated using the procedures described above. The carbohydrate values for the California data were doubled because a factor-of-two error was made in the carbohydrate calculations in the earlier papers. We also used data from Stickney and Torres (1989) for the proximate composition of midwater fishes from the eastern Gulf of Mexico to provide a comparison with another tropical region.

In order to compare the compositions of the fishes from these regions, it was necessary to make the comparisons in such a way that the variation with depth and the different depth distributions at the two sites did not bias the results. Regression lines of the form $y = ax^b$ were fitted to these data by linear regression using log-transformed data, with y being a given component in percent wet weight, and x being the minimum depth of occurrence. The power equation was chosen for this analysis after comparing the fits of the linear ($y = a + bx$) equation and the logarithmic ($y = a + b \ln x$) equation with those of the power equation for the Hawaii and California data as well as data from the eastern Gulf of Mexico (Stickney and Torres 1989). For most parameters, at most geographic locations, the relationship between y and x was most highly correlated when the power transformation was used. Further, visual inspection of the residuals suggested that the log-transformed data used in fitting the power curve were linear. In addition to these considerations, it is apparent that the linear equation is not an appropriate model for these relationships, since for most of the parameters studied the fitted line passed through the x -axis within the observed depth range, while the measured components can never go to zero in a living organism. The power and log equations provide a more realistic model of the changes in composition at greater depths. Of these two, the power equation (fitted as a linear equation using log-trans-

formed data) appeared to be the best compromise for fitting both the Hawaii and the California data sets. For the same reason, the analysis of covariance (ANCOVA) was carried out on log-transformed data because these were more nearly linear in most cases than the nontransformed data.

The initial examinations indicated that, for some components, the Hawaii data appeared to lie consistently above or below those of the California data while the slopes of the relationships appeared similar. The slopes of the power equations fitted for each component as a function of minimum depth of occurrence (MDO) were compared using an *F*-test (Sokal and Rohlf 1981). Since no significant differences in slopes were found, the lines were compared by ANCOVA for homogeneity of the *y*-intercepts. The mean values for each component adjusted to the mean \ln MDO of the two groups combined (\bar{y}_{adj}) are presented as an additional comparison of the elevations of the data sets. Where one or both of the regions failed to have a significant relationship between a component and MDO, the Mann-Whitney *U* test was used to compare the values of that parameter in the two regions. Statistical computations were either done manually following Sokal and Rohlf (1981), or done by computer using the programs Statview SE+ (Abacus Concepts), SuperANOVA (Abacus Concepts), and Fastat (Systat Inc.).

Results

The data from the chemical analyses are presented in Table 1. The regressions of the various components (% wet wt) as functions of minimum depth are given in Table 2. In general, the Hawaiian data consist of relatively more shallow-living species (mean MDO = 257 m) than do the Californian data (mean MDO = 440 m). None of the regression coefficients are significantly different between the Hawaiian and Californian data sets (Table 2, ANCOVA, *F*-test; Sokal and Rohlf 1981). The data presented here are generally similar in magnitude to data from analyses of ten species of midwater fishes from the central North Pacific Gyre north of the Hawaiian Islands (Bailey and Robison 1986), except that those data show lower water and higher lipid contents for most species.

Water

The water content of Hawaiian midwater fishes increases significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = 0.446$, $P < 0.0001$; Fig. 1 A, Table 2). There is no significant difference between the slopes or intercepts of the regressions of water content as a function of MDO of Hawaiian and Californian fishes (Table 2).

Ash-free dry weight

The ash-free dry weights (% wet weight) of Hawaiian midwater fishes decline significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = -0.421$; $P < 0.0001$; Table 2). There is no significant difference between the slopes or intercepts of the regressions of ash-free dry weight as a function of MDO of Hawaiian and Californian fishes (Table 2).

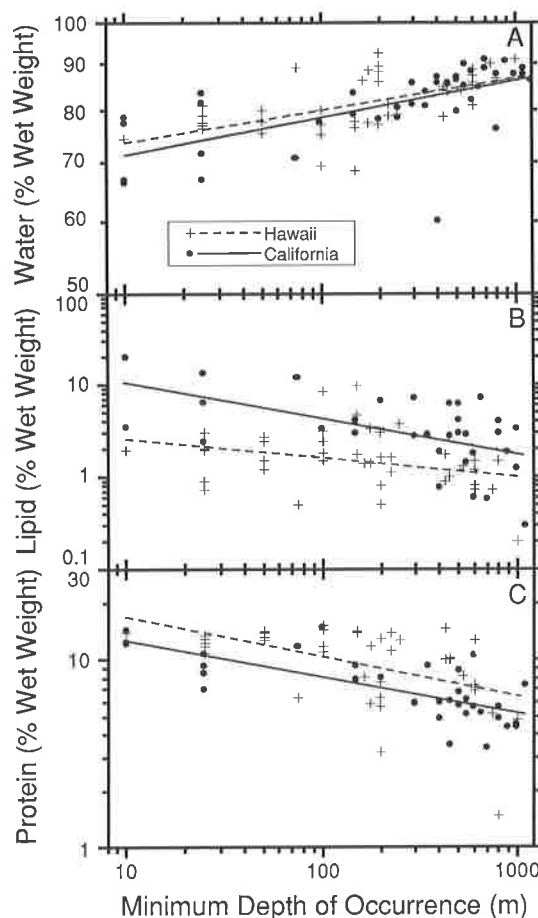


Fig. 1. Relationships between water (A), lipid (B), and protein (C) contents and minimum depth of occurrence of Hawaiian midwater fishes compared with those for Californian midwater fishes. Regression equations for lines are given in Table 2

Carbohydrate

The carbohydrate contents (% wet weight) of Hawaiian midwater fishes decline significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = -0.293$, $P = 0.0066$; Table 2). Since there is no significant relationship between carbohydrate content and MDO for Californian fishes (Kendall rank correlation, $\tau = -0.195$, $P = 0.14$; Table 2), the Hawaiian and Californian carbohydrate contents were compared by the Mann-Whitney *U* test and found to be significantly different ($P = 0.043$).

