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Relationship of oxygen consumption to swimming speed in *Euphausia pacifica*

1. Effects of temperature and pressure

J. J. Torres[1] **and J. J. Childress**[2]

[1] **Department of Marine Science, University of South Florida; 140 Seventh Avenue South, St. Petersburg, Florida 33701, USA**

[2] **Oceanic Biology Group, Marine Science Institute and Department of Biological Sciences, University of California; Santa Barbara, California 93106, USA**

Abstract

Oxygen consumption rate was measured as a function of swimming velocity for the vertically migrating euphausiid *Euphausia pacifica* at two temperatures (8° and 12 °C) and pressures (1 and 40 atm) typical of its bathymetric distribution. Increased swimming speed (x; $\mathrm{m\,h^{-1}}$) required increased oxygen consumption (y; $\mu\mathrm{l\,O_2}$ mg dry weight^{-1} $\mathrm{h^{-1}}$), described by the equation $y = 0.012x + 0.64$ at 8 °C, and by $y = 0.020x + 0.85$ at 12 °C. The current concept of low swimming costs of zooplankton, based on determinations of dead drag in copepods, is contradicted by our measurements. Temperature had a more profound effect on metabolism at higher swimming speeds ($112\,\mathrm{m\,h^{-1}}$; $Q_{10} = 2.8$) than on standard metabolism ($0\,\mathrm{m\,h^{-1}}$; $Q_{10} = 2.0$), indicating that activity is more costly at higher temperatures. Pressure caused a small but significant ($P > 0.05$) rise in the relationship of respiratory rate to swimming speed at both temperatures. The energy cost of vertical migration for *E. pacifica* was estimated by applying our data on oxygen consumption vs swimming speed to published observations on sonic scattering layer movement and the day-night distribution pattern of this species. Results indicate that the cost of a diel migration of 254 m, through a temperature change of 4 °C (8° to 12 °C), would cancel any energetic benefit gained by time spent at the lower temperature typical of daytime depth. The act of vertical migration is energetically expensive; its cost should be thoroughly considered in attempts to describe the energetics of vertically migrating species.

Introduction

The metabolic energy expended by a vertically migrating zooplankter is dictated by its activity level and by the ambient temperature and pressure during each phase of its diel distribution cycle. To quantify daily energy usage, the effects of three variables on metabolism must be addressed: locomotory activity, temperature, and pressure. A number of investigations have focused on the latter two variables (Small *et al.*, 1966; Paranjape, 1967; Small and Hebard, 1967; Teal and Carey, 1967; Pearcy and Small, 1968); their results suggest a conventional response to temperature (Q_{10} about 2.0) and a negligible pressure effect. The influence of locomotory activity on the metabolism of zooplankton has received less attention, largely due to the technical difficulty of evaluating oxygen consumption vs swimming speed in small zooplankton. Five studies have dealt directly with locomotion and metabolism. Two studies used experimental methods (Foulds and Roff, 1976; Klyashtorin and Kuz'micheva, 1976), while three studies used calculations of dead drag (Vlymen, 1970; Klyashtorin and Yarzhombek, 1973; Svetlichnyi *et al.*, 1977) to evaluate energetic cost of swimming in zooplankton. The five studies concluded that active metabolism was at most 160% of standard metabolism. Their conclusions contradict a large body of literature (Ivlev, 1963; Halcrow and Boyd, 1967; Fry, 1971; Mickel and Childress, 1978; Quetin *et al.*, 1978; Brett and Groves, 1979 and others) that indicates increased swimming activity can increase metabolic oxygen demand by a factor of 3 to 10 in larger organisms.

It is of critical importance to understand locomotory requirements when modeling the bioenergetics of vertically migrating zooplankton. Though the act of vertical migration occupies a relatively small portion of each day (17–25%: Kampa and Boden, 1954; Clarke and Backus, 1964; Boden and Kampa, 1967), its metabolic cost may be disproportionately large. Previous studies on migration energetics (McLaren, 1963, 1974; Kerfoot, 1970; Enright, 1977) have either considered only the metabolic costs at the surface and daytime depth, ignoring the energetic cost of the migration itself, or have not quantified the costs of migration.

