

## Metabolic rates, enzyme activities and chemical compositions of some deep-sea pelagic worms, particularly *Nectonemertes mirabilis* (Nemertea; Hoplonemertinea) and *Poeobius meseres* (Annelida; Polychaeta)

ERIK V. THUESEN\* and JAMES J. CHILDRESS\*

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**Abstract**—Investigations of metabolic rate, enzyme activity and chemical composition were undertaken on two abundant deep-sea pelagic worms: *Nectonemertes mirabilis* (Nemertea; Hoplonemertinea) and *Poeobius meseres* (Annelida; Polychaeta). Six other species of worms (*Pelagonemertes brinkmanni* (Nemertea) and the following polychaetes: *Pelagobia* species A, *Tomopteris nisseni*, *Tomopteris pacifica*, *Tomopteris* species A, and *Traviopsis lobifera*) were captured in smaller numbers and used for comparison in the physiological and biochemical measurements. Polychaete worms had the highest oxygen consumption rates and, along with *N. mirabilis*, displayed significant size effects on metabolic rate. *Poeobius meseres* had the lowest rates of oxygen consumption and displayed no significant relationship of oxygen consumption rate to wet weight. No significant effect of size on the activities of citrate synthase, lactate dehydrogenase or pyruvate kinase was observed in *P. meseres* or *N. mirabilis*. Lipid content was higher than protein content for all the worms in this study. Carbohydrate was of little significance in these worms and was usually <0.01% of the total wet weight. Citrate synthase activities of pelagic worms showed excellent correlation with metabolic rates. It appears that polychaete worms as a group have higher metabolic rates than bathypelagic shrimps, copepods and fishes, and may be the animals with the highest metabolic rates in the bathypelagic regions of the world's oceans.

### INTRODUCTION

A significant amount of the organic matter produced in epipelagic waters and then transported below the pycnocline is thought to pass through the organisms inhabiting the mesopelagic zone, however few studies have been undertaken on the metabolism and biochemistry of zooplankters from the meso- and bathypelagic regions of the oceans compared with investigations on shallow living organisms. The elucidation of the physiology and biochemistry of the animals in these intermediate depths will further our understanding of the rates of biological recycling of organic matter in the oceans (CHILDRESS and THUESEN, 1992). In order to gain a more comprehensive knowledge of the metabolic capabilities of zooplankton, other than crustaceans, from the deep sea, studies were undertaken on two abundant deep-sea pelagic worms; *Nectonemertes mirabilis* (Nemertea; Hoplonemertinea) and *Poeobius meseres* (Annelida; Polychaeta). *N. mirabi-*

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\*Oceanic Biology Group, Marine Science Institute, University of California, Santa Barbara, CA 93106, U.S.A.

*lis* is a common cosmopolitan constituent of the zooplankton below 1000 m. Like other deep-sea nemerteans it is believed to be carnivorous, feeding on small crustaceans (COE, 1954). However, very few investigations have been made on its trophic relationships within the midwater community, and no direct observations on its feeding or behavior *in situ* have been reported. *P. meseres*, an aberrant polychaete (ROBBINS, 1965), is a common midwater animal typical of Subarctic water in the North Pacific below 500 m and can occur in numbers of over 200 animals  $1000\text{ m}^{-3}$  water (MCGOWAN, 1960). It feeds by extruding a mucous net on which it captures particles falling to the bottom (UTTAL-COOKE, 1992). Other species of worms were captured in smaller numbers and used for comparison in the physiological and biochemical measurements, including the deep-sea nemertean *Pelagoneustes brinkmanni* and the following polychaetes: *Pelagobia* species A, *Tomopteris nisseni*, *Tomopteris pacifica*, *Tomopteris* species A, and *Traviopsis lobifera*. Although not all these animals are closely related phylogenically, they can co-occur in the water column where they inhabit a relatively uniform environment.

Investigations on midwater fish (CHILDRESS and SOMERO, 1979; SULLIVAN and SOMERO, 1980; TORRES and SOMERO, 1988) and terrestrial vertebrates (HOCHACHKA *et al.*, 1988) have shown that reliable estimates of metabolic rates can be made based on activities of enzymes involved in aerobic and anaerobic metabolism. Metabolic potentials of these worms were estimated by measuring the activities of several key enzymes involved in aerobic and anaerobic metabolism and investigating the correlation of these activities with oxygen consumption rates. Analyses of water, protein, lipid, carbohydrate, carbon and nitrogen, followed by calculations of energy contents, were also undertaken on the worms in this investigation. Studies on the biochemistry and physiology of these animals will help us to understand how their energy is stored and utilized, and possibly shed light on their ecological relationships.

