

Respiration and chemical composition of the bathypelagic euphausiid *Bentheuphausia amblyops*

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Abstract

Bentheuphausia amblyops is a cosmopolitan bathypelagic euphausiid with a vertical range of from 280 to 7 000 m. Determinations of proximate and elemental composition show that *B. amblyops* has a more robust structure (lower water content and higher protein content) than is typical of other bathypelagic Crustacea. *B. amblyops* is a strong swimmer and is capable of employing its thoracic legs in raptorial fashion. Discrete depth trawls taken between depths of 400 and 2 500 m on a diel basis show no evidence of vertical migration. There was no significant difference in oxygen consumption within the species environmental temperature range (1.5° to 7.5 °C), which may be partially ascribed to a limited temperature effect and partially to variability in spontaneous activity at the different temperatures. Between 7.5° and 9.5 °C there was a marked temperature effect on metabolism ($Q_{10}=6.4$). The observed vertical distribution and metabolic response to elevated temperature preclude the migrations to the surface that have been postulated for *B. amblyops*. The robust composition of the species, its behavioral characteristics, and published diet information strongly suggest that the species is omnivorous with a strong predatory component in its foraging strategy.

Introduction

Bentheuphausia amblyops is a ubiquitous bathypelagic euphausiid found between Lat. 50°N and 50°S in all major ocean basins with sill depths greater than 1 000 m (Brinton, 1962, 1975; Mauchline and Fisher, 1969; Mauchline 1980). It occurs at depths as great as 7 000 m and is the most important component of the euphausiid biomass between depths of 2 000 and 4 000 m (Vinogradov, 1970). Euphausiids comprise up to 13% of the total planktonic biomass at those depths (Vinogradov, 1970).

B. amblyops (2.5 to 5 cm as adults) is recognized by Brinton (1962), Nemoto (1967), and Vinogradov (1970) as one of four truly bathypelagic euphausiid species, a group that also includes the three giant (6 to 14 cm as adults) *Thysanopoda* species, *T. egregia*, *T. cornuta*, and *T. spinicaudata*. *B. amblyops* is by far the most abundant of the four.

Despite its cosmopolitan distribution and its numerical importance below 2 000 m, the biology of *Bentheuphausia amblyops* has received limited attention; up until now virtually all studies have been restricted to diet analyses on dead specimens. The first published diet study of *B. amblyops* (Vinogradov, 1962) found digested remains of diatoms, leading to speculation that individuals performed extensive migrations to feed at the surface. Later work (Nemoto, 1968, 1977; Ponomareva and Nikolayeva, 1981) confirmed the presence of phytodetritus in stomachs of *B. amblyops* and added small crustaceans and radiolarians to the known diet. No chlorophyll *a* has been detected in the guts of *B. amblyops* (Nemoto, 1968), ruling out fresh phytoplankton as a substantive part of the diet. What is known about vertical distribution and diet of *B. amblyops* suggests that the species is a non-migrating, bathypelagic resident and an opportunistic feeder (cf. Zenkevich and Birstein, 1956).

This study examines the oxygen consumption rate of *Bentheuphausia amblyops* at temperatures within and just outside those typical of its bathymetric range. Vertical distribution, chemical composition, and gross behavioral observations are reported to enlarge the data base on this important cosmopolitan species.

Materials and methods

Collections

Bentheuphausia amblyops were collected using a 9.3 m² mouth-area, closing Tucker trawl towed at 2.5 knots. The

trawl was constructed of 6-mm knotless nylon mesh and equipped with a thermally protecting cod end (Childress *et al.*, 1978) and time-depth recorder. Trawling was done from the R.V. "Alexander Agassiz" or R.V. "Velero IV" on several cruises spanning the years 1976 to 1978. Sampling sites were located in the San Clemente Basin, in the vicinity of the San Juan Seamount off the coast of Southern California, and in the Guadalupe Basin off Baja California. All tows were discrete depth trawls; depth variability within a given trawl was less than ± 75 m.

Immediately upon reaching the surface, the entire catch was transferred to refrigerated sea water approximating that at the depth of capture (± 1 C°), virtually eliminating any thermal shock. The most active individuals were removed and placed in 4-l polyethylene jars filled with refrigerated sea water, covered with black plastic, and kept at the experimental temperature for a minimum of 6 h before determining oxygen consumption rate. *Bentheuphausia amblyops* in comparable condition will survive up to one month in the laboratory, with an average life expectancy of two weeks. After removal of experimental individuals, all remaining *B. amblyops* in each catch were counted and, in most cases, measured. The total capture data for all three collecting sites were combined to give the vertical distribution data. All temperatures were determined from the extensive CTD data presented in Scripps Institution of Oceanography (1965).

