Marine Biology 61, 27–40 (1980)

MARINE BIOLOGY

Patterns of Growth, Energy Utilization and Reproduction in Some Meso- and Bathypelagic Fishes off Southern California

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Abstract

We have studied growth, energy use and reproduction in 4 mesopelagic fishes and 5 bathypelagic fishes living off Southern California (USA). All of the mesopelagic species underwent diurnal vertical migrations, while none of the bathypelagic species did so. The life histories of these pelagic fishes were compared among themselves and with epipelagic sardines and anchovies studied by others. The epipelagic species had the highest growth rates (estimated from otoliths, expressed in standard length or kilocalories), the mesopelagic species had the lowest growth rates and the bathypelagic species had intermediate growth rates. The relatively rapid growth rates of the bathypelagic fishes were achieved by high relative growth efficiencies made possible by low metabolic rates. Of the species studied, the lifespans of the epipelagic and bathypelagic species ranged from 4 to 8 yr and the lifespans of mesopelagic species from 5 to 8 yr. Data on egg diameters suggest that the mesopelagic species first reproduce in their 3rd yr, while the bathypelagic species do so in their last year. Epipelagic fishes generally have a large size, rapid growth, long life and early, repeated reproduction. Mesopelagic fishes are characterized by small size, slow growth, long life and early, repeated reproduction. Bathypelagic fishes generally have large size, rapid growth, somewhat shorter lives and late reproduction, which is possibly a single event. The latter pattern is evidently feasible only in a rather stable environment where juvenile survivorship would always display relatively low variability. Many unusual characteristics of deep-living animals have possibly been selected by factors peculiar to the environment; however, such characteristics are just as likely to have been selected by factors equally present in many other environments, but not expressed there due to masking selective forces. In particular, we have in mind the darkness, stability and homogeneity of the bathypelagic realm as phenomena which represent the effective absence of many selective forces.

Introduction

The rates of physiological processes in deep-sea animals have been much studied in recent years. In general, such rates are slower in the deep-sea than elsewhere (Childress, 1969, 1971, 1975; Jannasch *et al.*, 1971; Jannasch and Wirsen, 1973; Smith and Teal, 1973; Smith and Hessler, 1974; Wirsen and Jannasch, 1976; Smith, 1978; Childress and Somero, 1979; Torres *et al.*, 1979). It has also been suggested that deep-sea animals grow slowly (Mauchline, 1972; Grassle and Sanders, 1973; Turekian *et al.*, 1975); in contrast, Childress and Nygaard (1973, 1974) have proposed that the low caloric density of some bethypelagic species could enable such animals to grow relatively rapidly. These and other adaptations to deep-sea life have often been related to the decrease in biomass with increase in depth (Vinogradov, 1968) and therefore lower food levels at greater depths.

Most of the foregoing studies cover only one part of the energy usage or a limited segment of the life history. The present study provides comparative information on 3 major parameters of life history and energy usage (growth, metabolism and reproduction) for deeper-living pelagic fishes. Our study includes 4 species of mesopelagic fishes, and 5 species of bathypelagic ones. Within each group, the species are similar in size and body shape and are generally representative of "typical" fishes within their depth range off California. All the fishes studied are similar in body shape, and none of the more radically structured species were studied.

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0025-3162/80/0061/0027/$02.80

Materials and Methods

The fishes were captured with midwater trawls from the research vessels "Alpha Helix," "Oconostota," "Velero IV," "Agassiz," and "Proteus" in basins off Southern California between 1971 and 1978. Two of the mesopelagic species (*Leuroglossus stilbius* and *Stenobrachius leucopsaurus*) were captured in the relatively shallow Santa Barbara Channel (550 m maximum depth). Two other mesopelagic species (*Triphoturus mexicanus* and *Lampanyctus ritteri* and all 5 bathypelagic species (*Poromitra crassiceps, Borostomias panamensis, Lampanyctus regalis, Bathylagus milleri,* and *Bajacalifornia burragei*) were captured in the San Clemente Basin (2000 m maximum depth). The trawls were either a 3 m Isaacs-Kidd midwater trawl (8 m^2 frontal area) or a 3.1 m Tucker Trawl (9.62 m^2 frontal area), towed at 2.5 to 3.5 knots. Such large trawls towed at moderate speeds appear to capture the largest individuals; moreover, we have also had available the largest individuals from a long period of deep trawling spread over 7 yr (a cumulative total of over 100 d). For these reasons, we believe that our largest specimens quite closely approach the maximum size for each species off Southern California. This assumption is strengthened by our largest individuals being comparable to or larger than the largest specimens reported in the literature.

Age Determinations

All ages were determined from the concentric zones or rings found in the otoliths (sagittae) of these fishes. Each translucent zone, or winter ring, was taken to correspond to 1 yr's growth (Fitch and Lavenberg, 1968; Pannella, 1974). This relationship has been shown to hold for two vertically migrating myctophids (Halliday, 1970; Smoker and Pearcy, 1970). To avoid ambiguities of interpretation, we studied only those species with distinct, alternating opaque and translucent zones. Because of the lack of sexual development in the smaller individuals of the deep-living species, we did not sex many individuals and did not keep growth data separated by sex for any of the species.

The otoliths were dissected either from freshly captured fish or from frozen specimens, immersed in anise oil, and illuminated from above against a black background; growth rings were then counted using a dissecting microscope. We examined the otoliths of the smallest specimens to find the size of the opaque core which is laid down by these fishes before the first translucent ring. Individuals with just this core or with the core and the beginning of a translucent ring were assigned an age of 0.5 yr. Fish with a completed translucent ring (opaque outer edge) were assigned an age of 1 yr. At succeeding numbers of rings, those otoliths with a partial to completed opaque ring were assigned to the fractional year group, while those with a partial to completed translucent ring were assigned to the whole year group.

We fitted various curves to the length versus age data including linear, polynomial and exponential relationships. Since our purpose in curve-fitting was to smooth the data for further use, we chose the polynomial curve with the most factors which fit the data without introducing dips and peaks into the curve.

Energy Budgets

For each species we constructed a table of standard length, wet weight and caloric content at every half year for the life of the fish. The lengths at each age were taken from the equation fitted to the length and age data, and wet weight was obtained from the wet weight-length relations (Table 1). The data for these regressions were obtained by either weighing fish brought back frozen to the laboratory or by weighing the fish at sea on a time-averaging balance (Childress and Mickel, 1980). Caloric contents were estimated from the wet weights at each age, from published proximate analysis data (Childress and Nygaard, 1973; Torres *et al.*, 1979) and caloric equivalents (kcal g^{-1}) of 5.7, 9.3 and 4.1 for protein, lipid and carbohydrate, respectively, Since we tended to analyze relatively large individuals in each species, this method tended to overestimate the caloric content of younger fish. To evaluate the magnitude of this problem, we determined the gross chemical composition of a range of sizes of the myctophid *Triphoturus mexicanus* by the methods described by Childress and Nygaard (1973); the energy budget of this species was based on this analysis (Table 2).