## MATERIALS AND METHODS

### *Capture of animals*

Animals were collected using an opening-closing Mother Tucker trawl with a 3-m<sup>2</sup> mouth fitted with a 30-l insulated cod end (CHILDRESS *et al.*, 1978). This cod end prevents heat injury to deep-living animals during recovery of the net through warmer upper layers. Tows were carried out on two cruises of the R.V. *Point Sur* (September 1989 in San Clemente Basin, and late July 1991 off Point Conception, California) and on three cruises of the R.V. *New Horizon* (June 1990 and 1991, and February 1991 off Point Conception). The ship speed was held below 1 knot to decrease the biomass in the cod end and minimize damage to less robust animals. Animals were transferred to 5°C sea-water upon recovery and either held for metabolic rate measurements or frozen in liquid nitrogen for later analyses of enzymatic activities or chemical compositions in the laboratory. Some animals were transferred to a -80°C freezer in the laboratory until enzyme activity or chemical composition analyses were performed.

Two species of Polychaeta included in this report are not found in reports on pelagic polychaetes of the Pacific Ocean (e.g. DALES, 1957; DALES and PETER, 1972; TEBBLE, 1960; BERKELEY and BERKELEY, 1960). *Tomopteris* sp. A is a relatively large animal that can reach over 10 cm in length and has distinctive purplish-brown pigmentation lining the gut. This large worm is commonly captured at depths >700 m in the eastern North Pacific off

California and Mexico using the Mother Tucker trawl. *Pelagobia* sp. *A* resembles *Pelagobia longicirrata* but it is larger, reaching 20 mm in length, and has orange pigmentation. This worm was captured on only one occasion in a discrete depth trawl off Point Conception at 2400 m. It was very abundant at this depth, and we never captured it in any of the numerous trawls at shallower depths above 1200 m.

#### *Oxygen consumption measurements*

Oxygen consumption measurements were carried out aboard ship immediately following collection at a hydrostatic pressure of 1 atm. An investigation on the effects of pressure on respiration rates of chaetognaths, medusae and *P. meseres* found no differences in respiration rates when measured at 1 and 101 atm (CHILDRESS and THUESEN, in press). Animals were transferred to glass syringes with filtered sea-water containing 25 mg l<sup>-1</sup> each of streptomycin and penicillin and incubated at 5°C. Water samples were withdrawn periodically from the incubation syringe through a three-way valve and the new incubation volume noted. Before withdrawal of the sample, syringes were turned end-over-end to mix the incubation medium. The water samples were drawn into 0.5 ml gas-tight syringes. These samples were then injected into an in-line extractor, and oxygen and carbon dioxide were analyzed on the attached gas chromatograph (CHILDRESS *et al.*, 1984). Control syringes without animals were run simultaneously and after the removal of animals. Syringes were run up to 8 h as controls for background respiration. No background respiration was detected in any of the control experiments. Oxygen consumption of the giant polychaete *T. nissenii* was measured in a water-jacketed respiration chamber equipped with a small stir-pump that consists of a magnetic stirring bar enclosed within a discrete plastic chamber. This mechanism allowed for the gentle mixing of water sufficient to bathe the Clarke-type oxygen electrodes (MICKEL *et al.*, 1983) without damage to the animal. Following completion of experiments which typically lasted around 24 h, animals were weighed at sea using the motion-compensated shipboard precision balance system (CHILDRESS and MICKEL, 1980) and frozen in liquid nitrogen for later analyses of enzyme activities.

#### *Enzyme activity analyses*

The following enzymes were surveyed as appropriate indicators of aerobic and anaerobic metabolic potential: citrate synthase (CS, E.C. 4.1.3.7), lactate dehydrogenase (LDH, E.C. 1.1.1.27), pyruvate kinase (PK, E.C. 2.7.1.40) and octopine dehydrogenase (E.C. 1.5.1.11). CS was chosen as an indicator of aerobic metabolic potential in all animals. LDH was chosen as an indicator of anaerobic metabolism in *Nectonemertes*. PK was chosen as an indicator of anaerobic metabolism in *Poeobius*, because its LDH activities are very low. CS is an important regulatory enzyme and functions in the first step of the citric acid cycle. PK is the regulatory enzyme that supplies pyruvate to LDH in the second to last step in glycolysis, and both PK and LDH are good indicators of anaerobic metabolic potential. CS, LDH and PK activities in fish muscle have been found to correlate well with oxygen consumption (CHILDRESS and SOMERO, 1979; SOMERO and CHILDRESS, 1990; SULLIVAN and SOMERO, 1980; TORRES and SOMERO, 1988).