Behavioral observations

During the experimental manipulation that accompanied the 4l O₂ consumption measurements reported in this study, we observed the behavior of *Bentheuphausia amblyops*. The observations were not controlled.

Chemical composition

Individuals used for chemical composition determinations were removed from the catch, blotted with paper towels, placed in airtight polyethylene vials and frozen for one month before analysis. They were analyzed for water, ash, protein, lipid, carbohydrate and total nitrogen, carbon and hydrogen using the methods of Childress and Nygaard (1974).

Oxygen consumption measurements

Oxygen consumption rates were determined by allowing individuals to deplete the oxygen in a sealed, water-jacketed chamber filled with sea water. Temperature was maintained within or slightly above environmental temperatures over the species bathymetric range (1.5° to 7.5°C \pm 0.1 C°) by a refrigerated water bath. Oxygen partial pressure (PO₂) was monitored using a Clark polarographic oxygen electrode (Clark, 1956). Electrodes were calibrated using air- and nitrogen-saturated sea water

at the experimental temperatures (Childress, 1971). The time required for consumption of oxygen to low levels (0 to 40 mm Hg) varied from 8 to 16 h. Filtered (0.45 μ pore size) seawater containing streptomycin and neomycin at concentrations of 25 mg l⁻¹ each was used. At the end of selected runs at each temperature, the individual was removed, its volume was replaced with fresh seawater, and oxygen consumption was again monitored for 2 to 4 h to measure the microbial oxygen consumption rate. In all cases the microbial oxygen consumption was not detectable.

Data were recorded on either a potentiometric strip chart recorder or a digital data-logger. Individual oxygen consumption runs were divided into 30-min increments and the oxygen consumption rate calculated for each increment. Oxygen consumption rate at a particular PO₂ was the 30-min rate that included the PO₂ within the decline of oxygen associated with that 30-min increment.

The maximum and minimum O₂ consumption rates are the means of the five highest and five lowest sustained (> 30 min) rates displayed by individuals at each of the experimental temperatures, at PO₂s above the P_c [that PO₂ where oxygen consumption ceases to be independent of external PO₂ (Prosser, 1973)]. The "110-70 rates" are the means of all oxygen consumption rates between partial pressures of 110 and 70 mm Hg. This range of partial pressures was used because it constitutes the flattest portion of the oxygen consumption vs PO₂ curve at all five temperatures (Fig. 1). The range of partial pressures is above the P_c in all cases, and allows 2 to 3 h for the individual to become accustomed to the chamber. The 110-70 rates are the closest approximation to a routine rate (Brett, 1972) in this study. The P_c was determined as the inflection point in the curves where the rate declined precipitously toward 0.

All statistical comparisons were made using the Student's *t*-test at the 0.05 level of significance.

Results

Vertical distribution

Bentheuphausia amblyops was present in all samples collected between depths of 500 and 2 500 m (Table 1). There was no pronounced difference in vertical distribution on a diel basis. Larger-sized individuals were found more often at greater depths. The abundance of *B. amblyops* was patchy in the vertical and horizontal planes.

Behavioral observations

Bentheuphausia amblyops is negatively buoyant. A swimming individual prodded from the rear often ceases all activity and sinks rapidly. *B. amblyops* swims with the flagellae of its first and second antennae pointed directly forward. The recurved tips of the six flagellae are of equal length and form a circle approximately equal to the cross-sectional area of the individual. *B. amblyops* prodded