From the work tables mentioned earlier, the energy devoted to growth in each year was calculated by subtraction of the energy content at the end of the previous year. To estimate the metabolic energy usage on a yearly basis, wet weight at each half-year was taken to represent the entire year; moreover, we used the O_2 consumption rates from Torres *et al.* (1979) with an energy equivalent of 4.63 kcal l^{-1} O_2 (Brett and Groves, 1979). The 5 °C metabolic rates from Torres *et al.* (1979) were used for the bathypelagic nonmigrators, while the 10 °C values (intermediate between these species' day and night temperatures) were used for the mesopelagic migrators. We did not correct metabolic rate for animal size, since Torres *et al.* (1979) found no correlation of O_2 consumption with size. We have not made any correction for "lethargy" at depth (Barham, 1971) in the mesopelagic migrators, since at most it would account for only about a 15% reduction in metabolic rate on a 24 h basis (rate halved for the 8 h spent at depth). This would be a still smaller adjustment in the overall energy budget. The energy devoted to both growth and energy metabolism was also summed on a yearly basis. All further manipulations of these data were also carried out on a yearly basis. Such data are sometimes presented as a total from the whole life by summing all the yearly values. In other cases we have averaged all the yearly values to produce a lifetime average. From these tables, we extracted the

Table 1. Growth and energy usage parameters for some pelagic fishes found off southern California. The wet weight-length relationships and the length-age relationships are based on fish collected for this study ("Materials and Methods"). G = growth in calories; M = energy metabolism in calories. Details of calculations involved are given in "Materials and Methods" section. na: not asymptotic

Parameters observed or estimated	Epipelagic	Mesopelagic migrators				Bathypelagic non-migrators				
	Sardinops caerulea[d]	*Leuroglossus stilbius*	*Stenobrachius leucopsaurus*	*Triphoturus mexicanus*	*Lampanyctus ritteri*	*Poromitra crassiceps*	*Borostomias panamensis*	*Lampanyctus regalis*	*Bathylagus milleri*	*Bajacalifornia burragei*
Minimal depth of occurrence (m)[a, b]	surface	surface[a]	surface[a]	surface[a]	75[a]	400[a]	500[a]	500[a]	550[a]	1000[b]
Energy density (kcal g^{-1} wet wt)	1.40[d]	1.00[a]	1.82[a]	1.74[a]	1.76[a]	0.41[a]	0.70[a]	0.60[a]	0.60[a]	0.57[b]
O_2 consumption $\mu l\ O_2\ mg^{-1}$ wet wt h^{-1}[b]	0.3	0.095	0.070	0.067	0.059	0.011	0.017	0.011	0.011	0.005
Maximum observed length (mm)	240	118	86	72	118	148	290	198	172	198
Energy content at maximum age (kcal)[c]	252	12.4	9.6	6.3	24.9	34.0	139.3	32.8	46.0	37.5
Wet wt (g) = a (length, mm)^{B}										
a	5.42	4.78	2.21	13.10	3.17	2.60	11.40	8.72	1.24	
B	3.07	3.15	3.31	2.92	3.41	3.20	2.95	3.11	3.39	
no. of individuals	23	44	21	30	24	13	30	8	32	
Polynomial equation fitting length (y, mm) versus age (x, yr) $y = a + bx + cx^2 + dx^3$: $a\ 10^{-6}$		8.70	7.73	27.80	15.85	42.04	64.53	19.71	11.08	63.80
b		42.40	21.43	5.77	28.01	0.106	41.21	36.44	100.40	31.49
c		7.21	–1.53	3.94	–1.77	16.42		22.4		
d		0.606		–0.679		–2.17			1.94	
n		80	99	40	138	46	52	75	34	47
Von Bertalanffy growth parameters										
K	0.39	0.24	0.31	0.63	0.36	na	0.05	0.17	na	na
L^{∞}	260	178	98.1	78.9	135		1342	342		
Growth (G, kcal, lifetime sum)	252	12.4	9.6	6.3	24.9	34.0	139.3	32.8	46.0	37.5
$G\ yr^{-1}$ over lifetime	42	2.4	1.3	1.3	4.5	4.0	28.0	7.2	9.2	9.4
$G\ yr^{-1}\ g^{-1}$ wet wt over lifetime	0.98	1.38	1.70	1.39	1.80	0.35	0.81	0.84	0.43	0.60
$G\ yr^{-1}\ kcal^{-1}$ over lifetime	0.69	1.38	0.94	0.87	1.0	0.85	1.61	1.41	1.35	1.00
Energy metabolism (M, kcal, lifetime sum)	7126	41.8	56.8	21.0	72.8	88.6	229.0	29.3	73	17.9
$M + G$ (lifetime sum, kcal)	7378	53.7	66.4	27.3	97.1	122.6	368.3	62.1	119.0	55.4
$(M + G)\ yr^{-1}$ over lifetime	1224	10.7	8.8	5.3	13.1	14.4	74.0	18.7	23.8	13.4
$(M + G)\ yr^{-1}\ g^{-1}$ wet wt over lifetime	13.33	3.45	4.70	4.11	4.16	0.78	1.16	1.29	0.80	0.79
$(M + G)\ yr^{-1}\ kcal^{-1}$ over lifetime	9.6	3.45	2.60	2.49	2.44	1.90	2.06	2.30	1.68	1.40
Relative growth efficiency (lifetime), $G\ (M + G)^{-1}$	0.03	0.23	0.15	0.24	0.26	0.38	0.38	0.52	0.39	0.68

[a] Values from Childress and Nygaard (1973)
[b] Values from Torres *et al.* (1979)
[c] Energy contents corresponding to average size at maximum ages in Figs. 1, 2 and 3
[d] Values based on Lasker (1970)

summary data in Table 1 and the figures concerning energy usage (Figs. 4, 5, 6).

Our energy budgets are only partial, since the costs of reproduction, specific dynamic action, excretion, etc. are not included. The resulting error is probably not large, since growth and energy metabolism are generally the dominant components in the energy budgets of fishes. For example, Lasker (1970) estimates that only about 1% of the energy budget of the Pacific sardine *Sardinops caerulea* is devoted to reproduction. Brett and Groves (1979) estimate that growth (29%) and metabolism (44%) total 73% of the ingested energy of an average carnivorous fish. We designate the energy (in kcal) devoted to growth and metabolism as G and M, respectively. The partial energy budget is $G + M$ and relative growth efficiency is $G(G + M)^{-1}$. We believe that these energy budget values are best regarded as indices useful for comparing energy partitioning among these species or with similarly derived values for other species.

Reproductive Studies

All fishes used for reproductive studies were from the midwater fish collection at the Los Angeles County Museum of Natural History. They had been captured in the same locations as the fishes used for the age determinations and had been preserved in formalin and stored in ethanol. The mean maximum diameter of oocytes was used as an index of reproductive state (Nikolsky, 1963). For each fish, 1 ovary was dissected and at least 10 oocytes of the largest size class were measured using an ocular micrometer in a compound microscope. The measurements were then averaged to give the mean maximum oocyte diameter for each fish. Fishes examined ranged from early juveniles to the largest individuals captured.

Results

Proximate Composition of *Triphoturus mexicanus*

The composition of *Triphoturus mexicanus* does change somewhat as a function of size (Table 2). Relative protein content decreases and relative lipid content increases with increasing size. As a result, the relative energy content increases somewhat with increasing size. This indicates that the method used for estimating caloric contents of the other species tends to overestimate the caloric content of smaller individuals, since we used only analyses of larger individuals. For *T. mexicanus* this method would overestimate the caloric content of the smallest fish by about 20%. This error lessens as one approaches the larger sizes. It would cause the estimated growth efficiency to be about 6% too high for the first-year fish. Such errors are not very great in the context of the large differences observed. Further, due to the low lipid levels (Childress and Nygaard, 1973) in the deep species (*T. mexicanus* is quite high), the possible error for them is much less.