Animals were weighed on a Mettler analytical balance and homogenized in 1 part weight/volume 0.01 M Tris homogenization buffer, pH 7.5 at 20°C using Duall hand held

glass homogenizers kept on ice. Samples were transferred to microfuge tubes and centrifuged at 6200 g for 5 min at 5°C. All assays were performed within 1 h of homogenization using a Shimadzu spectrophotometer equipped with a water-jacketed cuvette holder. Small amounts of sample supernatant (25 or 50  $\mu$ l) were used for assays. Measurements of enzyme activity were made in 1 ml final volume of assay medium in quartz cuvettes at 20°C under non-limiting conditions in order to estimate maximum metabolic potential and followed procedures essentially as described previously (CHILDRESS and SOMERO, 1979; SOMERO and CHILDRESS, 1980; THUESEN and CHILDRESS, in press). Enzyme activities are expressed as units ( $\mu$ mol substrate converted to product  $\text{min}^{-1}$ ) per gram wet weight of animal.

Citrate synthase activity measurements were performed in a medium containing 50 mM imidazole-HCl buffer (pH 7.8 at 20°C), 0.5 mM oxaloacetate, 0.1 mM acetyl-CoA, 0.1 mM 5,5-dithiobis (2-nitrobenzoic acid) (DTNB) and 1.5 mM  $\text{MgCl}_2$ . The increase in absorbance at 412 nm due to the reaction of the reduced coenzyme A generated by the enzymatic reaction with DTNB was recorded. Background activity was measured following the addition of homogenate supernatant, and this background rate was then subtracted from the rate after the assay reaction was initiated by addition of the oxaloacetate. Background activities were subtracted from total activities to arrive at enzyme activities in the samples.

Lactate dehydrogenase activity measurements were performed in a medium containing 80 mM Tris-HCl buffer (pH 7.2 at 20°C), 2 mM sodium pyruvate, 150  $\mu$ M NADH, and 100 mM KCl. PK activity measurements were performed in a medium containing 50 mM imidazole-HCl buffer (pH 7.8 at 20°C), 100 mM KCl, 10 mM  $\text{MgSO}_4$ , 0.1 mM fructosebisphosphate, 1.0 mM phosphoenolpyruvate, 5.0 mM ADP, 150  $\mu$ M NADH and excess LDH activity (rabbit muscle LDH, Sigma Chemical Co.). ODH activity measurements were performed in a medium containing 50 mM imidazole-HCl buffer (pH 7.0 at 20°C), 2 mM sodium pyruvate, 2 mM arginine, 150  $\mu$ M NADH, and 100 mM KCl. The assay reactions of LDH and PK were started by addition of the sample supernatant, and the decrease in absorbance at 340 nm due to NADH oxidation was recorded. ODH assay reactions were initiated by the addition of arginine after the decrease in absorbance at 340 nm due to LDH activity had been recorded.

#### *Chemical analyses*

After removal from liquid nitrogen or the freezer, sealed vials containing the specimens were weighed on an analytical balance when condensation no longer formed on the outside of the vial. The vials were then opened, and the samples were dried to a constant weight (usually ~24 h) at 60°C, then reweighed. Dried samples were homogenized in distilled water and aliquots were removed for chemical analyses. Protein was measured spectrophotometrically according to LOWRY *et al.* (1951). Lipid was extracted following the microextraction technique of REISENBICHLER and BAILEY (1991) and measured spectrophotometrically after charring with sulfuric acid (MARSH and WEINSTEIN, 1966). Carbohydrate was measured spectrophotometrically following the method of DUBOIS *et al.* (1956). Carbon and nitrogen were measured by combustion at the Marine Science Institute Analytical Laboratory of the University of California at Santa Barbara on a Control Equipment Corporation Model 240XA elemental analyzer. Energy values were calculated using the following conversion values: carbohydrate, 4.1 kcal  $\text{g}^{-1}$ ; lipid, 8.7 kcal

$\text{g}^{-1}$ ; protein,  $5.7 \text{ kcal g}^{-1}$  (BRETT and GROVES, 1979); and then converted to  $\text{kJ g}^{-1}$  using a conversion factor of  $4.1867 \text{ J cal}^{-1}$ .

#### Data analyses

All statistical analyses were performed with the Statview II program (Abacus Concepts, Inc., Berkeley, CA). Regressions of oxygen consumption and enzyme activity data were carried out in ln transformed data, and regressions of chemical composition data were carried out on arcsin transformed data to minimize non-linearity of the data (SOKAL and ROHLF, 1983). Oxygen consumption rates and enzyme activities were evaluated in relation to wet mass of the animals, and scaling coefficients from the well-known allometric equation  $y = aM^b$  were derived, where  $a$  is a constant for the species at the experimental temperature,  $M$  is the wet weight of the animal, and  $b$  is the scaling coefficient (SCHMIDT-NIELSEN, 1983). Wet mass was used as a measure of size rather than dry weight because this is the parameter of physiological significance determining constraints on animal locomotion, behavior, etc. The use of other parameters as indicators of size can lead to misinterpretations concerning the biology of the whole animal. The relative values of different parameters of body size in this regard have been discussed fully by CHILDRESS (1977) and CHILDRESS and SOMERO (1979). Enzyme activities were regressed with oxygen consumption rates to evaluate the potential of using enzyme activities as indicators of metabolic rates of pelagic worms.