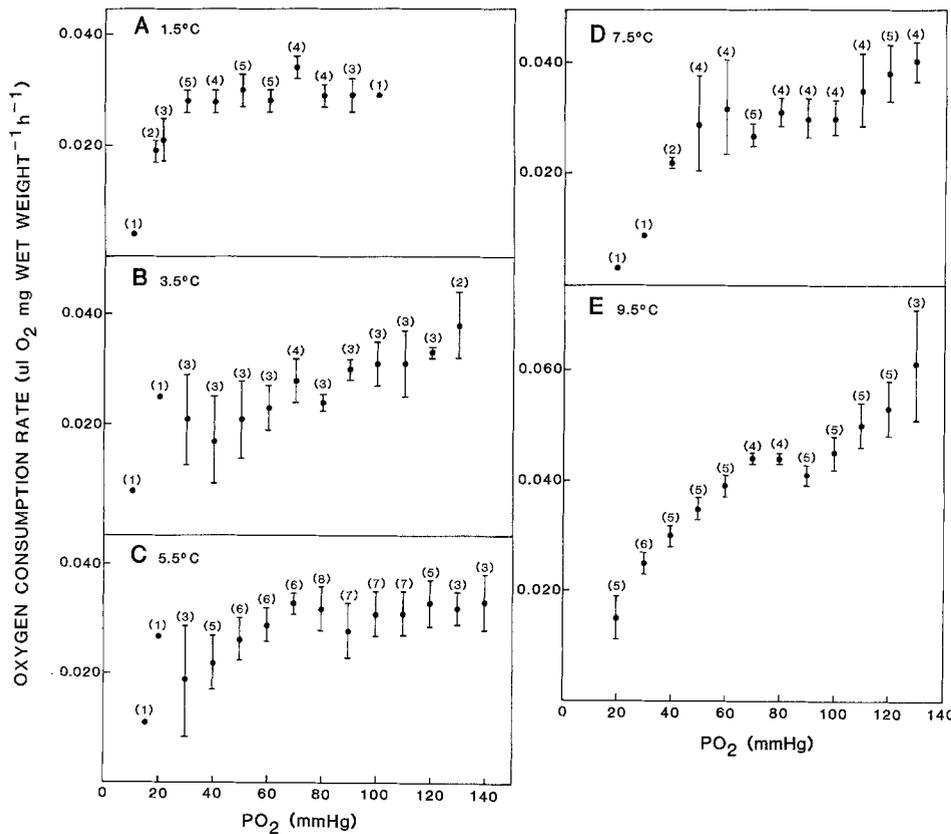


Fig. 1. *Bentheuphausia amblyops*. The relationship of oxygen consumption rate to PO_2 at 5 different temperatures. Numbers in parentheses are the numbers of individuals used to determine each point. Error bars indicate the standard error of the mean

Table 1. *Bentheuphausia amblyops*. Diel vertical distribution of *B. amblyops* between the depth of 400 and 2 500 m. The table combines trawl data from 3 station locations: San Clemente Basin, Guadalupe Basin, and in the vicinity of San Juan Seamount. See text

Maximum depth attained by net	Day					Night				
	No. of trawls	Total h trawled	Total catch	Catch/effort (individuals h^{-1})	Size range (mm)	No. of trawls	Total h trawled	Total catch	Catch/effort (individuals h^{-1})	Size range (mm)
400- 500	1	2	0	0	0	1	3	0	0	0
500- 600	1	2	6	3.0	13-25	3	7	11	1.6	15-25
600- 700	3	9	14	1.6	18-28	2	4	13	3.3	18-20
700- 800	7	20.5	83	4.0	14-25	2	12	20	1.7	-
800- 900	2	7	10	1.4	14-27	2	12	3	0.3	-
900-1 000	4	14	72	5.1	14-31	1	3	3	1.0	-
1 000-1 100	1	4	6	1.5	-	4	20	53	2.7	17-37
1 100-1 200	2	10	52	5.2	17-35	4	18	24	1.3	16-33
1 200-1 500	3	20	37	1.9	17-34	1	6.5	6	0.9	19-28
1 500-2 000	3	39	7	0.2	-	2	11	14	1.3	25-35
2 000-2 500	1	14	19	1.4	-	1	6	8	1.3	17-34

anteriorly often employs its thoracic legs in raptorial fashion to grab the prodding instrument.

Chemical composition

Bentheuphausia amblyops has a lower water content (78.4% of wet weight) and higher protein content (44.68% of ash-free dry weight) than other crustaceans of similar vertical distribution (Table 2; Childress and Nygaard, 1974). The relationship between size (x ; total length, mm) and wet weight (y ; mg) is: $\log y = 2.84 \log x - 1.84$ ($n = 57$;

$r^2 = 0.79$). Size and dry weight (d ; mg) show the relation $\log d = 2.95 \log x - 2.61$ ($n = 54$; $r^2 = 0.78$). Both equations describing the relation between size and weight in *B. amblyops* are quite similar to those of other euphausiid species (Mauchline and Fisher, 1969; Mauchline, 1980).