Data Analysis for Grouped Species

The subsequent data presentation will focus on 3 groups of species. Information on individual species is presented in Figs. 1, 2, 3, 4, 7 and 8 and Tables 1 and 2, but will not be extensively discussed species by species. The Pacific sardine *Sardinops caerulea* (Lasker, 1970) and the northern anchovy *Engraulis mordax* (Collins and Spratt, 1969) were chosen from the literature as species which are surface-living pelagic planktivores and constitute our epipelagic group for comparison with the deeper-living species. The next group of fishes are the mesopelagic migrators *Leuroglossus stilbius* (Bathylagidae), *Stenobrachius leucopsaurus* (Myctophidae), *Triphoturus mexicanus* (Myctophidae), and *Lampanyctus ritteri* (Myctophidae). These fishes spend the day at depths of 400 to 700 m and migrate to near the surface at night (*L. ritteri* remains somewhat deeper than the others). The final group is made up of the bathypelagic non-migratory species, *Poromitra crassiceps* (Melamphaidae), *Borostomias panamensis* (Astronesthidae), *Lampanyctus regalis* (Myctophidae), *Bathylagus milleri* (Bathylagidae) and *Bajacalifornia burragei* (Alepocephalidae). As a group these species live at depths between 400 and 1500 m and do not occur above 400 m once they have reached a length of about 50 mm. Some of them live considerably deeper than 400 m, as is indicated in Table 1.

Table 2. *Triphoturus mexicanus*, Proximate analyses in relation to length and wet weight. Results presented in form of regression equations shown in heading. Left-hand column (y) indicates dependent variable for equation values given in the other columns. a is constant, b is exponent, r is correlation coefficient, and n is number of analyses

y	$y = a$ (standard length, mm)^b			
	a	b	r	n
Wet wt (mg)	0.00221	3.310	0.981	21
Dry wt (mg)	0.000202	3.610	0.987	21
Ash-free dry wt (mg)	0.000183	3.613	0.978	21
Protein (mg)	0.000557	3.020	0.962	21
Lipid (mg)	0.000560	3.175	0.984	9
Energy content (cal)	0.00344	3.355	0.993	8
	$y = a$ (wet wt, g)^b			
Protein (mg)	0.168	0.892	0.959	21
Lipid (mg)	0.416	1.172	0.970	9

Growth Rates and Ages

The two epipelagic species *Sardinops caerulea* and *Engraulis mordax* (Fig. 1) show the fastest rates of growth early in life, but their growth slows greatly with increasing age (asymptotic growth pattern). They reach fairly large sizes and can have life spans of 6 yr or so. *S. caerulea* also has the fasted growth in caloric content (x symbols in Fig. 4; Table 1, G yr^{-1}) and reaches the highest caloric content (Table 1, G).

The bathypelagic species have the next highest rates of growth (Figs. 1–3). Their growth curves are linear (constant rate of growth) or, for *Poromitra crassiceps*, exponential (constant percentage growth). They never show clear asymptotic growth, and they grow almost as large as the epipelagic species and much larger than vertical migrators. The bathypelagic species apparently grow as old as fishes in the other two groups. The rates of growth in calories and maximum caloric contents (Fig. 4, Table 1) are lower for bathypelagic fishes than for *Sardinops caerulea*, but are considerably higher than those of the mesopelagic migrators. It is especially notable that the deepest living of the mesopelagic migrators, *Lampanyctus ritteri*, also shows the highest growth rate and greatest accumulation of calories within its group. Further, its very similar congener, *L. regalis*, which lives deeper and grows much larger, has a caloric growth curve almost identical to that of

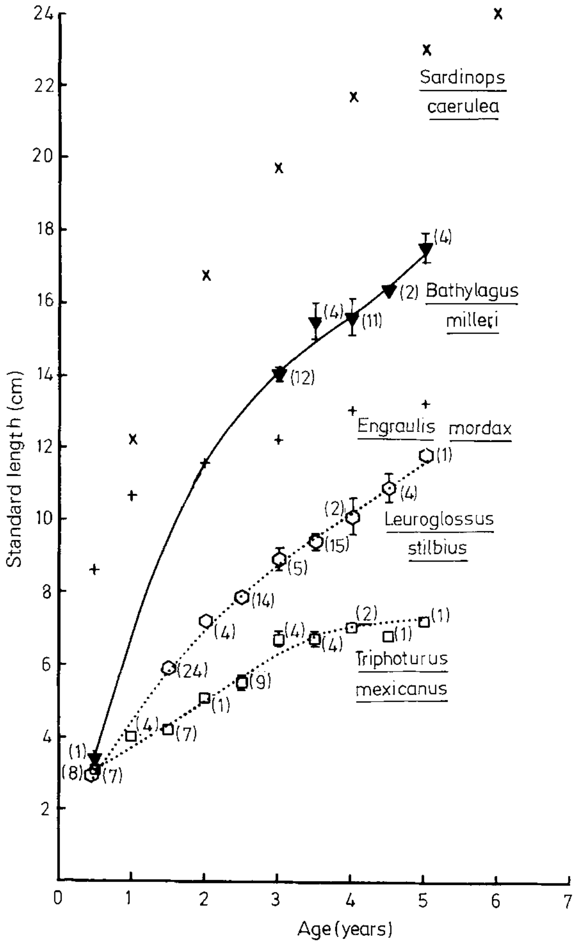

Fig. 1. Growth curves for 5 species of pelagic fishes off Southern California: the epipelagic species *Sardinops caerulea*, Lasker, 1970 and *Engraulis mordax*, Collins and Spratt, 1969; the mesopelagic migrators *Leuroglossus stilbius* and *Triphoturus mexicanus*; the bathypelagic *Bathylagus milleri*. Error bars indicate standard errors of the means, and numbers in parentheses are numbers of otoliths assigned to a given age. The bathypelagic species (minimum depth of occurrence > 400 m, Table 1), in this Fig. as well as Figs. 2 through 6 are represented by filled symbols and continuous lines. The mesopelagic migrators are indicated by open symbols and dashed lines in Figs. 1–6

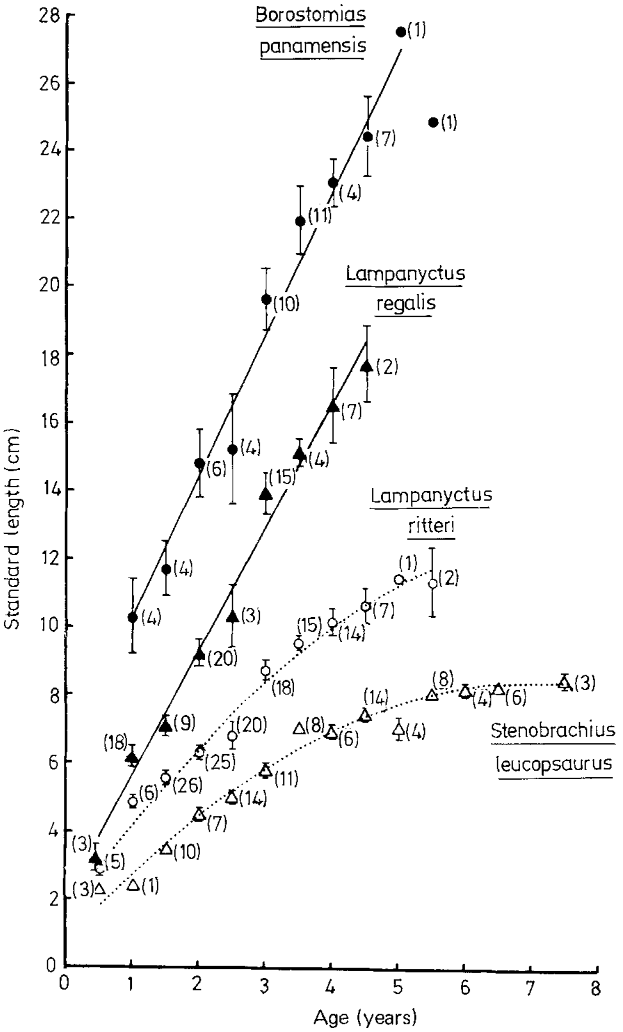

Fig. 2. Growth curves for 4 species of pelagic fishes off Southern California: *Stenobrachius leucopsaurus* and *Lampanyctus ritteri*, both mesopelagic migrators; *Borostomias panamensis* and *Lampanyctus regalis*, both bathypelagic species. Error bars represent standard errors of the means, and numbers in parentheses are numbers of otoliths assigned to a given age