## RESULTS

#### Oxygen consumption rates

*Nectonemertes mirabilis*, *P. meseres* and four species of more active polychaete worms were recovered in extremely good condition using the large insulated cod end. Both the robust *N. mirabilis* and the more flaccid *P. meseres* could be kept alive for several days on board ship when maintained in a refrigerator at  $5^\circ\text{C}$ . Animals were usually in good condition after the completion of experiments. For the less active species, oxygen was seldom depleted below one-half the initial concentration over the course of the run. Our oxygen consumption data are expressed as overall average uptake over the course of the experiment for these species (Table 1). However, the active tomopterid species depleted the oxygen to almost zero before the runs were ended, and only initial measurements ( $\sim 6$  h) were used in calculations of metabolic rates (Table 1). There was very close agreement between the weight measurements made at sea using the motion-compensated shipboard precision balance system and those made in the laboratory on the analytical balance ( $<2\%$ ).

Weight specific oxygen consumption rates declined significantly with increasing wet weight when data from all the animals investigated were combined (Fig. 1). Polychaete worms had the highest oxygen consumption rates, and the giant polychaete *T. nisseni* had a higher oxygen consumption rate than the smaller worms *N. mirabilis* and *P. meseres* (Fig. 1). *P. meseres* had the lowest rates of oxygen consumption. The allometric scaling of oxygen consumption rate of *N. mirabilis* had a negative slope significantly different from zero ( $y = 0.163x^{-0.54}$ ; 95% confidence interval (CI):  $\pm 0.44$ ;  $R = 0.68$ ;  $F$ -test for regression coefficient,  $P = 0.02$ ; Fig. 1). The polychaete worms also had negative allometric scaling

Table 1. Metabolic rates of the pelagic worms investigated in this study compared with the metabolic rates of some other deep-sea worms

Phylum Family Genus and species	Wet weight range (g)	T (°C)	Oxygen consumption (mean ± SE, number of specimens) ( $\mu\text{mol O}_2 \text{ g}$ wet weight <sup>-1</sup> h <sup>-1</sup> )	Source
Nemertea				
Nectonemertidae				
<i>Nectonemertes mirabilis</i>	0.1522–1.0554	5.0	0.295 ± 0.043, 11	This study
Annelida				
Poeobiidae				
<i>Poebius meseres</i>	0.1059–1.1995	5.0	0.068 ± 0.008, 17	This study
Phyllodocidae				
<i>Pelagobia</i> sp. A	0.0062–0.0444	5.0	2.395 ± 0.806, 4	This study
Tomopteridae				
<i>Tomopteris pacifica</i>	0.0126–0.0801	5.0	3.928 ± 2.298, 2	This study
<i>T. nissenii</i>	11.259	5.0	0.718, 1	This study
Typhloscolecidae				
<i>Traviopsis lobifera</i>	0.2385–0.2678	5.0	1.001 ± 0.142, 2	This study
Chaetognatha				
Sagittidae				
<i>Caecosagitta macrocephala</i>	0.0145–0.0297	5.0	0.779 ± 0.097, 9	THUESEN and CHILDRESS (in press)
Eukrohniidae				
<i>Eukrohnia fowleri</i>	0.0531–0.1655	5.0	0.349 ± 0.027, 10	THUESEN and CHILDRESS (in press)
Vestimentifera				
Riftidae				
<i>Riftia pachyptila</i>	5.9–27.5	2.5	0.63 ± 0.15, 5	CHILDRESS <i>et al.</i> (1984)

with a regression slope significantly different from zero ( $y = 0.892x^{-0.26}$ ; 95% CI:  $\pm 0.19$ ;  $R = 0.78$ ;  $F$ -test for regression coefficient,  $P = 0.01$ ; Fig. 1). However, for *P. meseres* there was no significant relationship of oxygen consumption rate to wet weight (Fig. 1).

#### Enzyme activity measurements

Citrate synthase and PK activities were measured on eight species of pelagic worms (Table 2). No significant effect of size on the enzymatic activity of CS, LDH or PK in *P. meseres* or *N. mirabilis* was observed. CS activities showed excellent correlation with metabolic rates when regressed against oxygen consumption (Fig. 2). Linear regression of ln transformed CS and oxygen consumption data was highly significant ( $p < 0.01$ ). PK activities and LDH activities were also significantly correlated with oxygen consumption rates (Figs 3 and 4).