Oxygen consumption rate

Temperature had no significant effect on minimum, maximum, or 110-70 oxygen consumption rates (Table 3) over the temperature range 1.5° to 7.5°C ($P > 0.05$, Student's

Table 2. *Bentheuphausia amblyops*. Chemical composition of *B. amblyops*¹ including a comparison with 2 other deep living species²

Order Genus and species	Euphausiacea <i>Bentheuphausia amblyops</i>	Mysidacea <i>Gnathophausia gracilis</i>	Mysidacea <i>Boreomysis californica</i>
Minimum depth (m)	280	900	600
Maximum depth (m)	7 000	1 500	> 1 100
Water (% wet weight)	78.94±2.04 ³	81.6 (± 0.4; 7) ⁴	82.6 (± 0.9; 5) ⁴
Ash free dry weight (% dry weight)	86.70±1.22	79.3 (± 1.4; 7)	81.0 (± 1.3; 4)
Skeletal ash (% wet weight)	0.05	0.99	0.45
Carbohydrate (% ash-free dry weight)	0.81±0.21	0.9 (± 0.1; 7)	0.7 (± 0.1; 2)
Lipid (% ash-free dry weight)	26.51±5.75	39.5 (± 3.8; 4)	32.9 (± 0.5; 2)
Protein (% ash-free dry weight)	44.68±7.68	37.6 (± 3.2; 7)	34.7 (± 3.5; 3)
Chitin (% ash-free dry weight)	1.64±0.86	8.1 (± 1.0; 4)	4.3 (± 0.2; 2)
Carbon (% ash-free dry weight)	45.20±3.67	52.8 (± 0.9; 7)	53.6 (± 1.3; 3)
Hydrogen (% ash-free dry weight)	6.72±0.68	8.7 (± 0.3; 7)	8.0 (± 0.5; 3)
Nitrogen (% ash-free dry weight)	7.34±0.89	8.8 (± 0.4; 7)	9.8 (± 1.0; 3)

¹ 5 sets of 3 pooled individuals were analyzed² Data for *G. gracilis* and *B. californica* from Childress and Nygaard (1974)³ $\bar{X} \pm 95\%$ confidence limits⁴ Numbers in parentheses: \pm standard error of the mean and numbers of individuals analyzed, as reported in Childress and Nygaard (1974)**Table 3.** *Bentheuphausia amblyops*. Metabolic rates of *B. amblyops* at 5 temperatures. All values are expressed as $\bar{X} \pm 95\%$ confidence limits. The number of observations used in calculating the metabolic rates are given in parentheses

Temperature (°C)	1.5	3.5	5.5	7.5	9.5
No. of individuals	5	4	8	5	5
110-70 rate ($\mu\text{l O}_2$ mg wet weight ⁻¹ h ⁻¹)	0.030±0.002 (17)	0.029±0.003 (16)	0.031±0.001 (34)	0.031±0.004 (20)	0.045±0.003 (23)
Maximum rate	0.077±0.005 (5)	0.080±0.005 (5)	0.075±0.007 (5)	0.077±0.006 (5)	0.128±0.006 (5)
Minimum rate	0.018±0.002 (5)	0.019±0.002 (5)	0.018±0.003 (5)	0.022±0.002 (5)	0.023±0.002 (5)
110-70 rate ($\mu\text{l O}_2$ mg dry weight ⁻¹ h ⁻¹)	0.142±0.009 (17)	0.137±0.014 (16)	0.147±0.005 (34)	0.147±0.019 (20)	0.213±0.014 (23)
Maximum rate	0.364±0.024 (5)	0.379±0.024 (5)	0.356±0.033 (5)	0.364±0.028 (5)	0.607±0.028 (5)
Minimum rate	0.085±0.009 (5)	0.090±0.009 (5)	0.085±0.014 (5)	0.104±0.009 (5)	0.109±0.009 (5)
110-70 rate ($\mu\text{l O}_2$ mg ash-free dry weight ⁻¹ h ⁻¹)	0.160±0.011 (17)	0.154±0.016 (16)	0.165±0.005 (34)	0.165±0.021 (20)	0.239±0.016 (23)
Maximum rate	0.410±0.027 (5)	0.426±0.027 (5)	0.400±0.037 (5)	0.410±0.032 (5)	0.681±0.032 (5)
Minimum rate	0.096±0.011 (5)	0.101±0.011 (5)	0.096±0.016 (5)	0.117±0.011 (5)	0.122±0.011 (5)
Pc (mm Hg)	10 < Pc < 20	10 < Pc < 20	10 < Pc < 20	40 < Pc < 50	60 < Pc < 70