This paper describes the effects of temperature and pressure on the relationship of oxygen consumption to swimming speed in the vertically migrating euphausiid *Euphausia pacifica.* The increased resolution gained by monitoring activity with oxygen consumption rate allows for a clear separation of the effects of temperature, pressure, and swimming velocity on metabolism. The data are used to describe energy consumption over the diel distribution cycle of *E. pacifica* and to quantify the cost of vertical migration.

Materials and methods

Oxygen consumption

Oxygen consumption rate was measured as a function of swimming speed in individual *Euphausia pacifica*, using an annular pressure respirometer (Torres *et al.*, 1982). The device is a Teflon-coated stainless steel annulus that allows unrestricted swimming while simultaneously monitoring swimming velocity and oxygen consumption rate. Oxygen consumption is measured with a polarographic oxygen electrode; activity is monitored using a photoresistor in conjunction with a light emitting diode (LED). Each revolution of an individual around the annulus (0.33-m circumference) is detected by the activity monitor, resulting in a spike on the dual channel strip chart recorder that also records O_2 consumption.

A single experiment consisted of placing an individual *Euphausia pacifica* in the annulus using a pipette, sealing the vessel, and allowing the individual to deplete the oxygen in the system for 12 h. The first 2 h of each run were discarded to minimize the effects of transfer into the vessel. After the first 2 h individuals settled into an intermediate period of activity during which swimming speeds varied from 0 to 150 m h^{-1}. The intermediate portion of each experiment was divided into 30-min increments; total activity and total oxygen consumption were determined for each increment to produce a single observation. Oxygen partial pressure during the intermediate period was between air saturation and 60 mm Hg, well above the levels at which oxygen becomes limiting to *E. pacifica* (Childress, 1975). Five to twelve individual *E. pacifica*, i.e. 5 to 12 single experiments, were used in each experimental treatment. A more complete description of experimental protocol may be found in Torres *et al.* (1982).

The extensive literature on metabolism of fishes (see Fry, 1971; Brett and Groves, 1979 for review) has defined three metabolic rates based on the relationship between activity and oxygen consumption. Standard metabolic rate is the rate at 0 activity and is determined by the intercept of the equation $y = a + bx$. Routine rate is the average oxygen consumption associated with spontaneous activity (Brett, 1972), the value of y at the mean of x in the present study. The active rate is generally considered to be the oxygen consumption at maximal sustained activity under conditions of forced swimming (3–5 body lengths s^{-1} for most teleosts; Alexander, 1970). Our study deals only with spontaneous activity; the maximal swimming speed exhibited by *Euphausia pacifica* could probably be elevated considerably if they were forced to swim at higher speeds (Fry, 1971). For comparisons, 30-min periods of greatest activity in each of the six experimental treatments were averaged to give an arbitrary figure for active metabolism.

Euphausia pacifica

Euphausia pacifica were captured in the Santa Barbara Channel with a 1.5-m (2.3-m^2 mouth area) Tucker trawl from the R. V. Lammer between July and November of 1979. Once on deck the krill were immediately sorted into 1-gallon (3.89 l) polyethylene jars and transported to the laboratory. There they were placed in 1.5-l cylindrical polypropylene containers at a density of two individuals per container. Holding temperature was cycled from 8 °C during daylight hours to 12 °C at night, rising and falling in a time span of 1.5 h. Log-phase cultures of the diatom *Ditylum brightwelli* were used for feeding at densities greatly exceeding the nutritional requirements of the individuals (Ross, 1979). Although *E. pacifica* can be maintained indefinitely, the individuals used in experiments had been in captivity for more than 2 d and less than 3 wk. The captive individuals were maintained in darkness after initial sorting, being exposed to indirect light only during feeding and transfer into the respirometer.