L. ritteri up to its third year. This apparent paradox is possible because the caloric density of *L. ritteri* (like the other mesopelagic migrators) is almost 3 times that of its deeper-living congener. *P. crassiceps* (Figs. 3, 4) differs somewhat from the general characteristics of the bathypelagic species because it has a very low initial rate of growth and subsequently grows exponentially. In spite of its low initial growth, *P. crassiceps* achieves the highest growth rate of any of these fishes during the second half of its life. It also reaches a relatively large size and caloric content (Table 1). The only comparable published growth rate for a deep-living species is Clarke's (1974) estimate that the stomiatoid *Chauliodus sloani* grows to 70 to 100 mm in 1 yr. This rapid growth is about the same as that for the stomiatoid *Borostomias panamensis* shown in this study.

The mesopelagic migrators have the lowest growth rates and the smallest maximum sizes, while they live as long as the deeper species (Figs. 1 and 2). The vertical migrators' growth curves generally approach an asymptote rather quickly. The rates of growth in energy content (Fig. 4) are also lower in these species than in the others studied. Our data on the growth in length of *Stenobrachius leucopsaurus* agree closely with Fast (1960)

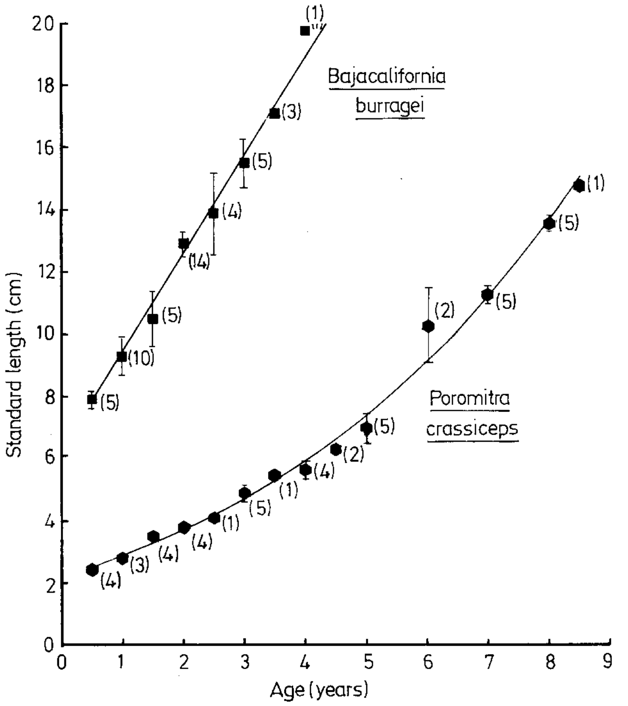

Fig. 3. Growth curves for 2 bathypelagic fish species, *Poromitra crassiceps* and *Bajacalifornia burragei*. Error bars represent standard errors of the means, and numbers in parentheses are numbers of otoliths assigned to a given age

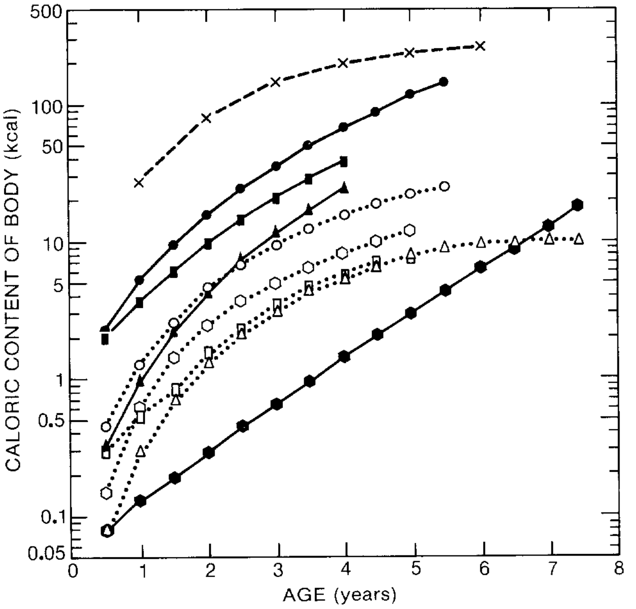

Fig. 4. Caloric growth curves of the pelagic fishes shown in Figs. 1–3 (energy conversions from Table 1). All symbols and lines as in Figs. 1–3. The epipelagic *Sardinops caerulea* is represented by x symbols and a dashed line. The mesopelagic migrators are represented by open symbols and dotted lines (*Leuroglossus stilbius*, open hexagons; *Triphoturus mexicanus*, open squares; *Stenobrachius leucopsaurus*, open triangles; *Lampanyctus ritteri*, open circles. The bathypelagic species are represented by filled symbols and continuous lines (*Poromitra crassiceps*, filled hexagons; *Borostomias panamensis*, filled circles; *Lampanyctus regalis*; filled triangles; *Bajacalifornia burragei*, filled squares)

for this species off central California and Smoker and Pearcy (1970) off Oregon for the same species, thus supporting the validity of our otolith reading and assumptions relating otolith zones and age in midwater fishes.

Standardized Growth Rates

The mesopelagic migrators, in comparison to the other two groups, have the lowest absolute growth rates; when caloric growth rates are standardized to wet weight (G yr^{-1} g^{-1} wet wt, Table 1) however, they have the highest weight-specific rate of calory accumulation, since their caloric densities are relatively high. Evidently, these migratory fishes are giving priority to energy storage (high lipid levels, Childress and Nygaard, 1973) over growth in size, while the bathypelagic fishes are giving priority to increase in size.

When caloric growth rates are standardized to energy content (G yr^{-1} kcal^{-1}, Table 1), all 3 groups accumulate energy relative to their body energy at roughly comparable rates. This suggests that all the fishes studied devote about the same relative amount of energy to growth, independent of body mass or particular composition. Therefore, the differences in absolute growth rates and weight-standardized growth rates apparently represent different, evolved strategies for using resources.

Energy Budgets

The lifetime totals of energy used for growth, energy metabolism and their sums are highest for the epipelagic *Sardinops caerulea* and comparatively lower for the bathypelagic species. In comparison to bathypelagic fishes, the mesopelagic migrators clearly devote less total energy to growth, however the migrators use only slightly less total energy for energy metabolism and for the sum of energy metabolism and growth. The interpretation of these data is complicated by the different sizes of the fishes studied; however, it appears that bathypelagic fishes conserve less energy than mesopelagic migrators, while bot these groups conserve much more energy than epipelagic species.