t-test). In contrast, a change in experimental temperature from 7.5° to 9.5°C resulted in a significant increase in both the maximum and 110-70 rates (Maximum=0.077 to 0.128 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹, $Q_{10} = 12.6$; 110-70=0.035 to 0.045 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹, $Q_{10} = 6.4$). Increased temperature affected the shape of the curves describing the relationship between oxygen consumption rate and PO_2 (Fig. 1). At temperatures between 1.5° and 5.5°C, *Bentheuphausia amblyops* regulates its oxygen consumption rate over a wide range of oxygen partial pressures, with a P_c between 10 and 20 mm Hg over the entire range.

At 7.5°C, and particularly at 9.5°C, oxygen consumption is much higher at higher oxygen partial pressures; the P_c increased to between 40 and 50 mm Hg at 7.5°C and to between 60 and 70 mm Hg at 9.5°C.

Discussion

The vertical distribution of *Bentheuphausia amblyops* extends from 500 m to the maximum depths sampled (2 500 m) in the present study. Our data complement and

corroborate those of Brinton (1962) for the eastern Pacific region, with the exception that *B. amblyops* were found in virtually all trawls below 500 m, and adults (> 25 mm total length) were captured as shallow as 500 to 600 m. Since our trawl was much larger in cross-sectional area (9.3 m² vs 1–3 m²) and towed for longer periods (2 h vs 0.33 to 0.66 h), it is not surprising that our capture of the patchily distributed *B. amblyops* was more consistent. Our trawl records strongly support Brinton's (1962) assertion that *B. amblyops* does not vertically migrate.

The raptorial behavior and strong swimming ability of *Bentheuphausia amblyops* suggests that the species is not restricted to filter feeding (cf. Nemoto, 1967), and is probably capable of active predation. This conclusion is consistent with data that include radiolaria and small crustaceans within the species' diet (Ponomareva and Nikolayeva, 1981) and the observation that opportunistic feeding behavior is a general characteristic of deep sea species (e.g. Ebeling and Cailliet, 1974). The cessation of movement by *B. amblyops* in response to being prodded from the rear is a particularly useful escape mechanism at aphotic depths. Since mechanoreception is believed to be an important mechanism for locating prey (e.g. in cetomimid whale fishes, Marshall, 1971) in the bathypelagic, cessation of movement accompanied by rapid sinking would likely suffice to remove individuals from immediate danger in close brushes with predators.

The relatively robust chemical composition of *Bentheuphausia amblyops* supports a case for a mobile, omnivorous life style over a passive filter-feeding one. The protein content of *B. amblyops* is uniformly higher than that of other bathypelagic Crustacea (Table 2; Childress and Nygaard, 1974), suggesting a larger muscle content, whereas its water and lipid content are low, contributing to the observed negative buoyancy of the species. *B. amblyops* must swim actively to prevent sinking, an observation more consistent with a foraging strategy that consists of seizing large particles than with filter feeding.

Quetin *et al.* (1980) reported a respiratory rate of 0.026 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹ for *Bentheuphausia amblyops* at 5.5 °C, which is slightly below our 110-70 rate (0.031 \pm 0.001 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹; $\bar{X} \pm 95\%$ C.L., Table 3), but within our overall range at 5.5 °C (0.018 \pm 0.003 to 0.075 \pm 0.007 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹). Childress (1975) presented respiration rates for a broad range of pelagic crustaceans with comparable vertical distribution. Assuming a minimum depth of occurrence of 700 m (that depth below which 90% of the population lives, Childress and Nygaard, 1973), based on our data and those of Brinton (1962) our 110-70 rate (0.030 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹) falls on the regression line describing respiratory rate and minimum depth of occurrence in 29 other species of midwater crustaceans (0.031 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹ predicted by Childress, 1975). The maximum and minimum rates for *B. amblyops* are most closely approximated by those of *Gnathophausia gracilis*, a lophogastrid mysid with depth distribution in

the range of *B. amblyops* (800–1500 m), the vertically migrating copepod *Gaussia princeps* (150–1100 m) and the mesopelagic penaeid *Sergestes phorcus* (350–600 m). All three of these species are active swimmers capable of extended horizontal and vertical movement.