Lipid

The lipid content of Hawaiian midwater fishes decreases significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = -0.273$, $P = 0.011$; Fig. 1 B; Table 2). There is no significant difference between the slopes ($P = 0.46$) of the regressions of lipid content as a function of MDO of Hawaiian and Californian fishes (Table 2). However, the Hawaiian fishes have significantly lower lipid contents (Fig. 1 B; Table 2). Examination of the scatterplot (Fig. 1 B) suggests that this dif-

Table 1. Composition of Hawaiian midwater fishes; all values are percent of wet weight. Where only a single analysis of a single specimen was done, no statistical information is given; where individuals were pooled in an analysis series, number pooled is given in parentheses after standard lengths (SL). ND for wet weights and standard lengths indicates individuals were pooled without being measured. Where two analyses were made, range is given in parentheses after mean; where three or more analyses were made, standard error of the mean is given in parentheses after mean. In all such cases, number of analyses is shown in water column, in parentheses, after standard error values, and applies to all analyses for a given species. The minimum depth of occurrence (MDO) data were taken from publications of T. Clarke as well as his unpublished trawling data, as described in "Materials and methods - Capture and proximate analysis of Hawaiian fishes". AFDW: ash-free dry weight; CHO: carbohydrate

Species	MDO (m)	Wet wt (g)	SL, mm (n)	Water, x (SE, n)	AFDW	CHO	Lipid	Protein	C	N	kJ g ⁻¹
<i>Chauliodontidae</i>											
<i>Chauliodontus sloani</i>	175	24.7	185	88.3	9.0	0.09	1.4	5.8	4.6	1.3	1.89
<i>Cyemidae</i>											
<i>Cyema atrum</i>	1000	2.8	118	91.0	4.0	0.07	0.2	4.8	2.4	0.7	1.23
<i>Derichthysidae</i>											
<i>Derichthys serpentinus</i>	175	0.6	ND	77.5	17.8	0.42	3.3	11.7	8.4	2.1	4.05
<i>Evermannellidae</i>											
<i>Evermannella indica</i>	100	1.7-3.1	62-71	76.9 (1.5, 2)	19.2 (0.8)	0.42 (0.22)	2.4 (1.4)	15.1 (2.7)	9.1 (2.7)	2.3 (0.4)	4.54
<i>Giganturidae</i>											
<i>Bathyleptus lisae</i>	750	1.5	ND	90.2	3.6	0.08	0.7	5.1	3.1	0.8	1.46
<i>Gonostomatidae</i>											
<i>Cyclothone alba</i>	425	ND	ND (>10)	85.0	10.0	0.07	0.9	9.9	5.3	1.5	2.69
<i>Cyclothone pallida</i>	600	ND	ND (>10)	85.9	9.0	0.10	0.8	7.3	4.8	1.5	2.05
<i>Cyclothone pseudopallida</i>	525	ND	ND (>10)	84.1	11.2	0.12	1.3	8.2	5.3	1.6	2.46
<i>Diplophos taenia</i>	50	4.9	151	75.3	20.4	0.27	2.7	13.7	9.6	3.0	4.29
<i>Gonostoma atlanticum</i>	150	0.55	39-52 (2)	76.5 (2.5, 2)	19.3 (2.5)	0.46 (0.14)	4.7 (1.9)	13.8 (2.0)	9.7 (1.5)	2.2 (0.2)	5.09
<i>Gonostoma ebelingi</i>	200	2.7-5.8	100-126	85.8 (0.3, 4)	9.9 (0.3)	0.26 (0.02)	1.6 (0.1)	7.6 (0.2)	5.2 (0.3)	1.4 (0.1)	2.41
<i>Gonostoma elongatum</i>	200	1.0-15.3	69-160	89.4 (0.5, 6)	6.6 (0.5)	0.12 (0.12)	0.8 (0.2)	5.6 (0.3)	3.7 (0.1)	1.0 (0.0)	1.66
<i>Malacosteidae</i>											
<i>Malacosteus niger</i>	600	10.9	118	88.9	6.4	0.13	0.8	6.8	3.6	1.1	1.93
<i>Melamphaidae</i>											
<i>Scopelogadus mizolepis</i>	200	1.9-3.5	49-58	88.0 (2.5, 2)	7.8 (1.2)	0.08 (0.05)	0.8 (0.2)	6.3 (3.5)	3.9 (1.1)	1.1 (0.4)	1.78
<i>Melanostomiidae</i>											
<i>Thysanactis dentex</i>	75	1.4-3.0	65-98	89.0 (2.4, 2)	6.4 (1.4)	0.14 (0.04)	0.5 (0.0)	6.3 (0.2)	4.0 (0.2)	1.2 (0.1)	1.72
<i>Myctophidae</i>											
<i>Benthosema suborbitale</i>	25	0.33	26-28 (4)	76.6	18.3	0.25	3.1	13.2	8.1	2.0	4.31
<i>Bolinichthys distofax</i>	225	7.9	85	78.8	16.9	0.15	1.1	13.9	9.0	2.9	3.74
<i>Bolinichthys longipes</i>	25	1.9	52	80.8	15.2	0.11	0.7	10.7	7.1	2.2	2.82
<i>Centrobranchus choerocephalus</i>	10	0.23	32-33 (2)	74.1	19.3	0.12	1.9	13.9	10.1	3.4	4.01
<i>Ceratospilus warmingi</i>	50	0.4-1.8	33-50	80.0 (0.5, 5)	15.3 (0.8)	0.17 (0.03)	1.5 (0.3)	12.5 (0.6)	7.9 (0.3)	2.2 (0.1)	3.56
<i>Diaphus brachycephalus</i>	150	1.5-2.5	42-51	77.5 (0.3, 4)	17.8 (0.3)	0.26 (0.02)	1.7 (0.1)	13.9 (0.4)	8.6 (0.1)	2.6 (0.1)	3.97
<i>Diaphus mollis a</i>	25	0.38	23-35 (4)	77.2	17.3	0.17	0.9	11.7	8.3	2.5	3.15
<i>Diaphus schmidti</i>	25	0.46	30-32 (7)	76.0 (1.0, 2)	18.1 (1.0)	0.16 (0.02)	1.9 (0.4)	12.8 (0.5)	9.8 (0.6)	2.3 (0.2)	3.76
<i>Hypogomphus reinhardtii</i>	50	0.7-1.6	39.2-52	77.7 (1.7, 2)	18.3 (2.0)	0.23 (0.04)	2.4 (1.0)	14.0 (0.8)	10.0 (0.5)	2.7 (0.2)	4.24
<i>Lampanyctus niger b</i>	165	2.6-4.4	71-92	86.1 (0.4, 4)	9.4 (0.4)	0.12 (0.01)	1.4 (0.2)	8.0 (0.8)	5.2 (0.6)	1.4 (0.2)	2.43
<i>Lampanyctus nobilis</i>	100	4.4-6.9	83-94	79.9 (1.0, 3)	15.9 (1.0)	0.16 (0.03)	1.8 (0.5)	11.7 (0.4)	8.1 (0.6)	2.3 (0.0)	3.48
<i>Lampanyctus steinbecki</i>	100	0.5-1.2	40-52	76.9 (0.7, 6)	19.3 (0.9)	0.24 (0.04)	3.1 (0.3)	14.4 (1.0)	9.7 (0.5)	2.6 (0.2)	4.61
<i>Lampanyctus tenuiformis</i>	250	23.1	130	79.0	17.5	0.19	3.7	12.6	8.4	2.3	4.36

Table 1 (continued)