When the partial energy budget is standardized to wet weight [$(G + M)$ yr^{-1} g^{-1}], a different picture emerges (Fig. 5, Table 1). The epipelagic species, with its high rate of metabolism, uses the most energy per unit of mass. The mesopelagic migrators are next in level of usage due to their high caloric density and moderate metabolic rates. The bathypelagic species use the least weight-specific energy as a consequence of low caloric densities and low metabolic rates. These results indicate that the epipelagic species are giving priority to large mass (high overall energy used for growth), robust musculature and high activity (high energy metabolism) and energy storage (high caloric density). The mesopelagic migrators on the other hand appear to be giving priority to activity and energy storage at the expense

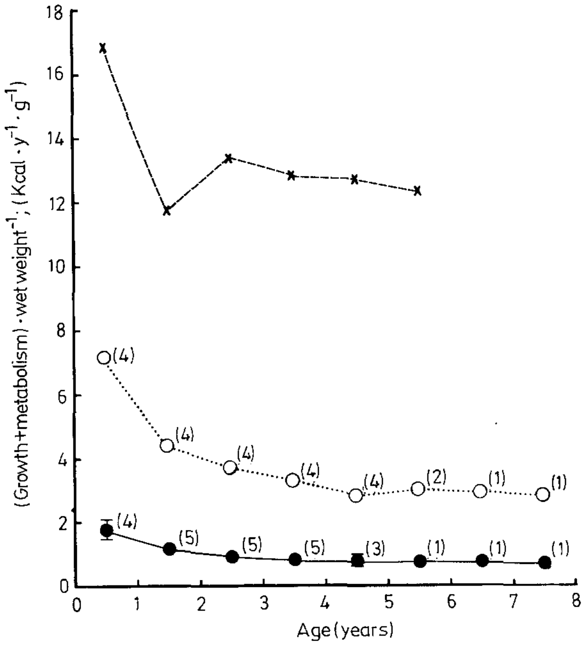

Fig. 5. Weight-specific energy usage for pelagic fishes shown in Figs. 1–3. x: California sardine; open circles: mesopelagic migrators; filled circles: bathypelagic species. Error bars represent standard errors of the means, and numbers in parentheses are number of species averaged

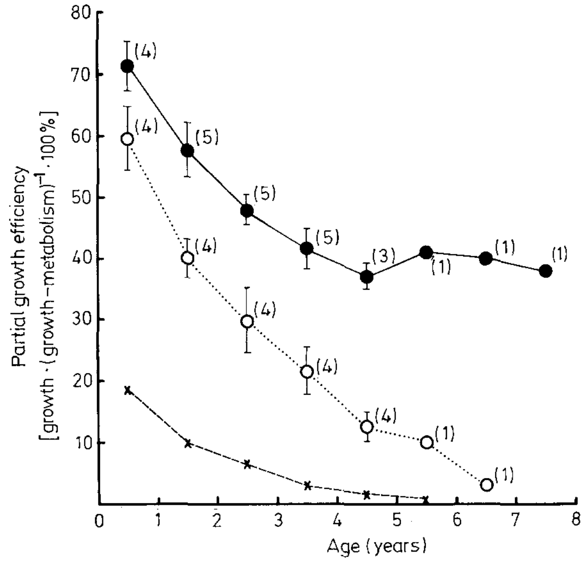

Fig. 6. Relative growth efficiencies of pelagic fishes shown in Figs. 1–3. x: California sardine; open circles: mesopelagic migrators; filled circles: bathypelagic species

of growth in mass. The bathypelagic species use the contrasting strategy of giving priority to growth in mass over energy storage and activity. The energy-specific partial energy budgets show the same general pattern [Table 1, $(G+M)$ yr^{-1} kcal^{-1}]. The epipelagic sardine uses much more energy than the mesopelagic migrators, which in turn use more energy than the bathypelagic species.

The partitioning of energy between growth and energy metabolism indicates the energetic priorities of these fish groups (Fig. 6; Table 1, "relative growth efficiency"). In all 3 groups the fraction of the energy devoted to growth declines with age. The epipelagic sardine and mesopelagic migrators display a dramatic decline in growth efficiency with increasing age so that little energy is used for growth near the end of life. The bathypelagic species have the highest relative growth efficiencies and channel much of their energy into growth throughout their lives. These high relative growth efficiencies in the bathypelagic species indicate once again the high priority given to growth within these species' life histories.

Reproduction

The mesopelagic *Leuroglossus stilbius, Stenobrachius leucopsaurus* and *Lampanyctus ritteri* evidently mature sexually during their third year (Fig. 7) and continue reproducing throughout the rest of their lives, which agrees with previous work on *S. leucopsaurus* by Pearcy (1970). Our mean maximum oocyte sizes for *S. leucopsaurus* are comparable to values reported by Smoker and Pearcy (1970) for mature oocytes. It is possible that we did not observe mature oocytes in *L. ritteri* or *L. regalis,* since the sizes observed are somewhat smaller than those of mature oocytes in a variety of myctophids (0.55 to 0.84 mm, Karnella and Gibbs, 1977; Robertson, 1977).

All the bathypelagic species examined appear to defer sexual maturation until late in their lives. Four species had large oocytes only in their last year of life (Fig. 7), although *Bathylagus milleri* had large oocytes in its last 2 yr of life. Deferral of reproduction to the last year of life suggests that these fishes may reproduce only once (semelparity), a pattern already documented for the bathypelagic mysid *Gnathophausia ingens* by Childress and Price (1978).

In addition to oocyte sizes, Fig. 7 shows the numbers of individuals with minute, undeveloped gonads. In the bathypelagic species, individuals up to about one-half the maximum age typically have minute, threadlike gonads and only the very largest individuals possess gonads with mature oocytes. This pattern is most extreme in *Poromitra crassiceps,* which shows virtually no development of ovaries until about the seventh year (100 mm standard length) and evidently has mature oocytes only in the ninth year (>140 mm standard length, SL). In agreement with these observations, Clarke and Wagner (1976) found no specimens of *P. crassiceps* with mature oocytes in collections from off Hawaii, even though the largest specimen was 130 mm SL. The same authors described mature eggs from only their largest specimens of the alepocephalid *Photostylus pyncopterus.* Similarly, Clarke (1974) found mature oocytes only in the largest individual of the astronesthid