Individual *Euphausia pacifica* can retain food in their stomachs for at least 4 d of starvation, and digestive-enzyme activity persists strongly during that period (Willason, personal communication). For consistency, all individuals were placed in the experimental vessel with no preceding period of starvation. Every individual started and finished each run with a full gut. All individuals were adult females ranging in length from 14 to 17 mm with a mean dry weight of 6.9 ± 0.7 mg ($\bar{x} \pm$ SE).

Temperature

The daytime depth of *Euphausia pacifica* is typically between 200 and 400 m (Brinton, 1962; Clarke, 1966). The cycling temperature regime described above approximates field conditions for this vertically migrating species (Scripps Institute of Oceanography, 1965; Clarke, 1966). Oxygen consumption experiments were conducted at 8° and 12 °C, the lower and upper temperatures of the cycling regime used in maintenance. All experiments at the lower temperature typical of daytime depth (8 °C) were executed during the day and those at 12 °C were conducted at night. This protocol, labelled cycling maintenance-temperature, is abbreviated as CMT.

A second experiment investigated individuals maintained at a constant temperature of 8 °C for at least 5 d. Oxygen consumption was measured at 8 °C (run during the day) and 12 °C (run at night) at atmospheric pressure. The experimental treatments are designated respectively 8 °C, 1 atm, 8 °C constant; and 12 °C, 1 atm, 8 °C constant.

Pressure

The pressure used, 40 atm, corresponds to the lower limit of *Euphausia pacifica's* bathymetric distribution (400 m; Brinton, 1962). Pressure was applied to the annulus using a liquid-chromatography pump (Altex) in concert with a relief valve, creating a flow-through system. Pressure was increased gradually to 40 atm over a period of 45 min at a flow rate of 6 ml min^{-1}. Flow was continued until the oxygen electrode reached a stable calibration point. The entire process required 1 to 2 h. The effects of pressure were tested at both 8° and 12 °C, using the photoperiod-temperature relationship described above. All individuals used in the pressure treatments were maintained in the cycling-temperature bath. These two experimental treatments are designated 8 °C, 40 atm, CMT; and 12 °C, 40 atm, CMT.

A thermistor, encased in epoxy and inserted into the bomb, recorded no change in temperature within the annulus with an increase in pressure during several trials of the experimental procedure. Thus, experimental individuals experienced a slow rise in pressure without a temperature change.

Results

Each of the six experimental treatments was used to generate a curve of oxygen consumption vs activity using the methods described above (Figs. 1–6). The relationship of oxygen consumption (y; μl O_2 mg dry weight^{-1} h^{-1}) to swimming speed (x; m h^{-1}) was best described by an equation of the form $y = a + bx$. The average of the greatest activity in each of the six experimental treatments, indicating active metabolism, was 112 ± 32.6 ($\bar{x} \pm SD$) m h^{-1}. In one preliminary experiment, a swimming speed of 350 m h^{-1} was recorded for an individual, indicating a capacity to swim much more rapidly than 112 m h^{-1}.

Increased swimming speed in all six experiments resulted in a marked increase in oxygen consumption rate (Table 1, Figs. 1–6). Slopes of the six lines ranged from 0.009 to 0.020. They were consistently higher at 12 °C than at 8 °C, resulting in higher Q_{10}'s for active than for standard metabolism (Table 1).

Temperature

The six experiments fall into three pairs, within each pair, only temperature differs between the treatments. These three pairs are: 8 °C, 1 atm, CMT and 12 °C, 1 atm, CMT (Figs. 1 and 2); 8 °C, 40 atm, CMT and 12 °C, 40 atm, CMT (Figs. 3 and 4); 8 °C; 1 atm, 8 °C constant and 12 °C, 1 atm, 8 °C constant (Figs. 5 and 6). The regression lines of each pair are highly significantly different ($P < 0.0001$); analysis of covariance, Barr *et al.*, 1979.