Species	MDO (m)	Wet wt (g)	SL, mm (n)	Water, x (SE, n)	AFDW	CHO	Lipid	Protein	C	N	kJ g ⁻¹
<i>Lobianchia gemellari</i>	150	3.0	55	68.4	25.2	0.20	9.6	14.1	14.3	2.2	6.88
<i>Myctophum selenoides</i>	100	5.4	65	75.1	19.7	0.21	1.5	11.0	8.0	2.4	3.22
<i>Notolycmus valdiviae</i>	100	0.1	23 (3)	69.2	25.9	0.13	8.3	15.0	17.3	2.1	6.63
<i>Taaningichthys bathyphils</i>	600	0.7–1.3	45–54	80.8 (1.3, 2)	14.5 (0.1)	0.10 (0.02)	1.2 (0.5)	12.5 (3.0)	8.0 (0.4)	2.2 (0.2)	3.44
<i>Taaningichthys minimus</i>	200	1.6–2.6	56–62	77.1 (0.8, 3)	18.8 (0.9)	0.21 (0.06)	3.0 (0.4)	12.9 (0.5)	9.9 (0.7)	2.1 (0.1)	4.19
<i>Triphoturus nigrescens</i>	25	0.17	26–36 (15)	78.7	15.7	0.23	2.0	12.1	7.9	2.3	3.67
Nemichthyidae											
<i>Avocettinops infans</i>	600	21.0	ND	87.3	8.1	0.12	1.5	7.1	5.1	1.4	2.27
Oneirodidae											
<i>Oneirodes acanthias</i>	800	1.3	18	86.9	6.5	0.25	1.5	1.5	3.0	0.7	0.97
Opisthoproctidae											
<i>Opisthoproctus soleatus</i>	450	6.0–15.8	57–78	83.8 (0.5, 3)	11.6 (0.3)	0.12 (0.02)	1.0 (0.1)	10.0 (1.1)	6.2 (0.1)	1.9 (0.1)	2.78
Photichthyidae											
<i>Vinciguerrria nimbaria</i>	50	0.27	25–33 (5)	77.7	17.4	0.45 (0.16)	1.2	13.1	8.4	2.5	3.64
Rondeletidae											
<i>Rondeletia lorricata</i>	200	8.1–25	66–100 (2)	92.5	3.3	0.05	0.5	3.2	2.6	0.7	0.95
Sternoptychidae											
<i>Argyropelicus aculeatus</i>	225	5.7–6.0	56–59	81.0 (0.2, 2)	13.4 (0.3)	0.22 (0.04)	1.6 (0.4)	11.2 (2.5)	6.0 (1.3)	1.8 (0.5)	3.30
<i>Danaphos oculus</i>	430	0.35	32–36 (4)	78.5 (0.7, 2)	18.4 (1.4)	0.16 (0.01)	1.7 (0.2)	14.6 (1.6)	8.4 (0.5)	2.2 (0.0)	4.13
<i>Sternoptyx diaphana</i>	450	1.4–4.2	26–40	85.2 (2.4, 2)	10.6 (2.6)	0.22 (0.13)	1.0 (0.3)	10.2 (2.0)	5.6 (1.3)	1.9 (0.0)	2.83

Table 2. Regression equation ($y = ax^b$) relating percent composition (y) to minimum depth of occurrence ($x = m$) of midwater fishes. These equations were fit and the ANCOVA were run using ln transformation to linearize the data. Hawaiian data are given in Table 1 of present paper, Californian data, plus four sets of unpublished analyses, are from Childress and Nygaard (1974) and Torres et al. (1979). 95% confidence intervals (95% CI) are given after b values, which are underlined when significantly different from 0.0. Equations whose slopes are not significantly different from 0.0 are shown so that their confidence intervals may be compared with those of the significant regressions. \bar{y}_{adj} values are mean y values adjusted to common mean x value for both groups combined for each parameter. Significance of differences in \bar{y}_{adj} was tested in the ANCOVA, and the P value for the null hypothesis is shown. The null hypothesis that the slopes are equal for the two groups was tested in the ANCOVA ("Slopes"); when slopes were not significantly different, ANCOVA was used to test for significant differences between intercepts ("Intercepts"); when either one or both regressions for a given parameter were not significant ($P > 0.05$), significance of the difference between the two regions was tested with Mann-Whitney U test (results shown in parentheses in "Intercepts" column)

Component	Hawaiian fishes					Californian fishes					ANCOVA, $P =$		
	a	$b \pm 95\% \text{ CI}$	R^2	n	P	a	$b \pm 95\% \text{ CI}$	R^2	n	P	\bar{y}_{adj}	Slopes	Intercepts
y , % wet wt													
Water	67.70	0.036 ± 0.017	0.30	42	<0.0001	64.77	-0.041 ± 0.016	0.41	42	<0.0001	0.66	0.40	0.67
AFDW	51.28	-0.236 ± 0.164	0.29	42	<0.0001	43.84	-0.217 ± 0.058	0.65	33	<0.0001	0.13	0.35	0.12
CHO	0.35	-0.154 ± 0.137	0.11	42	0.028	0.38	-0.114 ± 0.147	0.08	29	0.12			(0.043)
Lipid	4.14	-0.201 ± 0.195	0.10	42	0.044	26.51	-0.390 ± 0.202	0.33	33	0.0004	<0.0001	0.46	<0.0001
Protein	27.16	-0.207 ± 0.115	0.25	42	0.0008	19.46	-0.192 ± 0.065	0.53	34	<0.0001	0.0044	0.59	0.004
Carbon	19.64	-0.217 ± 0.105	0.30	42	0.0002	24.86	-0.229 ± 0.075	0.57	31	<0.0001	0.038	0.99	0.036
Nitrogen	5.25	-0.215 ± 0.097	0.36	42	<0.0001	3.31	-0.154 ± 0.070	0.41	31	<0.0001	0.037	0.26	0.040
kJ g^{-1}	7.80	-0.193 ± 0.115	0.22	42	0.0015	13.00	-0.266 ± 0.090	0.54	33	<0.0001	0.095	0.33	0.096
% AFDW													
Lipid	8.08	0.074 ± 0.139	0.03	42	0.29	62.30	-0.182 ± 0.169	0.14	32	0.037			<0.0001
Protein	52.96	0.068 ± 0.083	0.07	42	0.10	44.43	0.025 ± 0.059	0.02	33	0.40			<0.0001

ference continues at greater depths. Comparison of the lipid contents of Hawaiian ($n=8$) and Californian ($n=15$) fishes with MDO values of 500 m or greater supported this ($P=0.028$, Mann-Whitney).

Protein

The protein contents (% wet weight) of Hawaiian midwater fishes decline significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = -0.368$; $P=0.0006$; Fig. 1C; Table 2). There is no significant difference between the slopes ($P=0.59$) of the regressions of protein content as a function of MDO of Hawaiian and Californian fishes (Table 2). However, the Hawaiian fishes have significantly higher protein contents (Fig. 1C; Table 2). Examination of the scatterplot (Fig. 1C) suggests that this difference does not continue at greater depths. Comparison of the protein contents of Hawaiian ($n=8$) and Californian ($n=15$) fishes with MDO values of 500 m or greater supported this ($P=0.37$, Mann-Whitney).

Carbon

The carbon contents (% wet weight) of Hawaiian midwater fishes decline significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = -0.411$, $P < 0.0001$; Fig. 2A, Table 2). There is no significant difference between the slopes ($P=0.26$) of the regressions of carbon content as a function of MDO of Hawaiian and Californian fishes (Table 2). However, the Hawaiian fishes have significantly lower carbon contents (Fig. 2A; Table 2).