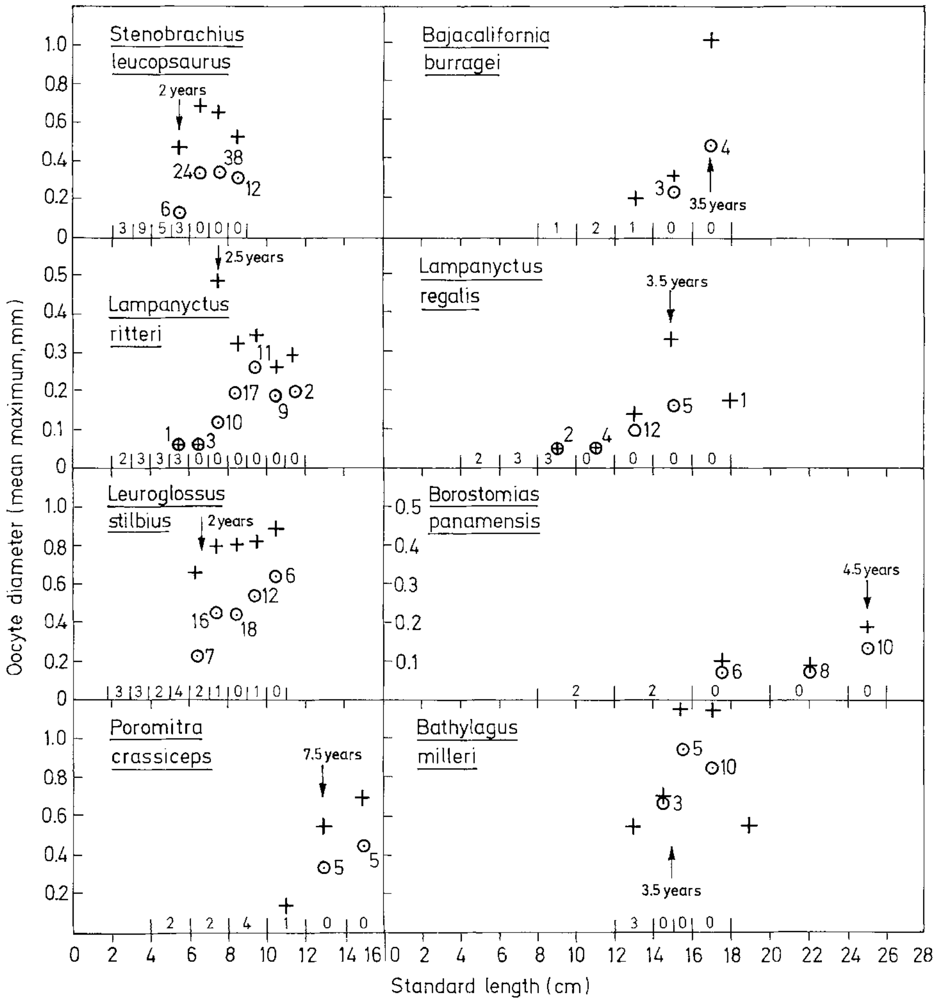

Fig. 7. Oocythe diameter (mean diameter of largest size class of eggs present in a given ovary) as a function of standard length for 3 mesopelagic fishes (*Stenobrachius leucopsaurus, Lampanyctus ritteri and Leuroglossus stilbius)* and 5 bathypelagic fishes. All data are presented in terms of the intervals indicated by the x-axis marks (nos. between x-marks indicate no. of individuals with minute gonads, not examined for oocyte development). Circles are mean maximum oocyte diameters (number of fishes making up the means is shown near the circle). Cross indicates the single largest oocyte diameter (mean maximum diameter) for individuals (within the indicated intervals) examined which had minute threadlike gonads (obviously not near maturity)

Astronesthes indicus (estimated age of 3 to 4 yr), and only in the largest individuals of the chauliodontid *Chauliodus sloani*. Such observations, along with ours, suggest that larger bathypelagic fishes in general tend to defer reproduction until very late in their lives.

Two of the mesopelagic fishes, *Leuroglossus stilbius* and *Stenobrachius leucopsaurus* appear to spawn in the winter and spring (Fig. 8). This is in agreement with Smoker and Pearcy (1970), who report December to March as the spawning season for *S. leucopsaurus* off Oregon. The limited data for *Lampanyctus ritteri* give no evidence of seasonality, and those for *Bathylagus milleri* weakly suggest summer spawning.

Discussion

Difficulties Encountered in Presenting Life-Cycle Data

The data in this paper could have been presented in many different ways and we have explored a variety of them; however, it was difficult to interpret the patterns and rates of growth, especially in relation to sizes of the organisms. Our first problem was that, while much attention has previously been given to the ecological importance of organism size, virtually all such work has been done on organisms which spend much of their lives at or near a maximal size. Bathypelagic fishes apparently do not have this kind of growth pattern and, as a result; cannot be considered to have any characteristic size. In additon, because of the wide variation in proximate compositon of these species (Childress and Nygaard, 1973), growth in size can differ markedly from growth in energy in these fishes.

We deal with these problems by treating the data in the following ways. The first treatment is to calculate the absolute size, energy content or energy usage over a lifetime or a period within a lifetime. In this form, the data give some idea of the differences in size of the different species. However, since such data vary widely even for fishes within a single shallow environment, their significance is probably more closely tied to the size-specific ecological strategy of a particular species than to the general characteristics of the habitat. The remaining 3 treatments of the data are intended to get away from the size-specificity resulting from the conspicuous differences in the sizes from one group to the next, so that underlying differences in energetic strategies

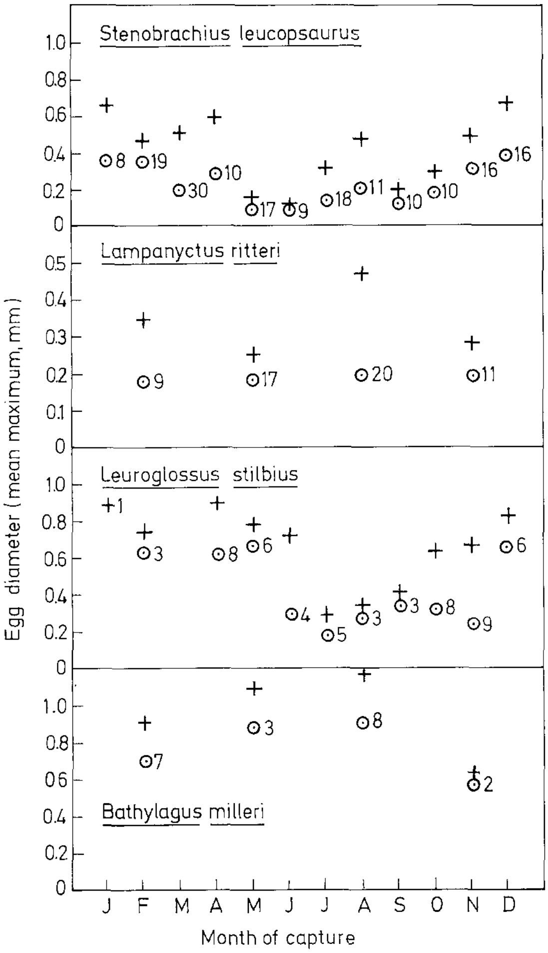

Fig. 8. Oocyte diameter (mean diameter of largest size class of eggs present in a given ovary) as a function of month of year for 4 species from Fig. 7. Circles are mean values for each month of quarter, depending on the species, and crosses represent highest individual mean maximum. Numbers beside symbols indicate numbers of individuals whose eggs were measured

may be examined. The second treatment is to calculate the ratio of energy for growth relative to that for growth plus metabolism. This ratio is independent of size and allows one to compare metabolic priorities of different ages and species. The third treatment is to standardize the energy used for growth to the wet weight of the fish to demonstrate the relative costs of producing and operating bodies of different sizes, shapes, etc. (We used wet weights instead of dry ones, since some ecological parameters such as predator-prey interaction are determined by the live size of the animal, and wet weight standardization gives an index of the costs per unit of live size.) the fourth treatment is to express the energy usage relative to the caloric content of the body; This relation is relatively independent of body size or composition.

Several examples may help clarify important differences between wet weight and caloric standardization. If the first of two fish has a high numeric value for caloric growth standardized against caloric content, then the first is accumulating energy faster. On the other hand, if the first of two fish has a relatively high value for caloric growth standardized against wet weight, the first is accumulating energy more rapidly than the second relative to its size; however, depending on the relative compositions of the two fish, the first might actually be growing more slowly in size or caloric content than the second.

Our interpretation of otolith rings as annuli may properly be questioned in light of the conventional description of the deep ocean as stable. However, there is considerable evidence of seasonal fluctuations of micronekton biomass (Legand, 1969; Blackburn *et al.*, 1970; Tranter, 1973; Brown, 1974) as well as populations (Legand *et al.*, 1970; Pearcy, 1970; Clarke, 1973, 1974). One would expect these seasonal fluctuations to be reflected in the nutritional status of the longer-lived deeper, predatory species such as those considered here. Studies in our laboratory have indicated that the bathypelagic mysid *Gnathophausia ingens* has clear seasonal differences in nutritional status (caloric density) off California (own unpublished observations). Since such fluctuations produce annual otolith rings in shallow-living fishes, our interpretation of the perceived rings as annuli seems reasonable. This is further supported, since spawning is the only other phenomenon which is likely to have a sufficiently major effect on a deep-living fish as to affect its otolith growth, yet, as shown below, the smaller individuals of deeper-living species do not spawn but do have translucent otolith rings. None of the species studied here have the greatly distensible stomachs characteristic of some deep-sea fishes (*Chiasmodon* sp., *Eurypharynx* sp., and angler fishes) and therefore cannot take gigantic meals which might affect the otolith patterns.