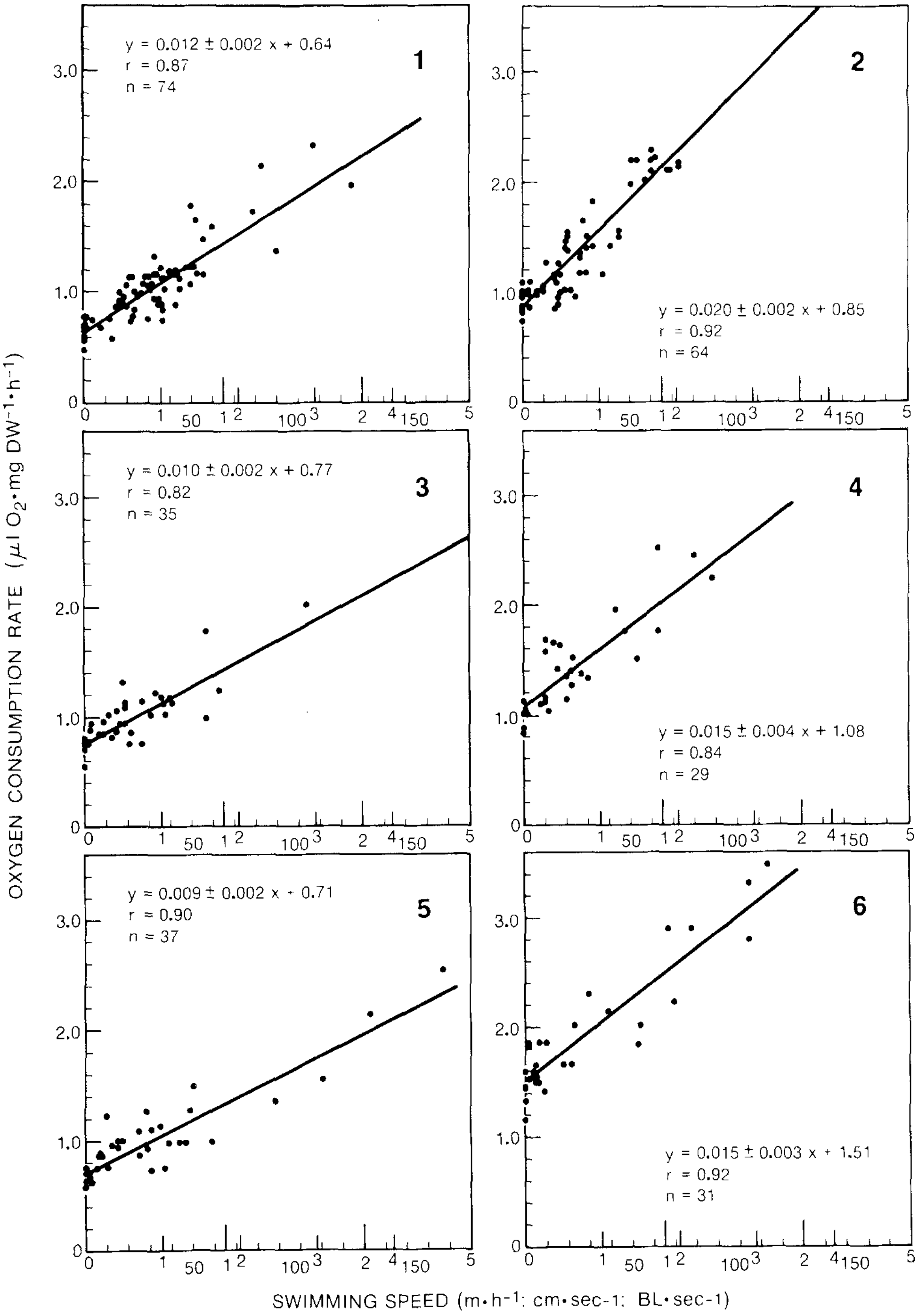
The standard rate observed for the treatment 8 °C, 1 atm, CMT (Fig. 1; Table 1) was 0.64 μl O_2 mg DW^{-1} h^{-1}. This value compared to that of its experimental counterpart, 12 °C, 1 atm, CMT (0.85 μl O_2 mg DW^{-1} h^{-1}), results in a Q_{10} of 2.0 over the temperature range.