Nitrogen

The nitrogen contents (% wet weight) of Hawaiian midwater fishes decline significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = -0.472$, $P < 0.0001$; Fig. 2B; Table 2). There is no significant difference between the slopes ($P=0.26$) of the regressions of nitrogen content as a function of MDO of Hawaiian and Californian fishes (Table 2). However, the Hawaiian fishes have significantly higher nitrogen contents (Fig. 2B; Table 2).

Energy content

The energy contents (kJ g^{-1} wet weight) of Hawaiian midwater fishes decline significantly with increasing minimum depth of occurrence (Kendall rank correlation, $\tau = -0.353$, $P=0.001$; Fig. 2C, Table 2). There is no significant difference between the slopes ($P=0.33$) or the intercepts of the regressions of energy content as a function of MDO of Hawaiian and Californian fishes (Fig. 2C; Table 2).

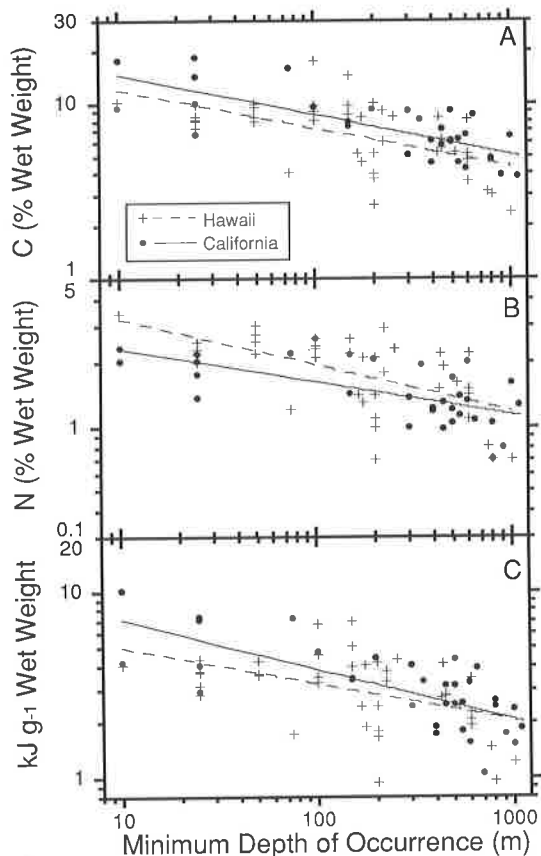


Fig. 2. Relationships between carbon, nitrogen, and energy contents and minimum depth of occurrence of Hawaiian midwater fishes compared with those for Californian midwater fishes. Regression equations for lines are given in Table 2

Lipid and protein as % ash-free dry weight

When lipid and protein are compared on an ash-free dry weight basis (Table 2), the partitioning of organic matter between these components is made more obvious. While neither lipid (% AFDW) nor protein (% AFDW) have significant regressions with MDO, protein (% AFDW) does show a significant increase with increasing depth (Kendall rank correlation, $\tau = 0.389$, $P = 0.0003$) while lipid (% AFDW) does not (Kendall rank correlation, $\tau = 0.044$, $P = 0.68$). Since the regressions of these components (% AFDW) as functions of MDO were not significant, Mann-Whitney U tests were used to compare the Hawaiian and Californian fishes. The Hawaii species have lower lipid as percent ash-free dry weight ($P < 0.0001$). As expected, the opposite is true of protein, with the Californian fishes having significantly less of their organic matter in the form of protein ($P < 0.0001$).

Biomass comparison

The biomasses of the major micronekton groups found off Hawaii and California are presented in Table 3. The total abundances of fishes, crustaceans, cephalopods, or cnidarians are not significantly different between the two regions. The Oahu site has significantly more biomass of

anguilliform fishes and caridean crustaceans, while the California site has significantly more biomass of mysid crustaceans. Other differences are found in groups which were not quantified (because of very low abundance) in one of the areas. For example, the bathylagid and melamphaid fishes are more abundant off California, while fishes of the genus *Gonostoma* are important components off Oahu but not off California. The data available for the central gyre north of Hawaii suggest that it has similar or lower biomass values compared with the Oahu site, depending on the group being considered (Table 3).

Discussion

The midwater fishes off Hawaii have lower lipid and carbon contents and higher protein and nitrogen contents (% wet weight) than those off California. Bailey and Robison (1986) found generally similar relationships when comparing 12 central North Pacific Gyre midwater-fish species with the same or closely related species from the California Current. However, their analyses indicate that the gyre fish, except for the sternoptychids, from the location more remote from Hawaii have appreciably higher lipid contents than we found in fish off Oahu. Like Bailey and Robison, we believe that the differences between California and gyre species must result from environmental differences between these two regions. Although our central Pacific site is close to Oahu, while Bailey and Robison's site is several hundred miles north and east, and our California site is within the Southern California borderland while theirs is just outside it, the fish compositions show similar trends between the California sites and the central Pacific sites. The Oahu site probably has higher primary productivity than the central gyre site due to the island-mass effect (Gilmartin and Revelante 1974), and this is apparently reflected in the biomasses at higher trophic levels (Table 3), although both central Pacific sites lie within the North Pacific Central Gyre faunal province (McGowan 1986). The general similarity in compositions of fishes at the two central Pacific sites compared to the California sites leads us to believe that they must share the property(s) which are responsible for the differences between the central Pacific and California regions. Thus, in our discussion of differences between the regions, we will combine data from large areas which, while each may be somewhat heterogeneous internally, differ substantially from each other. The differences in temperature at shallow depths, water clarity at shallow depths, average food supply, and variability in food supply are those most likely to be important in understanding the compositional differences.

Temperature at shallow depths

The surface temperature off Hawaii is about 10°C warmer than that off Southern California (San Clemente Basin), and temperature is elevated down to about 400 m. Below 400 m the difference is less than 1°C . This difference could have little effect on deeper-living non-migratory species, but would be expected to have a substantial effect on the metabolic rates of surface-living and verti-

Table 3. Micronekton standing stocks (biomass, g wet wt 100 m⁻²) in top 1 400 m of ocean in San Clemente Basin off Southern California (the first 11 trawls described in Table 1 of Childress and Price 1978), in top 1 200 m off lee side of Oahu, Hawaiian Island (Maynard et al. 1975), and in top 1 000 m of North Pacific Central Gyre and California Current (Bailey 1984). One standard deviation is shown in parentheses following means. San Clemente values are means of 11 trawls taken on 4 cruises, Oahu values are means of 9

trawls taken on 1 cruise; Bailey's values are not from oblique trawls like the others, but are integrations of discrete depth trawls. Null hypotheses comparing San Clemente and Oahu data sets were tested using a test of equality of the means of two samples whose variances are assumed to be unequal (Box 13.3; Sokal and Rohlf 1981). The San Clemente and Oahu studies used nets with 6.44 mm mesh on each side, Bailey nets with 4.5 mm mesh