Estimated Rations for Midwater Fishes

One can evaluate the validity of the proposed energy budgets by estimating the required rations which correspond to them. Averaged by years across the fish's whole lifetime the epipelagic sardine would require 2.7% d^{-1} of its body energy, the mesopelagic migrators 0.65% d^{-1} and the bathypelagic species 0.50% d^{-1} for their growth and metabolism. If we correct these to food ingested using Brett and Groves' (1979) average of 73% of the ration being equal to metabolism plus growth, the sardine requires 3.6% d^{-1}, the mesopelagic migrators 0.87% d^{-1} and the bathypelagic species 0.68% d^{-1}. These appear to be generally reasonable estimates, although the mesopelagic migrators and bathypelagic species have relatively low rates of energy usage.

Some of our values can be compared with those estimated by Clarke (1978) from stomach contents. His value for the vertically migrating myctophid *Hygophum proximum* (18 to 46 mm SL) is 5.7% dry wt d^{-1}. Since the zooplankton prey of these species may have lower caloric densities than the fishes themselves by a factor of about 2 (Childress and Nygaard, 1974), the percentage dry wt d^{-1} for the California mesopelagic migrators should be about 1.7%. These estimates can be brought closer by taking into account the higher night temperatures and smaller average size (30 mm) for *H. proximum* compared to the California migrators. If we use only the first-year data for the California migrators (28 mm average length) and double the estimated energy into metabolism (to correct for temperature) as well as correct for the differences in caloric density and fraction of the rations, we arrive at a value of 5% dry wt d^{-1} for the California migrators. Considering how crude these estimates are, this is rather good agreement between Clarke's method, and our own.

Clarke (1978) also estimated the rations of a non-migratory deeper-living species, *Danophos oculatus* (27 to 49 mm SL, 450 to 650 mm depth), as 1.9% dry wt d^{-1}. This agrees with the overall trend in our data that deeper living species need less energy. This value is somewhat greater than the 0.68% cal d^{-1} estimated for the bathypelagic species, but if we consider only the first year for the deep species (average SL = 52 mm) the estimated rations are 1.1% cal d^{-1}. Further, if *D. oculatus* is like the other sternoptychids which we have examined, it probably has a higher caloric density than most deeper-living fishes (Childress and Nygaard, 1973) as well as a higher metabolic rate (Childress and Somero, 1979). These factors should bring these estimates closer, again giving reasonable agreement between the two methods.

Comparison of Life Histories

The apparently rapid growth rates of deeper-living fishes in this study are at odds with the traditional belief in slow growth rates in deep-sea animals (Mauchline, 1972; Grassle and Sanders, 1973; Turekian *et al.*, 1975). Our bathypelagic fishes apparently live relatively short lives, become fairly large, and use moderate amounts of energy for their growth and metabolism. Our findings require a reevaluation of ideas about the rates of processes at depth and the factors selecting for such rates. We will first examine the growth rates and how they are achieved, and then the more general issues raised.

We found rather similar growth rates (length and mass) for the epipelagic and bathypelagic species (Figs. 1–3), indicating that the latter grow at relatively rapid rates. In comparison, the mesopelagic vertical migrators have much lower rates of growth in length and mass. Further, the bathypelagic species apparently use more energy over their lives for both growth and metabolism than do the mesopelagic migrators, and both use much less than a typical epipelagic fish, the Pacific sardine. In both the mesopelagic migrators and the bathypelagic group, the major saving is in their lower metabolic rates compared to the epipelagic sardine (Table 1). Some energy is also saved by the low growth rates of the mesopelagic migrators, and the low caloric densities of the bathypelagic species (Table 1). This energetic strategy of bathypelagic fishes permits rapid growth to large size and maintenance of the body at a low energetic cost relative to size (Table 1, Fig. 5).

As a rule, when fishes approach maturity they typically reduce the energy devoted to growth as they increase that devoted to gonadal development (Iles, 1974). This results in a rapid decline in growth efficiency with a resulting decline in growth rate as maturity is approached (for example, compare Figs. 1, 2, 3, and 7 to see the relations of sexual maturity, growth and growth efficiency). As less energy is devoted to growth at approaching maturity, the growth curves become asymptotic. In contrast, the bathypelagic species appear to free more resources for growth by deferring reproductive maturity and the corresponding changes in growth efficiency and pattern until the ends of their lives. Such fishes thus maintain a faster growth rate with a non-asymptotic growth curve, achieving a given size faster for a given energy input and also decreasing the energetic cost to reach a given size.

The life-history pattern of bathypelagic fishes is not, however, an energy-conserving strategy, because large size itself has appreciable costs due to the proportionality of metabolism and size. For example, if *Bajacalifornia burragei* with its metabolic rate, caloric density and lifespan, were to grow no larger than the mesopelagic *Triphoturus mexicanus,* it would require only about 6% of the energy which it uses. It is difficult to conceive that the growth patterns of the deep species have been primarily selected by factors related to energy limitation, since these species could save so much more energy by being smaller. This point is further emphasized by marked similarities in the energy-specific, energy growth rates of these species (G yr^{-1} $kcal^{-1}$; Table 1). Therefore the bathypelagic species do not seem to conserve energy in their growth patterns either with respect to total calories accumulated or to rate of caloric growth. Instead, physiological priorities of these fishes appear to have been selected to produce the maximum size for a given input of energy. Evolutionarily, bathypelagic fishes appear to have responded to this selection by (1) maintaining the energy devoted to growth at a relatively high level, but greatly reducing the caloric density and thus achieving much greater body sizes for a given caloric input; (2) greatly reducing their metabolic rates and thereby increasing their growth efficiencies; and (3) deferring reproduction until near the end of their lives, thus allowing higher growth efficiencies later in their lives. These factors emphasize the importance of size, and not energy conservation as the parameter primarily selected for in the life histories of the bathypelagic species.

In considering size, one should bear in mind that such species are relatively large for much of their lives; however, due to their non-asymptotic growth patterns, they have no characteristic sizes and they are at their maximum sizes for only brief periods at the ends of their lives. The attainment of maximum size and reproduction only near the end of life may well explain the common observation that trawls capture very few specimens of deeper-living midwater fishes that are of maximum size and sexually mature (Clarke, 1973; Clarke and Wagner, 1976). The foregoing authors have attributed this pattern to net avoidance, but our data suggest that these mature individuals are so short-lived once they reach maximum size that they constitute only a small fraction of the population at any given time.

Dominant hypotheses for factors selecting for large size in bathypelagic animals involve either advantages of large size in predator-prey interactions (Mauchline, 1972), or the disproportionately greater fecundity per individual and energy investment per offspring possible for larger individuals (Childress and Price, 1978). However, these ecological questions cannot be addressed so directly as the main concern of this paper, i.e., the physiological priorities of energy usage in midwater species.