The routine rates obtained from the treatments 8 °C, 1 atm, CMT and 12 °C, 1 atm, CMT (Figs. 1 and 2; Table 1) are 1.05 μl O_2 mg DW^{-1} h^{-1} and 1.3 μl O_2 mg DW^{-1} h^{-1} respectively. The Q_{10} for routine rate, 1.74, reflects the difference in mean activity between the two temperatures (32.2 m h^{-1} at 8 °C; 23.3 m h^{-1} at 12 °C).

The metabolism-activity curves at 8° and 12 °C are divergent (Figs. 1 and 2), indicating that increased swim-

Table 1. *Euphausia pacifica.* Metabolic rates, Q_{10}'s, and the relationship of oxygen consumption to swimming speed. Means are given with 95% confidence limits unless otherwise stated

Treatment	8°, 1 atm, CMT	12°, 1 atm, CMT	8°, 40 atm, CMT	12°, 40 atm, CMT	8°, 1 atm, 8° CON	12°, 1 atm, 8° CON
Equation	$y = 0.012x + 0.64$	$y = 0.020x + 0.85$	$y = 0.010x + 0.77$	$y = 0.015x + 1.08$	$y = 0.009x + 0.71$	$y = 0.015x + 1.5$
b ± 95% CI	0.012 ± 0.002	0.020 ± 0.002	0.010 ± 0.002	0.015 ± 0.004	0.009 ± 0.002	0.015 ± 0.003
r	0.87	0.92	0.82	0.84	0.90	0.92
n	74	64	36	29	37	31
No. of individuals	12	9	8	6	5	5
Mean Dry Weight (mg, $\bar{X} \pm SD$)	7.3 ± 1.3	5.6 ± 1.4	6.9 ± 1.8	7.8 ± 3.3	7.1 ± 1.5	6.7 ± 2.0
Standard Rate (μl O_2 mg DW^{-1} h^{-1})	0.64 ± 0.12	0.85 ± 0.16	0.77 ± 0.11	1.08 ± 0.11	0.71 ± 0.15	1.51 ± 0.25
Q_{10}	2.0		2.3		6.6	
Routine Rate (μl O_2 mg DW^{-1} h^{-1})	1.05 ± 0.07	1.31 ± 0.11	1.00 ± 0.08	1.45 ± 0.15	1.01 ± 0.12	1.94 ± 0.20
Q_{10}	1.7		2.5		5.1	
Active Rate (μl O_2 mg DW^{-1} h^{-1})	2.00 ± 0.25	3.06 ± 0.46	1.92 ± 0.32	2.72 ± 0.54	1.78 ± 0.27	3.18 ± 0.51
Q_{10}	2.8		2.4		4.3	
Mean Activity (m h^{-1}; $\bar{x} \pm SD$)	32.3 ± 24.4	23.3 ± 21.2	22.8 ± 22.1	24.9 ± 24.9	31.8 ± 38.0	27.7 ± 35.2



Figs. 1–6. *Euphausia pacifica.* The relationship of oxygen consumption rate to swimming speed for all six experiments. Curves derived as in Torres *et al.* (1982). Swimming speed is expressed in $m \cdot h^{-1}$ (small hash-marks), $cm \cdot s^{-1}$ (medium hash-marks), and body lengths $\cdot\ s^{-1}$ (large hash-marks). **Fig. 1:** 8 °C, 1 atm, Cycling Maintenance Temperature (CMT). **Fig. 2:** 12 °C, 1 atm, CMT. **Fig. 3:** 8 °C, 40 atm, CMT. **Fig. 4:** 12 °C, 40 atm, CMT. **Fig. 5:** 8 °C, 1 atm, 8 °C constant. **Fig. 6:** 12 °C, 1 atm, 8 °C constant

ming velocity has a greater effect on metabolism at higher temperature.

The experiments at 8 °C, 40 atm, CMT (Fig. 3) to 12 °C, 40 atm, CMT (Fig. 4) can be compared. The Q_{10} for standard rate is 2.3 (Table 1), largely due to the increased standard rate of the 12 °C, pressure treatment. The slope of the 12 °C curve is greater than that of the 8 °C curve (Table 1), a Q_{10} for active metabolism of 2.4.