The highest CS activity was measured in an individual of the epipelagic species *T. pacifica* at 3.364 U CS g wet weight<sup>-1</sup> (total body weight of 12.6 mg). The highest PK activity was measured in an individual of *Pelagobia* sp. A at 9.325 U PK g wet weight<sup>-1</sup> (total body weight of 6.2 mg). The highest LDH activity was measured in an individual of

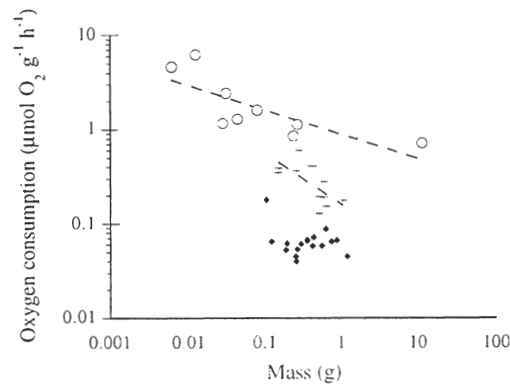


Fig. 1. Oxygen consumption rates of *Nectonemertes mirabilis* (+), *Poebobius meseres* (◆), and other polychaete worms (○) as a function of their wet weight. The slope of the regression line for *P. meseres* is not significantly different from a slope of zero. The regression line for *N. mirabilis* is  $y = 0.163x^{-0.54}$ ; 95% confidence interval (CI):  $\pm 0.44$ ;  $R = 0.68$ ;  $F$ -test for regression coefficient,  $P = 0.02$ . The regression line for the other polychaete worms is  $y = 0.892x^{-0.26}$ ; 95% CI:  $\pm 0.19$ ;  $R = 0.78$ ;  $F$ -test for regression coefficient,  $P = 0.01$ .

Table 2. Enzyme activities of some deep-sea worms. Chaetognath data are from THUESEN and CHILDRESS (in press)

Family Genus and species	Wet weight range (g)	Enzymatic activity ( $U\ g^{-1}$ , mean $\pm$ SE, number of specimens)			
		CS	LDH	PK	ODH
Nectonemertidae <i>Nectonemertes mirabilis</i>	0.1522–1.0554	0.401 $\pm$ 0.076, 11	0.132 $\pm$ 0.039, 10	3.998 $\pm$ 0.076, 3	n.d.
Pelagonemertidae <i>Pelagonemertes brinkmanni</i>	0.3569	0.059, 1	0.046, 1	0.406, 1	n.d.
Poeobiidae <i>Poebobius meseres</i>	0.1059–1.1995	0.93 $\pm$ 0.010, 19	0.002 $\pm$ 0.0, 2	0.100 $\pm$ 0.010, 17	0.002, 1
Phyllodocidae <i>Pelagobia</i> sp. A	0.0062–0.0444	n.d.	n.a.	6.702 $\pm$ 1.021, 4	n.a.
Tomopteridae <i>Tomopteris pacifica</i>	0.0126–1.1072	1.654 $\pm$ 0.714	1.310, 1	4.167 $\pm$ 1.070, 4	0.043, 1
<i>T. nisseni</i>	11.259	2.048	n.a.	5.037	n.a.
<i>Tomopteris</i> sp. A	0.9779–1.3497	0.563 $\pm$ 0.026, 2	4.949 $\pm$ 1.726, 2	4.488 $\pm$ 0.193, 3	0.038, 1
Typhloscolecidae <i>Traviopsis lobifera</i>	0.2193–0.3513	n.d.	0.038, 1	5.187 $\pm$ 0.384, 4	n.a.
Sagittidae <i>Caecosagitta macrocephala</i>	0.0110–0.0297	1.317 $\pm$ 0.093, 18	n.d.	1.114 $\pm$ 0.106, 18	n.a.
Eukrohniidae <i>Eukrohnia fowleri</i>	0.0502–0.1655	0.513 $\pm$ 0.044, 17	n.d.	0.202 $\pm$ 0.024, 17	n.d.

n.a., Not analyzed; n.d., not detected.