The mesopelagic migrators display a very different pattern of growth and reproduction in comparison to the other fishes studied. The migrators use energy at a lower rate than the epipelagic sardine, largely because of their smaller sizes (lower total energy metabolism) and slower growth rates. They show no other shifts in their physiology or composition to achieve lower energy usage. In essence, they appear to be smaller, slower growing surface fishes which spend their nights at depth. Much has previously been made in the literature of the supposed energetic benefits of vertical migration (McLaren, 1963; Enright, 1977). On both a weight-specific and a calorie-specific basis, the migrators, as compared to the deeper species, use more energy per unit of body, suggesting that spending the night in the surface layers may allow the migrators to capture more food per unit of body than if they remained at depth. However, with reference to the "energy bonus" of downward migration, the migrators fare less well than the sardine by virtually all the energetic criteria except weight- and calorie-specific caloric growth. The higher values for the latter result from differences in the shapes of the growth curves over the fishes' whole lives as well as differences in caloric density. Therefore, these values do not indicate any energy benefit for the vertical migrators, since their growth rates are much less than those of the sardine during the early phase of its life when it is actively growing.

The ideal test for the "energy bonus" of downward migration would be to compare the energy usage of an epipelagic species and a mesopelagic migrator, each of which reaches a particular size in the same amount of time and commences reproduction at the same age. We do not know of any such pair of species for comparison and, therefore, suggest that selection has resulted in the evolution of different life histories in these two groups. This makes energetic comparisons complex; however, it appears to us that our data do not support the existence of an energy bonus of downward migration and do suggest that the migrators are at an energetic disadvantage compared to the epipelagic species. However, we are reluctant to accept this conclusion, because the vertical migrators are smaller than the fishes living above or below them and, therefore, much of their pattern of energy usage is probably determined by the factors selecting for small size in this group.

Life-History Strategies of Midwater Fishes

Consideration of the life-history strategies of midwater fishes may place the patterns of energy usage in better perspective. Data on the life history of the Pacific sardine *Sardinops caerulea* have been published previously (Murphy, 1968; Lasker, 1970). Murphy suggested that long life and repeated reproduction is an adaptation to the highly variable survival of the immature sardines. The mesopelagic migrators off California show life histories which are similar to the Pacific sardine. As in the sardine, their later reproduction results in a lower rate of population increase (r). This pattern of relatively low reproductive effort with "bet-hedging" can be selected either by high and relatively predictable adult survival or by low and unpredictably variable juvenile survival (Warner, in press). The latter possibility seems the most likely for shallow-living populations in the relatively unstable Southern California borderland. In contrast, there is now evidence that the dominant mesopelagic migrators in the tropics are much smaller than those in temperate regions and apparently live only 1 yr, reproducing at the end of it (Clarke, 1973; Karnella and Gibbs, 1977; Mauchline, 1977). Clarke's data show that these tropical migrators grow to about 30 to 40 mm in 1 yr, about the same growth rate as the larger mesopelagic migrators off California have in their first year. The selective advantage of early reproduction is evidently derived from a higher rate of population increase (r), which is sensitive to generation time (Cole, 1954; Lewontin, 1965; Meats, 1971). This pattern of early maturity and short life is also found in tropical clupeoids (Murphy, 1968) and has been attributed to a lowered variability of juvenile survival in the stable tropics.

The life histories of the bathypelagic species are quite different from the shallower species. Age at first reproduction is delayed to an extreme degree in these species. Mertz (1971) and Hirschfield and Tinkle (1975) have pointed out that in stationary populations there is no selective advantage in the early production of young. Childress and Price (1978) have suggested that long deferred reproduction in the bathypelagic mysid *Gnathophausia ingens* allows individuals to maximize their contribution of offspring to the next generation through the development of large body size in the parent. The limit to this strategy is the increased probability of mortality with increasing age of the parent. Female specimens of *G. ingens* off California reproduce only once before dying. This lack of "bet-hedging" may reflect the relative stability of greater depths and the isolation from many of the surface fluctuations which apparently select for iteroparous reproduction among surface-living fishes in the same region. The deep-living fishes appear to follow a pattern similar to that of *G. ingens*, and presumably the selective factors are the same.

An Hypothesis for Energy Usage Adaptations of Deep-Sea Animals

One of the important reasons for doing the present research was to identify the selective values of the low metabolic rates and low caloric densities of deep-living fishes. The results reported are complex and, in our opinion, do not readily fit any one consistent picture of selection for conservation of energy in deep-sea animals. This has led us to reevaluate the problem in the following manner. It is generally accepted that, at carnivorous trophic levels, aquatic animal communities are usually limited by energy. There is evidence supporting this conclusion for oceanic animals living down to considerable depths (Vinogradov, 1968; Blackburn, 1973, 1977; Rowe *et al.*, 1974; Reid, 1977). Therefore, populations of many species, shallow as well as deep-living, are probably also limited by energy. As a consequence, food limitation alone cannot be responsible for selecting the various adaptations of deeper-living animals. This point is supported by the similarity in biomass of surface zooplankton in low-productivity oceanic areas and of zooplankton at 1000 m in productive areas (Vinogradov, 1968). However, the animals at the surface in the low-productivity areas are surface types of animals and do not possess obvious deep-sea-type adaptations. Therefore, energy limitation alone is not a sufficient selective factor to explain the evolution of the lower metabolic rates, reduced structure, and other characteristics of deep-sea animals.

We suggest that the evolution of the distinctive energy-conserving characteristics of these animals has come about not through selection by a greater degree of resource limitation in the deep sea but rather through a diminution with depth of selective forces which run counter to energy conservation. This diminution has allowed the evolution of energy-conserving characteristics at greater depths. This is supported by our earlier observation that the bathypelagic species have features such as their size which are not energy conserving and therefore indicate the existence of strong selective forces acting counter to selection for energy conservation even at greater depths. However, the dramatic modifications and reductions of the bodies of the bathypelagic species provide substantial evidence of the great reduction of these counter-selective forces at greater depths.

Recent studies (Childress, 1975; Childress and Somero, 1979; Somero and Childress, 1980) have suggested that the lower metabolic rates of deeper-living animals are a result of greatly reduced locomotory abilities in these animals. Evidently, the critical selective factor(s) is not energy conservation but selection for well-developed locomotion in species which live near the surface and the relative weakness and progressive diminution of such selective pressure at greater depths. The following factors might select for locomotory abilities and decrease progressively with depth: visual predation, water turbulence and whatever selects for vertical and horizontal migrations. If one were to find an animal occupying a niche in the deep sea which required high locomotory abilities, one would expect it to have a correspondingly high metabolic rate. In other words, patterns of structural and metabolic reduction with depth in pelagic animals are made possible by the diminution with depth of selective factors which are strongest at the surface, and these selective factors have little to do with energy supply *per se*, but rather with the locomotory abilities of the organisms. This hypothesis can be tested, since it leads to predictions that the structural properties and metabolic rates of oceanic animals should vary as a function of depth and other physical factors as well as habits, but not as a function of food availability given comparable animals.

Acknowledgements. This research was supported by NSF Grants GB 18929, GA 33232, OCE76-10407 and OCE78-08933 to J. J. Childress. The fishes were captured on NSF-funded cruises of the research vessels "Alpha Helix," "Oconostota," Velero IV, "Agassiz," and "Proteus" between 1971 and 1978. We thank J. Fitch for advising us on the aging of the otoliths. We also thank R. Lavenberg for making available preserved fishes from the Los Angeles County Museum. The original manuscript was greatly improved by the critical reading of B. Robison, R. Carney, K. Smith, R. Warner, and T. Mickel. J. J. Childress appreciates the patience which R. Carney has shown in listening to his ideas.

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Date of final manuscript acceptance: September 5, 1980.
Communicated by N.D. Holland, La Jolla