The experiments at 8 °C, 1 atm, CMT and 8 °C, 1 atm, 8 °C constant (Figs. 1 and 5) can be compared. The curves are not significantly different by analysis of covariance ($P > 0.496$) and are very similar. In contrast, if the experiments at 12 °C, 1 atm, CMT and 12 °C, 1 atm, 8 °C constant are compared (Figs. 2 and 6; Table 1), the two lines are significantly different by analysis of covariance ($P < 0.0001$).

There is a much larger Q_{10} for the two curves from the 8 °C constant regime than in either of the two comparisons with cycling individuals. Standard rates have a Q_{10} of 6.55. The data suggest metabolic overshoot and indicate that *Euphausia pacifica* is capable of thermal acclimation.

Pressure

The effects of pressure at 8 °C, 1 atm, CMT (Fig. 1) can be compared with 8 °C, 40 atm, CMT (Fig. 3). Analysis of covariance showed these lines to be significantly different ($P > 0.054$), indicating that pressure is a significant, but small, cause of variability in the data. The effect of pressure at 12 °C, 1 atm, CMT (Fig. 2) and 12 °C, 40 atm, CMT (Fig. 4) are very similar. The curves are significantly different by analysis of covariance ($P > 0.056$).

Discussion

The energy demand of increased locomotory activity can result in a more than three-fold increase in oxygen consumption rate in *Euphausia pacifica.* This is consistent with results from investigations on larger swimming crustaceans (Ivlev, 1963; Halcrow and Boyd, 1967; Mickel and Childress, 1978; Quetin, 1979) but disagrees with existing literature on energy costs of swimming in zooplankton (Lasker, 1966; Vlymen, 1970; Foulds and Roff, 1976; Klyashtorin and Kuz'micheva, 1976; Svetlichnyi *et al.*, 1977).

Prevailing views on the cost of swimming to zooplankton are primarily based on determinations of dead drag (cf. Webb, 1975) in copepods and euphausiids (Vlymen, 1970; Klyashtorin and Yarzhombek, 1973; Svetlichnyi *et al.*, 1977). Metabolic power required for swimming was computed by those authors as the product of thrust power required to overcome dead drag and an overall efficiency factor of 0.05 (assuming a metabolic-contractile efficiency of 0.1 and an efficiency of 0.5 for paddle propulsion; Vlymen, 1970 did not allow for biological inefficiency in his calculations and clearly stated so). Calculated values were compared to those obtained in respiration measurements resulting in a maximal cost of 1.4 to 1.6 times the "basal" rate for increased swimming activity.

A major cause for disagreement between our conclusions and those of Vlymen (1970), Klyashtorin and Yarzhombek (1973) and Svetlichnyi *et al.* (1977) is in their failure to recognize the difference between standard (basal) and routine metabolism. All values quoted as standard were actually routine rates, because activity was not monitored or controlled. Routine rates are elevated well above standard or resting metabolism because normal spontaneous activity is incorporated into the measured metabolic rate. The confusion between standard and routine respiration has resulted in very low estimates for swimming costs in zooplankton. Increases in respiration due to activity are actually nearly three times the resting rate. A second source of discrepancy is that previous estimates of swimming efficiency are based on similar determinations for fishes two to three orders of magnitude larger in size. No data exist on swimming efficiency in fishes weighing less than 1 g, or for efficiency of the multiple paddle propulsive systems typical of pelagic crustaceans. Analyses by Webb (1975) indicate that swimming efficiencies in sockeye salmon (*Oncorhynchus nerka*) may decrease radically below a weight of 8 g. Thus, efficiency in smaller (1 to 100 mg) swimming animals is presently a matter of conjecture.