Group	San Clemente	Oahu	P	Gyre	California Current
Myctophidae	71.2 (32.4)	65.7 (20.4)	NS	36.9	129.4
Cyclothone	59.8 (15.7)	45.9 (11.3)	NS	58.3	44.9
Other Gonostomatidae		14.9 (8.5)		5.5	0.5
Sternoptychidae	13.1 (15.7)	25.1 (14.0)	NS	10.3	17.9
Other Stomiatoidei	27.3 (38.9)	15.6 (12.5)	NS	12.0	93.2
Anguilliformes	10.7 (10.9)	48.2 (43.7)	<0.05	12.7	4.3
Bathylagidae	17.0 (10.4)			1.9	19.4
Melamphidae	18.8 (13.1)			5.3	41.7
Miscellaneous fishes	42.4 (50.6)	41.4 (40.2)	NS	8.2	8.5
Caridea	18.1 (5.0)	50.5 (21.1)	<0.001	42.5	36.1
Penaeidea	42.6 (20.7)	31.6 (10.6)	NS	42.4	39.5
Euphausiacea	6.2 (4.9)	18.5 (4.0)	NS	5.1	40.9
Mysidacea	61.5 (28.3)	8.8 (9.8)	<0.001	26.8	57.6
Miscellaneous Crustacea	4.2 (4.2)	1.1 (1.9)	NS		
Total fishes	260.3 (71.80)	256.7 (81.3)		151.1	359.8
Total Crustacea	133.1 (50.64)	110.5 (36.2)		119.9	181.1
Total Cephalopoda	128.5 (151.9)	48.7 (47.5)	NS	6.8	173.5
Total Cnidaria	45.6 (20.15)	40.9 (46.9)		4.2	20.7

cally-migrating species. All else being equal, one would also expect the Hawaiian fishes which enter the surface waters to have greater muscle power available to them due to decreased contraction times made possible by the higher temperatures (Bennett 1984).

Water clarity at shallow depths

The central Pacific waters have greater clarity, as indicated by a depth to 1% light of 80 to 120 m (Cullen and Eppley 1981, Hayward et al. 1983, Hayward and McGowan 1985) as compared to 30 to 66 m (Owen 1974, Cullen and Eppley 1981, Smith et al. 1987) off California. This translates to overall attenuation coefficients of 0.04 to 0.06 in the central Pacific compared with 0.07 to 0.15 off California. As a result of the difference in water clarity and surface irradiance, daytime irradiance is greater at depth off the lee shore of Oahu (Young et al. 1980) than in the Southern California Borderland (San Diego, Trough, Kampa 1970). One would also expect similar differences in nighttime irradiance near the surface. The higher irradiance off Hawaii at the depths occupied by these midwater fishes means that predators and prey of given sizes at comparable depths could detect each other visually at appreciably greater distances off Hawaii than off California.

Average food supply

The primary production off California is about two to three times that in the Central Pacific (Owen 1974, Cullen

and Eppley 1981, Hayward and Venrick 1982, Hayward 1986) and off the lee shore of Oahu (Station 19 in Gilmartin and Revelante 1974, Bienfang et al. 1984). The macrozooplankton biomass is also greater off California than in the central Pacific (Reid 1962, Owen 1974, McGowan and Williams 1973, Loeb et al. 1983, Hayward 1986) or off Hawaii (Nakamura 1967). Thus, it appears that the standing stock of potential food organisms for midwater fishes is greater by a factor of 2 to 4 or more off California. The standing stock of midwater fishes and other micronekton off California, however, is not significantly greater. Maynard et al. (1975) measured the total biomass (including the plankton component captured by their trawl) in the upper 1 200 m off the lee side of Oahu as 2.6 g wet wt m⁻² using a "10 foot" Issacs-Kidd midwater trawl. They also measured the biomasses of particular micronekton components. Using similar size gear and procedures, we found no significant difference between the two areas in the major micronekton groups (Table 3). Bailey (1984), using different gear and sampling procedures, found considerably lower biomasses in the central North Pacific Gyre than off California. His central gyre biomasses were also generally below those of Maynard et al. for Hawaii (see Table 3 of present study).

Spatial and temporal variability in food supply

The meso- and large-scale spatial variability in primary production and zooplankton biomasses off California is much greater than that in the central North Pacific (Hay-

ward 1986). However, it is not clear whether this would have much effect on midwater fishes, which may be mobile enough to find the denser patches. The seasonal and interannual temporal variability in primary production and macrozooplankton also is greater off California than in the Central Pacific by a factor of about 2 to 3 (Smith and Eppley 1982, Hayward et al. 1983, Hayward 1986). The primary production off the lee side of Oahu (Bienfang et al. 1984) has about the same degree of variability as at the more remote gyre site, and much less than off California. The zooplankton biomass off the lee of Oahu also has very low seasonal variability in macrozooplankton (15 to 30 ml 1 000 m⁻³ in the top 60 m during the day and 25 to 55 ml 1 000 m⁻³ at night, with a 0.656 mm net over 19 mo of monthly sampling; Shomura and Nakamura 1969). Thus, the fishes off California are exposed to food abundances ranging from about the same as in the central North Pacific to much greater, depending upon where and when they are feeding. The central North Pacific fishes would always have about the same amount of food available to them. Thus, mechanisms to compensate for fluctuations in food would have little adaptive value for the central North Pacific Gyre fishes. On the other hand, populations in more variable environments would, in the absence of compensatory mechanisms, be limited by the minimum food supply which they encounter. The most obvious compensatory mechanism is the storage of materials in the body during periods of abundance for use during periods of relative deprivation.

Basis of compositional differences

The observed differences in composition could be either ecophenotypic responses to different environmental conditions or evolved differences (adaptations), selected for by the different environmental conditions. The simplest explanation would be that one or some combination of the suggested factors reduces the energy and material available for growth, resulting in relatively less deposition of material. The contrasting differences of lipid and protein concentrations in fishes from the two environments argues against such a simple ecophenotypic response, since food limitation results in the utilization of both lipid and protein in fish (Love 1970, 1980). The growth rates of Hawaiian midwater fishes are similar to those of Californian fishes (Smoker and Percy 1970, Childress et al. 1980, Clarke 1974, Clarke and Wagner 1976). This would be unlikely if the observed differences are ecophenotypic responses, since reduction of energy and material availability sufficient to produce compositional changes should affect growth rates in the absence of compensating adaptations.

Therefore, the observed differences in composition are probably the result of evolved differences in the species and populations in the different regions and not ecophenotypic responses to environmental differences. Bailey and Robison (1986) also support this view. The observation that standing stocks of midwater animals are similar off Oahu and California further suggests that the compositional properties of these fishes are evolved for

the environment and not the result of phenotypic responses to limited food. The adaptive roles of lipid and protein must be considered to understand adaptation to the possible factors.