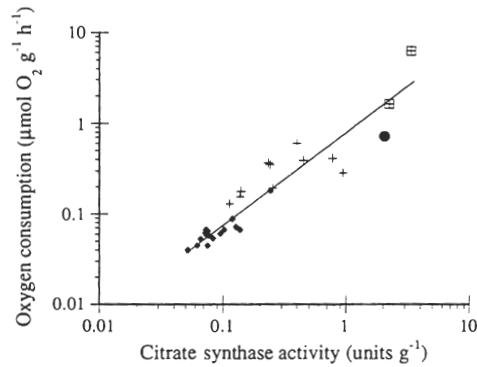


Fig. 2. The relationship between citrate synthase (CS) activity and oxygen consumption rate for pelagic worms. The regression line is  $y = 0.773x^{0.98}$ ; 95% CI:  $\pm 0.13$ ;  $R = 0.94$ ;  $F$ -test for regression coefficient.  $P < 0.01$ . Symbols are given in Fig. 1, except for the polychaetes: *Tomopteris* sp. A (●) and *T. pacifica* (⊠).

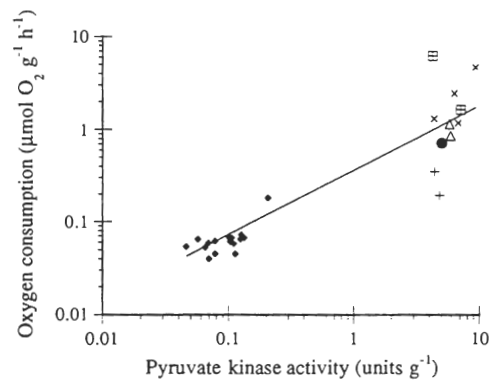


Fig. 3. The relationship between pyruvate kinase (PK) activity and oxygen consumption rate for pelagic worms. The regression line is  $y = 0.347x^{0.72}$ ; 95% CI:  $\pm 0.12$ ;  $R = 0.92$ ;  $F$ -test for regression coefficient.  $P < 0.01$ . Symbols are given in Figs 1 and 2, except for *Traviopsis lobifera* (Δ) and *Pelagobia* sp. A (×).

the bathypelagic polychaete *Tomopteris* sp. A at 6.675 U LDH g wet weight<sup>-1</sup> (total body weight of 1.252 g). The lowest enzyme activities were measured in the midwater species *P. meseres* at 0.052 U CS g wet weight<sup>-1</sup> (total body weight of 258.5 mg), 0.046 U PK g wet weight<sup>-1</sup> (total body weight of 266.3 mg), and 0.002 U g wet weight<sup>-1</sup> of both LDH and ODH. Background values for CS were extremely high for *Pelagobia* sp. A specimens and it could not be measured reliably. CS was not detected in *T. lobifera*. The one specimen of *P. brinkmanni* in our study had considerably lower enzyme activities than the other nemertean, *N. mirabilis*.

The metabolic poise of most of these worms appeared anaerobic, i.e. PK activities were considerably higher than CS activities in all species (Table 2). The exception to this trend was *P. meseres* which had very balanced PK and CS activities. LDH activities were lower

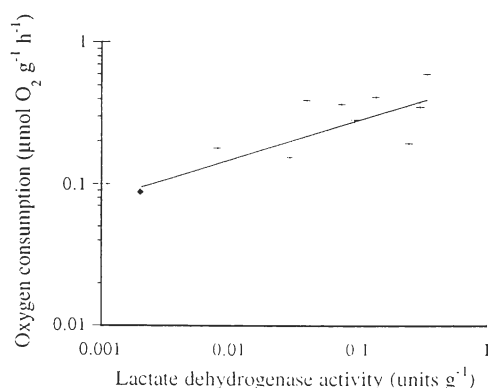


Fig. 4. The relationship between lactate dehydrogenase (LDH) activity and oxygen consumption rate for *Nectonemertes mirabilis* (+) and *Poebobius meseres* (◆). The regression line is  $y = 0.542x^{0.27}$ ; 95% CI:  $\pm 0.19$ ;  $R = 0.74$ ;  $F$ -test for regression coefficient,  $P < 0.01$ .

than both CS and PK activities in all worms except *Tomopteris* sp. *A* which had LDH activities that were even higher than its PK activities. Although low ODH activities were measured in three species of polychaetes, this enzyme was not detected in either of the two nemerteans (Table 2).

#### Chemical compositions

Results of lipid, protein, carbohydrate, water, carbon and nitrogen assays are presented in Table 3. There was no significant effect of size (wet weight) on the chemical constituents of these worms. All components showed significant negative correlation with water content ( $P < 0.001$  for all comparisons). Lipid and protein contents were highly correlated with carbon and nitrogen contents, respectively ( $P < 0.01$  for all comparisons). Lipid was higher than protein for all the worms in this study. Carbohydrate was of little significance in these worms and was usually  $< 0.01\%$  of the total wet weight. *P. meseres* had the highest water content and was the lowest in organic constituents of the worms investigated in this report. *N. mirabilis* had the highest organic content of all the worms. This nemertean has considerable lipid reserves which were two to four times higher than those of the polychaete worms. *T. lobifera* was the one species of worm that had protein contents almost as high as lipid contents.