Empirical determinations of energy consumption in zooplankton swimming have also indicated that increased swimming speed results in only a small increase in respiration over the routine rate (Foulds and Roff, 1976; Klyashtorin and Kuz'micheva, 1976). Both studies used groups of organisms in their determinations of routine respiration and swimming costs (Foulds and Roff, 1976; 12 individuals per experiment; Klyashtorin and Kuz'micheva, 1976; 200–300 individuals per experiment). That factor would elevate routine metabolism and mask costs of swimming either through asynchrony in individual swimming speeds within the group, or through drafting effects. In addition, routine rates vary with the amount of spontaneous activity during the measurement. In our study (8 °C; 1 atm) routine respiration corresponds approximately to swimming speeds between 8 and 57 $m\ h^{-1}$ (mean activity ± SD). Thus, Foulds and Roff (1976) and Klyashtorin and Kuz'micheva (1976) determined cost of swimming by a comparison of energy consumption at a known activity level (0.7 to 3.6 $cm\ s^{-1}$, Foulds and Roff, 1976) with that of an unknown: routine metabolism. Both the techniques employed and their method of determining swimming costs raise serious questions about the validity of their conclusions.

Temperature is the most important physical factor influencing the metabolic rate of *Euphausia pacifica.* The observed Q_{10} for standard rate (2.0) in individuals maintained at fluctuating temperature does not support a case for metabolic compensation. However, neither does it show the overshoot typically seen in the metabolism of ectotherms after an abrupt change in temperature (Prosser, 1973). The standard metabolism of those individuals maintained in cycling temperature reacts to the temperature change of 4 °C as if acclimated to both 8° and 12 °C, affording the individual a small degree of temperature independence resulting from the lack of metabolic undershoot at 8 °C or overshoot at 12 °C.

The Q_{10} for routine metabolism of individuals maintained in cycling temperature (1.74) shows the confounding effect of locomotory activity in any assessment of temperature effects on metabolic rate (cf. Holeton, 1974). The difference in mean activity between the two temperatures (32.2 $m\ h^{-1}$ at 8 °C; 23.3 $m\ h^{-1}$ at 12 °C) and the effect of temperature itself interacted to produce a Q_{10} of less than 2.0. Routine metabolic rate, while defined as the average oxygen consumption rate associated with spontaneous activity (Brett, 1972), is widely used to describe any measurement of oxygen consumption in which activity is unmonitored. All previous measurements of oxygen consumption in *Euphausia pacifica* are examples of this type of routine rate. Values for the oxygen consumption rate of *Euphausia pacifica* at 10 °C range from $0.79 \pm 0.22\ \mu l\ O_2\ mg\ DW^{-1}\ h^{-1}$ ($\bar{x} \pm 95\%$ CI; Paranjape, 1967) to $1.65 \pm 0.12\ \mu l\ O_2\ mg\ DW^{-1}\ h^{-1}$ (Pearcy and Small, 1968), with all values except those of Paranjape above the value of $1.18\ \mu l\ O_2\ mg\ DW^{-1}\ h^{-1}$ obtained by averaging our routines rates at 8° and 12 °C (cf. Lasker, 1966: $1.47\ \mu l\ O_2\ mg\ DW^{-1}\ h^{-1}$; Small *et al.*, 1966: $1.28\ \mu l\ O_2$

mg DW^{-1} h^{-1}; Small and Hebard, 1967; 1.31 μl O_2 mg DW^{-1} h^{-1}; Pearcy *et al.*, 1969: 1.34 μl O_2 mg DW^{-1} h^{-1}). Our value of 1.18 μl O_2 mg DW^{-1} h^{-1} is within the previously reported range of values, below the values of all of the manometric methods, and between the values of the two Winkler-bottle determinations (Paranjape, 1967; Pearcy and Small, 1968). Those techniques either confine (Winkler) or confine and agitate (Gilson, Warburg) euphausiids, resulting in unpredictable activity levels. Our apparatus allows for unrestricted swimming, and our results suggest the existence of possible bias in the other methods.

Temperature had a more profound effect at higher activity levels (Q_{10}'s = 2.8; 2.4 for individuals maintained in cycling temperature) suggesting that increased swimming speed costs more energy at the surface than at daytime depth. There was no evidence for thermal compensation on the part of *Euphausia pacifica* ($Q_{10} \leqslant 2.0$) despite the fact that the individuals were maintained in a fluctuating temperature regime approximating field conditions, i.e. the metabolism of *Euphausia pacifica* showed no independence from temperature that would suggest a constant metabolic rate at the surface and at daytime depth. The small effect of pressure would not change that conclusion (cf. Teal and Carey, 1967).