Lipid

Beyond the small amounts of lipid present in cell membranes, the primary roles of lipids in these fishes are as density-reducers and stores of energy and material. The lower lipid levels of the Hawaiian fishes indicate that these species rely more on mechanisms other than lipid (gas bladders or active swimming) to maintain their positions in the water column. The energetic consequences of this are unclear, but might result in a slight increase in metabolic energy demand, although Childress (1975) found no relationship between buoyancy and metabolic rate in midwater crustaceans. The magnitude and functions of lipid stores in marine fishes and invertebrates have been reviewed extensively by previous authors (Slobodkin and Richman 1961, Love 1970, 1980, Lee et al. 1971, Lawrence 1976, Griffiths 1977, Clarke 1983, 1988, Norrbin and Båmstedt 1984, Clarke and Holmes 1986). The reviews cited indicate that the major function of stored lipid is as a reserve of material and energy available for use during periods of increased demand (such as reproduction) or decreased ingestion (seasonal or other temporal variation in food availability). These studies do not support the concept that higher lipid stores are the result of higher food levels *per se*.

It appears, then, that lipid storage would be most strongly adaptive under conditions in which either reproductive output represents a large fraction of the fish's energy and material reserves and is discontinuous, or where the food supply is variable to the extent that energy and material are partitioned to storage to allow the fish to pass through periods of low food with little effect. Therefore, one would expect low lipid storage to be adaptive in the absence of high variability (spatial or temporal) in food supply or where discontinuous reproductive output is not a large fraction of the fish's energy and material budget. A lower level of lipid storage would allow more of the fish's resources to be put into more rapid growth in body size or more rapid achievement of maturity and reproduction. The presence of a relatively high micronekton biomass off Oahu, although primary and secondary production are apparently low, is a possible result of such an adaptation.

Of the four suggested factors affecting the adaptive value of body organic composition, we believe that water clarity is irrelevant for lipid storage. Temperature effects on lipid storage are apt to be only indirect, either through their generally inverse correlation with stability of production or through reduction of metabolic rates at lower temperatures making more energy available for other uses such as storage.

Among the possible responsible factors, food level must be considered, since primary production and zooplankton biomasses differ greatly between the central Pacific and the California sites. In addition, lipid contents

in individual fish respond to feeding intensity (Love 1980). However, the higher lipid contents found for the lower biomasses at the site away from Oahu (Bailey and Robison 1986) suggest that food availability and lipid content are not closely associated. The higher protein contents in the Hawaiian fishes show that the lower lipid contents of these fishes are not simply part of an overall reduction in the organic content or energy content. If they are related to lower food levels, they must be part of an adaptive strategy for surviving in this environment by partitioning less of the ingested food energy to lipid and more to protein. Food-supply differences cannot explain the higher protein contents of the Hawaiian fishes. On this basis, we can reject the hypothesis that the lower lipid contents result from an overall selection for lower energy content. It is possible that the low lipid contents are the result of genetically based differences in partitioning of food energy to lipid due to the selective pressure of lower food supplies in the central Pacific, but this is not consistent with the reviews cited above.

The fourth explanation, that the lipid levels are low in the Hawaiian fishes because of lack of spatial or temporal variation in food supply or energy demand is the most probable. Variability in supply would seem to be the most important, since Clarke (1984) has shown that mesopelagic fishes from off Hawaii generally have low fecundity and low gonad masses, properties which would reduce the variability in energy and material demand. A variety of evidence from many different environments indicates that variability in food supply selects for high levels of lipid storage (Slobodkin and Richman 1961, Love 1970, 1980, Lee et al. 1971, Lawrence 1976, Calow and Jennings 1977, Griffiths 1977, Clarke 1983, Norrbin and Båmstedt 1984). The higher lipid levels found seasonally in more polar pelagic species could be a necessary adaptation to the highly variable, seasonal pattern of primary production. The seasonal variation in production is much less in the central Pacific. Hayward (1986) estimated that the seasonal variation in macrozooplankton biomass is more in the California Current (factor of 3) than in the central North Pacific (factor of <1.5). He also estimates that interannual variation is much greater in the California Current (factor of 5) compared with the central North Pacific (factor of 1.5). Further, the spatial variation is also much greater off California than in the central Pacific, a factor which might also select for increased lipid storage off California. For example, Hayward estimates that the spatial variation in macrozooplankton biomass at the mesoscale has a range of 50-fold in the California Current while it varies by only a factor of 2 to 3 in the central North Pacific. Such differences in food-supply variability could select for greater lipid storage in the more variable California habitat.

The presence of significant differences in lipid content in fishes with MDO values of 500 m and greater suggests that deeper-living species also encounter spatial and temporal variation in food supply. However, because their metabolic rates are lower, the magnitude of lipid stores can be smaller than those of the shallower-living fishes. This release from the need for large energy stores may enable these deeper-living species to reach much larger

sizes for a given energy investment in growth, due to their low energy densities (Childress et al. 1980).

Protein

The protein contents of midwater fish, as Bailey and Robison (1986) and Stickney and Torres (1989) noted, are not correlated with food availability. The higher protein contents of the Hawaiian fishes indicate that these fishes are more structurally robust than those off California. At the higher water temperatures off Hawaii they should have greater muscle power (Bennett 1984), all else being equal. This would require more robust skeletal and connective tissue structure to support the use of this higher muscle power. Thus, the higher protein contents probably reflect the structural demands of higher muscle-power outputs in the shallower-living Hawaiian fishes. The adaptive value of such a difference in properties might be explained by greater water clarity and irradiance in the surface layers off Hawaii compared to California. Such a difference would presumably increase the "reactive distances" for predators and prey of particular sizes and therefore select for greater swimming abilities off Hawaii to compensate for this (Somero and Childress 1980).

If the increased water clarity and irradiance off Hawaii are important selective factors, one would predict that smaller body size, to increase reactive distances, as well as greater muscle power, to compensate for reduced reactive distances, would be adaptive. In fact, as Clarke (1973) has shown, the shallower migrating myctophids off Hawaii generally mature at much smaller sizes and reach much smaller maximum sizes than do myctophids of similar depth range off California. This is consistent with the proposed importance of visual predator-prey interactions as a selective factor in midwater environments (Childress et al. 1980, Childress and Mickel 1985, Bailey and Robison 1986, Stickney and Torres 1989, Childress and Somero 1990, Somero and Childress 1990). The absence of significant differences in protein content in fishes with MDO values of 500 m or greater, where light levels would be expected to be quite low and comparable in both regions due to bioluminescence (Cowles 1987), also supports the hypothesis that visual predator-prey interaction, or its attenuation, is the key selective factor responsible for the variation with depth in protein content as well as metabolic rates.