## DISCUSSION

#### Metabolic rates

The highest metabolic rates measured in this study were for the active polychaete worms. This is not surprising as both epi- and bathypelagic species of polychaete worms were constantly swimming after capture and during the time they were held for study. They often swam during respiration measurements. The aberrant polychaete *P. meseres* was relatively inactive and only occasionally was observed to be swimming. *N. mirabilis* usually alternates active periods with periods of quiescence. We believe that these observations likely reflect their behavior in the natural environment.

Table 3. Chemical compositions of pelagic nemertean and polychaete worms from off California. Values are per cent wet weight with standard error and number of specimens given in brackets. No n is given if the preceding value used the same number of specimens

Class	Family	Genus and species	Wet weight (g)	Water (SE, n)	CHO	Lipid	Protein	C	N	C/N
Enopla										
	Nectonemertidae									
	<i>Nectonemertes</i>									
		<i>mirabilis</i>	0.1441-0.6908	89.21 (0.62, 9)	0.062 (0.0008, 5)	6.01 (0.92)	2.03 (0.21)	4.19 (0.31, 9)	0.90 (0.10)	4.6 2.67
Polychaeta										
	Poeciidae									
		<i>Poecobius</i>								
		<i>mexeres</i>	0.1042-0.9363	95.00 (0.20, 11)	0.012 (0.0008, 7)	1.38 (0.24)	0.61 (0.10)	0.88 (0.14, 11)	0.19 (0.04)	4.6 0.65
	Phyllodoceidae									
		<i>Pelagobia</i> sp. A	0.173-0.341	89.39 (2.25, 4)	n.a.	n.a.	n.a.	n.a.	n.a.	n.a. n.a.
	Tomopteridae									
	<i>Tomopteris</i>									
		<i>pacifica</i>	1.8304-2.3115	94.88 (0.25, 2)	0.080 (0.0024)	1.88 (0.11)	0.95 (0.09)	0.93 (0.16)	0.17 (0.04)	5.5 0.91
		<i>T. nissenii</i>	11.2586	n.a.	n.a.	n.a.	0.891	n.a.	n.a.	n.a. n.a.
		<i>Tomopteris</i> sp. A	0.7633-1.2981	91.92 (2.50, 3)	0.102 (0.006)	2.39 (0.04, 2)	1.00 (0.17, 3)	2.47 (1.31)	0.58 (0.24)	4.3 1.11
	Typhlosolecidae									
	<i>Traviopsis</i>									
		<i>lobifera</i>	0.1683-1.4669	90.64 (0.97, 7)	0.083 (0.0007, 5)	2.65 (0.38)	2.00 (0.33)	3.54 (0.63, 7)	0.88 (0.17)	4.0 1.44

n.a. Not assayed.

The low oxygen consumption rates of *P. meseres* and *N. mirabilis* are within the range of those measured for deep-sea medusae (THUESEN and CHILDRESS, in preparation). The oxygen consumption rates of the other worms in this study are higher than the metabolic rates of most chaetognaths (THUESEN and CHILDRESS, in press) and are higher than many of the rates measured previously for meso- and bathypelagic shrimp and copepods (CHILDRESS, 1975; COWLES *et al.*, 1991). The metabolic rates of pelagic crustaceans and fishes decline rapidly with increasing depth of occurrence (reviewed in CHILDRESS *et al.*, 1990). It thus appears that, as a group, polychaete worms may have the highest metabolic rates in the meso- and bathypelagic zones of the oceans.

The allometric scaling of oxygen consumption rates in these worms appears to be within the range of that observed for most animals (SCHMIDT-NIELSEN, 1984). However, there is no effect of size on the metabolic rate of *P. meseres*. This phenomenon has been observed for a variety of gelatinous organisms (BIGGS, 1977; LARSON, 1986; THUESEN and CHILDRESS, in press).

The effect of low hydrostatic pressures on the metabolic rates of animals that continually live below 1000 m depth can be acute (CHILDRESS *et al.*, 1990; MICKEL and CHILDRESS, 1983). In another study, we performed experiments on the effects of pressure on the metabolic rates on *P. meseres*, three species of Chaetognatha and two species of medusae (CHILDRESS and THUESEN, in press). We observed no significant differences in the metabolic rates of any of these animals measured at 1 and 101 atm. Meso- and bathypelagic organisms usually display little or no significant effect of hydrostatic pressure on their metabolic rates when measured within the range of their normal habitat pressures or slightly outside this range (BELMAN, 1978; QUETIN and CHILDRESS, 1976; SMITH and TEAL, 1973; TEAL and CAREY, 1976; TORRES and CHILDRESS, 1983).