Temperatures of 1.5° to 7.5 °C are within the bathymetric range of *Bentheuphausia amblyops* off the coast of California (Brinton, 1962; Scripps' Institution of Oceanography, 1965; GEOSECS, 1981) and in the eastern Pacific in general. A temperature of 7.5 °C corresponds to depths of 250 to 400 m depending on location (Scripps Institution of Oceanography, 1965), and represents the extreme upper limit of *B. amblyops* vertical range (280 m, Brinton, 1962). *B. amblyops* is in fact quite rare above a depth of 500 m (Table 1; Brinton, 1962). A temperature of 9.5 °C (150–200 m; Scripps Institution of Oceanography, 1965) is well above that encountered by *B. amblyops* in the field.

Temperature had no significant effect on maximum, minimum, or 110-70 rates at temperatures between 1.5 and 7.5 °C. This is largely due to variability in metabolic rate caused by differences in spontaneous activity at different temperatures. Experimental temperatures were chosen for this study on the basis of metabolic responses to temperature in extremely stenothermal, high-latitude fishes (Wohlschlag, 1960, 1964; Somero *et al.*, 1968), where metabolic rates can double with an increase of as little as 4 °C (Wohlschlag, 1963). In extreme cases, such as the nototheniid fishes, upper lethal limits are reached at 6° to 8 °C (Wohlschlag, 1964). It appears that the metabolic temperature responses of *Bentheuphausia amblyops* are not analogous to those of higher latitude fishes despite the similar temperature stability in the bathypelagic zone.

The Antarctic euphausiid *Euphausia superba* and *B. amblyops* show a strikingly similar relationship of metabolism to temperature. *E. superba* exhibits a very low Q_{10} (1.24) over its normal environmental temperature range (0° to 5 °C) and a substantial increase in metabolic rate (Q_{10} 2.3) above it (McWhinnie and Marciniak, 1964). Similarly, in *B. amblyops* the increase in experimental temperature from 7.5° to 9.5 °C resulted in a 45% increase in 110-70 rate, and a 66% increase in maximum rate, while the minimum rate remained essentially unchanged. Clearly, temperatures above those encountered in nature are stressful to *B. amblyops*, as indicated by the large Q_{10} between 7.5° and 9.5 °C (110-70=6.4; maximum=12.6) and the high P_c at 9.5 °C (60 mmHg < P_c < 70 mmHg). The small change in minimum rate (0.018 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹ at 1.5 °C to 0.23 $\mu\text{l O}_2$ mg wet weight⁻¹ h⁻¹ at 9.5 °C) over the experimental temperature range is typical of several invertebrate and fish species (cf. Brett, 1964; Prosser, 1973). It is probably more indicative of the relative insensitivity to temperature of the metabolism associated with lower activity levels than of any independence of metabolism from temperature effects.

The vertical distribution of *Bentheuphausia amblyops* overlaps the regions of lowest oxygen concentration within the oxygen minimum layer of the eastern North Pacific (O_2 : 0.2–0.5 ml l⁻¹; depth range: ~ 500 to 1000 m

depending on location; Scripps Institution of Oceanography, 1965; GEOSECS, 1981). The P_c of 10 to 20 mm Hg ($\sim 0.45\text{--}0.90\text{ ml l}^{-1}$) recorded at 3.5° and 5.5°C (temperatures roughly corresponding to this depth range) would not allow the species a totally aerobic existence at the lowest PO_2 s encountered within the layer. It appears that *B. amblyops* must rely on anaerobiosis to supply a fraction of its metabolic needs while residing in those areas. This conclusion is consistent with Brinton's (1979) data that show *B. amblyops* to be absent from the severely oxygen deficient waters of the eastern tropical Pacific ($\text{O}_2 < 0.1\text{ ml l}^{-1}$).

Both the observed vertical distribution and metabolic response to elevated temperatures almost certainly preclude the migrations of *Bentheuphausia amblyops* to surface waters postulated by Vinogradov (1970). Phytodetritus in the guts of *B. amblyops* (Nemoto, 1968; Ponomareva and Nikolayeva, 1981) is probably refractory material contained in the guts of prey captured by *B. amblyops* (cf. Foxton and Roe, 1974) or present in bathypelagic marine snow (Silver and Alldredge, 1981). The relatively robust composition, observed predatory behavior, and strong swimming capability of this species indicate an opportunistic foraging strategy with a strong predatory component. *B. amblyops* may rely on anaerobiosis for part of its metabolic energy demand during excursions up into the core of the oxygen minimum layer.

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