Comparison with fishes from the eastern Gulf of Mexico

Stickney and Torres (1989) have analyzed the proximate composition of midwater fishes from the eastern Gulf of Mexico, another tropical, low-productivity, relatively stable region. Their results are quite similar to our results off Hawaii. ANCOVA of their complete data set with our data sets from Hawaii and California (Table 4) showed no significant differences in slope among the three areas and highly significant correlations with MDO for water, ash-free dry weight, carbohydrate, lipid, protein and energy. The intercepts were also not significantly different between the Hawaiian and eastern Gulf fishes for any components. Further, when the 11 species analyzed in

Table 4. Comparison of proximate composition of fishes from off Hawaii and Southern California (present study) and eastern Gulf of Mexico (data set of 31 species from Stickney and Torres 1989). Independent variable in all cases was minimum depth of occurrence (MDO). ANCOVA was carried out on log-transformed (both dependent and independent variables) data. *P* values (*F*-test) are given for probability that there is no significant variation with depth for

all three regions combined or no significant difference among the three regions in the slopes or intercepts for relationship of each parameter with depth. In all three regions, only species with measurements of all listed components were used for tests of any of the components. Games-Howell is *post-hoc* test of significance of differences among the groups (Games and Howell 1976); differences shown correspond to $P < 0.05$

Dependent variable	<i>n</i>	Slopes	In MDO	Intercepts	Games-Howell
ln % H ₂ O	101	<i>P</i> =0.62	<i>P</i> <0.0001	<i>P</i> = 0.155	—
ln % AFDW	101	<i>P</i> =0.16	<i>P</i> <0.0001	<i>P</i> = 0.299	—
ln % CHO	101	<i>P</i> =0.71	<i>P</i> 0.0033	<i>P</i> = 0.0063	Calif. > EGulf
ln % lipid	101	<i>P</i> =0.093	<i>P</i> <0.0001	<i>P</i> = <0.0001	Calif. > Haw. = EGulf
ln % protein	101	<i>P</i> =0.21	<i>P</i> <0.0001	<i>P</i> = 0.0013	Haw. = EGulf > Calif.
ln kJ g ⁻¹	101	<i>P</i> =0.058	<i>P</i> <0.0001	<i>P</i> = 0.238	—

both studies were compared (Wilcoxon sign-rank test), there was no significant difference in water, ash-free dry weight, carbohydrate, lipid, protein or energy contents (% wet wt) between the regions. Thus, tropical, low-productivity, stable midwater habitats appear to result in the same compositions in midwater fishes whether these habitats are central oceanic regions or more limited areas. As for the Hawaii vs California comparison, the Californian fishes had higher lipid and lower protein contents than the fishes from the eastern Gulf of Mexico (Table 4). One surprising aspect of this comparison is that there was no significant difference in energy content of fishes among the three regions. This apparently results because of the increase in energy due to increased protein (5% wet wt) replacing the decrease due to reduced lipid.

Conclusion

We propose that differences in lipid and protein contents between Hawaiian and Californian midwater fishes are selected for by different factors. The lower lipid content off Hawaii is apparently allowed by the much lower levels of spatial and temporal variation in food supply there. The lipid contents of deeper-living fishes are apparently affected by this variation, but the lipid contents are reduced at greater depths because the metabolic demands are reduced. The higher protein contents in the Hawaiian fishes are probably selected for by predator-prey interactions acting over greater distances in the clearer, more strongly illuminated surface waters off Hawaii. The absence of a significant difference in protein in the deeper-living species indicates that in terms of the factor selecting for decreased protein contents in the deeper-living species, these two environments are equivalent. However, since the macrozooplankton and micronekton biomasses are higher off California and therefore presumably the food supply is higher, food availability is not the critical selective factor determining the protein contents of deeper-living fishes.

Acknowledgements. This research was supported by NSF Grants GA 33232, OCE76-10407, and OCE85-00237 to J. J. Childress. We thank T. Clarke for making the specimens available to us, identifying the specimens analyzed and advising us on the depth distribu-

tions of the fishes. We thank B. Robison, G. Cailliet and A. T. Barnes for their help in carrying out the exhausting sorting and identification involved in the oblique trawls. We thank T. Bailey, B. Robison, N. Sanders and E. Thuesen for critically reading this manuscript.

Literature cited

- Bailey, T. G. (1984). Distribution, abundance, and aspects of the life histories of midwater fishes from three regions of the eastern North Pacific. Ph. d. dissertation. University of California, Santa Barbara
- Bailey, T. G., Robison, B. H. (1986). Food availability as a selective factor on the chemical compositions of midwater fishes in the eastern North Pacific. *Mar. Biol.* 91: 131–141
- Bennett, A. L. (1984). Thermal dependence of muscle function. *Am. J. Physiol.* 247: R217–R229
- Bienfang, P. K., Szyper, J. P., Okamoto, M. Y., Nada, E. K. (1984). Temporal and spatial variability of phytoplankton in a subtropical ecosystem. *Limnol. Oceanogr.* 29: 527–539
- Brett, J. R., Groves, T. D. (1979). Physiological energetics. In Hoar, W. S., Randall, D. J. (eds.) *Fish physiology*. Vol. VIII. Academic Press, New York, p. 279–351
- Childress, J. J., Mickel, T. J. (1985). Metabolic rates of animals from the hydrothermal vents and other deep-sea habitats. *Bull. Biol. Soc. Wash.* 6: 249–260
- Childress, J. J., Nygaard, M. H. (1973). The chemical composition of midwater fishes as a function of depth of occurrence off Southern California. *Deep-Sea Res.* 20: 1093–1109
- Childress, J. J., Nygaard, M. H. (1974). Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off Southern California. *Mar. Biol.* 27: 225–238
- Childress, J. J., Price, M. H. (1978). Growth rate of the bathypelagic crustacean *Gnathopausia ingens* (Mysidacea: Lophogastridae). I. Dimensional growth and population structure. *Mar. Biol.* 50: 47–62
- Childress, J. J., Price, M. H. (1983). Growth rate of the bathypelagic crustacean *Gnathopausia ingens* (Mysidacea: Lophogastridae). II. Accumulation of material and energy. *Mar. Biol.* 76: 165–177
- Childress, J. J., Somero, G. N. (1979). Depth-related enzymatic activities in muscle, brain and heart of deep-living pelagic marine teleosts. *Mar. Biol.* 52: 273–283
- Childress, J. J., Somero, G. N. (1990). Metabolic scaling: a new perspective based on scaling of glycolytic enzyme activities. *Am. Zool.* 30: 161–163
- Childress, J. J., Taylor, S. M., Cailliet, G. M., Price, M. H. (1980). Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. *Mar. Biol.* 61: 27–40