#### *Enzyme activities*

In some invertebrates one or more of the opine dehydrogenases function along with, or take the place of, LDH during anaerobic metabolism (HOCHACHKA and SOMERO, 1984; LIVINGSTONE, 1991). Although some benthic nemerteans are known to have ODH (GÅDE and CARLSSON, 1984; LIVINGSTONE *et al.*, 1990), it was not detected in the two pelagic nemertean worms in this study. The more robust nemertean in our study, *N. mirabilis*, had considerably higher enzyme activities than the flaccid *P. brinkmanni*.

The metabolic poise of the worms investigated in this report differs dramatically from pelagic arrowworms investigated previously from the same region (THUESEN and CHILDRESS, in press). Chaetognaths usually have higher CS than PK activities and thus appear aerobically poised. *Tomopteris* sp. *A* has very high LDH activities compared with the other worms. We interpret this as an adaptation for burst swimming, which could be useful during a sustained swimming effort during an escape response or when following an odor plume to catch prey.

The high correlation between metabolic rates and enzymatic activities, especially CS, suggests that these correlations may be useful in the estimation of metabolic rate. This is advantageous since many more enzyme activity analyses can be run on a greater number of animals in a single day than can oxygen consumption experiments. Furthermore, those deep-living species not captured in sufficiently healthy condition for metabolic rate measurements could be readily assayed for enzymatic activity and their metabolic rates estimated with reasonable precision. There were two notable exceptions to the usefulness

of CS as an indicator of metabolic rate. No CS was detected in *T. lobifera*, and high background values for the *Pelagobia* sp. A specimens resulted in unreliable measurements. Despite these two exceptions it is apparent that CS has value as a predictive tool in estimating the metabolic rates of pelagic polychaetes and nemerteans.

#### *Chemical compositions*

The chemical compositions of the worms in this report suggest that lipid is an important component in their energy budgets. The lipid and protein contents reported here for worms are within the range of those values reported for midwater fishes (CHILDRESS and NYGAARD, 1973) and pelagic crustaceans (CHILDRESS and NYGAARD, 1974) from the same region. Carbohydrate is of little importance in these pelagic worms. Other workers have suggested that carbohydrate is of little importance in other kinds of zooplankton (RAYMONT and KRISHNASWAMY, 1960; CHILDRESS and NYGAARD, 1974; PERCY and FIFE, 1981; LARSON, 1986). The types of worms investigated in this report resemble mesopelagic crustaceans which typically have lipid contents that are higher than their protein contents.

The weight specific energy content of *N. mirabilis* is very similar to that of the benthic nemertean *Parborlasia corrugatus* from Antarctica, however the amount of lipid in *N. mirabilis* is much higher than it is in *P. corrugatus* (PEARSE and GIESE, 1966; HEINE *et al.*, 1991). This large nemertean has a much higher protein content than lipid content and, in contrast to *N. mirabilis*, apparently uses protein as its primary energy storage component. High lipid content may also be a buoyancy adaptation, allowing *N. mirabilis* to maintain its position in the water column.

Since pelagic crustaceans are prey for the carnivorous species of worms studied here, we have calculated their significance in the energy budget of *N. mirabilis*. Assuming an oxyenergetic equivalent of  $13.61 \text{ J mg}^{-1} \text{ O}_2$  (derived from ELLIOTT and DAVISON, 1975), and using the oxygen consumption data from Table 1, the calculated energy demand of a 0.5 g specimen of *N. mirabilis* is  $1.54 \text{ J day}^{-1}$ . This means that the energy content in a 0.03 g bathypelagic copepod (*Gaussia princeps*; CHILDRESS and NYGAARD, 1974) would supply the above nemertean with enough energy for 79 days assuming a conservative assimilation efficiency of 85% and not accounting for any energy that would be diverted into growth or reproduction. This worm could live on its own lipid reserves for 711 days.

*Poebius meseres*, on the other hand, feeds primarily on fecal pellets, but also consumes diatoms and other particulate matter (UTTAL-COOKE, 1992). A 0.5 g *P. meseres* requires  $0.36 \text{ J day}^{-1}$ , and assuming a  $10 \mu\text{g}$  (dry weight) fecal pellet has 0.098 J (JOHANNES and SATOMI, 1966), then five fecal pellets of this size and energy content each day would support its daily energy requirements. In turn, using the same method of calculation, a 0.5 g *N. mirabilis* and a 0.5 g *P. meseres* would supply the bathypelagic myctophid *Lampanyctus regalis* (3.0 g; TORRES *et al.*, 1979) with enough energy for 77 and 19 days, respectively. This demonstrates that these worms are energy-rich as prey items for fish, crustaceans and other carnivorous zooplankton, especially for deeper living fishes and crustaceans that have much lower metabolic rates and organic contents than shallower living species.

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