- Clarke, A. (1983). Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanogr. mar. Biol. A. Rev.* 21: 341–453
- Clarke, A. (1988). Seasonality in the Antarctic marine environment. *Comp. Biochem. Physiol.* 90B: 461–474
- Clarke, A., Holmes, L. J. (1986). Lipid content and composition of some midwater crustaceans from the Southern Ocean. *J. exp. mar. Biol. Ecol.* 104: 31–51
- Clarke, T. A. (1973). Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fish. Bull. U.S.* 71: 401–434
- Clarke, T. A. (1974). Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. *Fish. Bull. U.S.* 72: 337–351
- Clarke, T. A. (1984). Fecundity and other aspects of reproductive effort in mesopelagic fishes from the North Central and Equatorial Pacific. *Biol. Oceanogr.* 3: 147–165
- Clarke, T. A., Wagner, P. J. (1976). Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. *Fish. Bull. U.S.* 74: 635–645
- Cowles, D. C. (1987). Factors affecting the aerobic metabolism of midwater crustaceans. Ph. D. dissertation, University of California, Santa Barbara
- Cullen, J. J., Eppley, T. W. (1981). Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance. *Oceanol. Acta* 4: 23–32
- Donnelly, J., Torres, J. J. (1988). Oxygen consumption of midwater fishes and crustaceans from the eastern Gulf of Mexico. *Mar. Biol.* 97: 483–494
- Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A., Smith, F. (1956). Colorimetric method for determination of sugars and related substances. *Analyt. Chem.* 28: 350–356
- Folch, H., Lees, M., Stanley, G. H. S. (1956). A simple method for the isolation and purification of total lipids from animal tissues. *J. biol. Chem.* 226: 497–509
- Games, P. A., Howell, J. F. (1976). Pairwise multiple comparison procedures with unequal n's and/or variances: a Monte Carlo study. *J. educ. Statist.* 1: 113–125
- Gilmartin, M., Revelante, N. (1974). The island mass effect on the phytoplankton and primary production of the Hawaiian islands. *J. exp. mar. Biol. Ecol.* 16: 181–204
- Griffiths, D. (1977). Caloric variation in Crustacea and other animals. *J. Anim. Ecol.* 46: 593–605
- Hayward, T. L. (1986). Variability in production and the role of disturbance in two pelagic ecosystems. In: Pierrot-Bults, A. C., van der Spoel, S., Zahuranec, B. J., Johnson, R. K. (eds.) *Pelagic biogeography: proceedings of an international conference*. UNESCO, Paris, p. 133–139
- Hayward, T. L., MacGowan, J. A. (1985). Spatial patterns of chlorophyll, primary production, macrozooplankton biomass and physical structure in the central North Pacific Ocean. *J. Plankton Res.* 7: 147–167
- Hayward, T. L., Venrick, E. L. (1982). Relation between surface chlorophyll, integrated chlorophyll and integrated primary production. *Mar. Biol.* 69: 247–252
- Hayward, T. L., Venrick, E. L., McGowan, J. A. (1983). Environmental heterogeneity and plankton community structure in the central North Pacific. *J. mar. Res.* 41: 711–729
- Kampa, E. M. (1970). Photoenvironment and sonic scattering. In: Farquhar, G. B. (ed.) *Proceedings of an international symposium on biological sound scattering in the ocean*. Maury Center for Ocean Science, Department of the Navy, Washington, D.C., p. 51–59
- Lawrence, J. M. (1976). Patterns of lipid storage in post-metamorphic marine invertebrates. *Am. Zool.* 16: 747–762
- Lee, R. F., Hirota, J., Barnett, A. M. (1971). Distribution and importance of wax esters in marine copepods and other zooplankton. *Deep-Sea Res.* 18: 1147–1165
- Loeb, V. J., Smith, P. E., Moser, N. G. (1983). Ichthyoplankton and zooplankton abundance patterns in the California current area, 1975. *CalCOFI Rep.* 24: 109–131
- Lowry, O. H., Roseborough, N. J., Farr, A. L., Randall, R. J. (1951). Protein measurement with the folin phenol reagent. *J. biol. Chem.* 193: 265–275
- Love, R. M. (1970). *The chemical biology of fishes*. Academic Press, New York
- Love, R. M. (1980). *The chemical biology of fishes*. Vol. 2. Advances 1968–1977. Academic Press, New York
- Maynard, S. D., Riggs, F. V., Walters, J. F. (1975). Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock and diel vertical migration. *Fish. Bull. U.S.* 73: 726–736
- McGowan, J. A. (1986). The biogeography of pelagic ecosystems. In: Pierrot-Bults, A. C., van der Spoel, S., Zahuranec, B. J., Johnson, R. K. (eds.) *Pelagic biogeography: proceedings of an international conference*. UNESCO, Paris, p. 191–200
- McGowan, J. A., Williams, P. H. (1973). Oceanic habitat differences in the North Pacific. *J. exp. mar. Biol. Ecol.* 12: 187–217
- Nakamura, E. L. (1967). Abundance and distribution of zooplankton in Hawaiian waters, 1955–56. *Spec. scient. Rep. U.S. Fish Wildl. Serv. (Fish.)* 544: 1–37
- Norrbin, F., Båmstedt, U. (1984). Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. A comparison of energetic strategies in marine organism groups. *Ophelia* 23: 47–64
- Owen, R. W., Jr. (1974). Distribution of primary production, plant pigments, and Secchi depth in the California Current region, 1969. *Calif. coop. ocean. Fish. Invest. Atlas* 20: 98–117
- Reid, J. L., Jr. (1962). On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. *Limnol. Oceanogr.* 7: 287–306
- Siebenaller, J. F., Yancey, P. H. (1984). Protein composition of white skeletal muscle from mesopelagic fishes having different water and protein contents. *Mar. Biol.* 78: 129–137
- Shomura, R. S., Nakamura, E. I. (1969). Variations in marine zooplankton from a single locality in Hawaiian waters. *Fish. Bull. U.S.* 68: 87–100
- Slobodkin, L. B., Richman, S. (1961). Calories/gm in species of animals. *Nature, Lond.* 191: p. 299
- Smith, K. L., Jr., Laver, M. B. (1981). Respiration of the bathypelagic fish *Cyclothone acclinidens*. *Mar. Biol.* 61: 261–266
- Smith, P. E., Eppley, R. W. (1982). Primary production and the anchovy population in the Southern California Bight: comparison of time series. *Limnol. Oceanogr.* 27: 1–17
- Smith, R. C., Bidigare, R. R., Prézelin, B. B., Baker, K. S., Brooks, J. M. (1987). Optical characterization of primary productivity across a coastal front. *Mar. Biol.* 96: 575–591
- Smoker, W., Percy, W. G. (1970). Growth and reproduction of the lanternfish *Stenobrachius leucopsaurus*. *J. Fish. Res. Bd Can.* 27: 1265–1275
- Sokal, R. R., Rohlf, F. J. (1981). *Biometry. The principles and practice of statistics in biological research*. 2nd ed. W. H. Freeman & Co., San Francisco
- Somero, G. N., Childress, J. J. (1980). A violation of the metabolism-size scaling paradigm: activities of glycolytic enzymes in muscle increase in larger-size fish. *Physiol. Zool.* 53: 322–337
- Somero, G. N., Childress, J. J. (1990). Scaling of ATP-supplying enzymes, myofibrillar proteins, and buffering capacity in fish muscle: relation to locomotory habit. *J. exp. Biol.* 149: 319–333
- Stickney, D. G., Torres, J. J. (1989). Proximate composition and energy content of mesopelagic fishes from the eastern Gulf of Mexico. *Mar. Biol.* 103: 13–24
- Torres, J. J., Belman, B. W., Childress, J. J. (1979). Oxygen consumption rates of midwater fishes as a function of depth of occurrence. *Deep-Sea Res.* 26A: 185–197
- Torres, J. J., Somero, G. N. (1988). Metabolism, enzymic activities and cold adaptation in Antarctic mesopelagic fishes. *Mar. Biol.* 98: 169–180
- Young, R. E., Kampa, E. M., Maynard, S. D., Mencher, F. M., Roper, C. F. E. (1980). Counterillumination and the upper depth limits of midwater animals. *Deep-Sea Res.* 27A: 671–691