Euphausia pacifica is capable of thermal acclimation if maintained at a fixed temperature for a period of time. Thermal acclimation involves an inducible adjustment in the quantity or quality of enzymes involved in oxidative metabolism for more efficient metabolic function at a new temperature (Hochachka and Somero, 1973). It should be distinguished from thermal compensation which, in this case, would indicate a metabolic machinery that does not increase its overall reaction velocity in response to increasing temperature, even if the change in temperature is abrupt. The metabolism of *Euphausia pacifica* adjusts to temperature over time, as indicated by the high Q_{10} (6.6) obtained for standard rate of individuals held at 8 °C and measured at 12 °C. *Euphausia pacifica* does not appear capable of maintaining a constant metabolic rate when exposed to abrupt changes in temperature, even if it is maintained in a fluctuating temperature regime. The results of the acclimation treatments suggest that maintenance protocol is an important consideration in any study of the metabolism of vertically migrating species.

The underestimation of locomotory costs in zooplankton has misled several authors (Kerfoot, 1970; McLaren, 1974; Steele, 1974; Enright, 1977) into dismissing the cost of the vertical migration in consideration of the bioenergetics of the phenomenon. Both Vlymen (1970) and Foulds and Roff (1976) specifically stated the qualifications on any direct application of their data to the field situation. However, their qualifications have been consistently ignored by those desiring to model the flow of energy in planktonic systems.

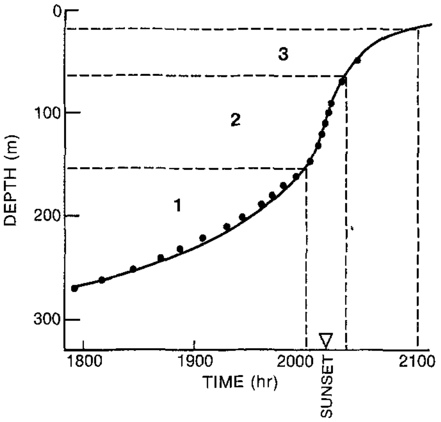


Fig. 7. *Euphausia pacifica.* Ascent of 17.5 KH_z scattering layer (solid line) and 10^{-4} $\mu W \cdot cm^{-2}$ isolume (dots), in San Diego Trough, 30 June 1954. The three phases of the migration used to deduce swimming speeds are delineated 1, 2 and 3. Figure redrawn from Kampa and Boden (1954)

The best example of migratory behavior for *Euphausia pacifica* is that of Kampa and Boden (1954) for the ascent of the 10^{-4} μW cm^{-2} isolume and its associated sound-scattering layer in the San Diego Trough (Fig. 7). The ascent of the scattering layer to the surface is triphasic and is completed during a time span of 3 h. The first portion of upward movement occurs about 2.2 h before sunset as the isolume and its associated scattering layer ascend at a velocity of 60 m h^{-1} from a depth of 270 m to a depth of 150 m. Just before (0.2 h) sunset, the scattering layer rapidly rises to the surface at a velocity of 270 m h^{-1}. That velocity is sustained for 0.33 h, whereupon the ascent is slowed to 68 m h^{-1} in the last 0.67 h as the isolume reaches its nighttime depth of 16 m.

The two most important factors influencing the energetic cost of the vertical migration are the temperature profile of the water column through which movement occurs and the swimming speeds in each portion of the migration. We have used the thermal profile of the water column typical of the upwelling season in Santa Barbara Basin (Scripps Institute of Oceanography, 1965) for calculation. It may be roughly characterized as having a linear rise in temperature with depth from about 8 °C at 270 m, to about 12 °C at 16 m. In order to be conservative about the energy expended in swimming, we calculated the mean slope for all six curves of oxygen consumption vs activity (Figs. 1–6; Table 1) as the index for the cost of increasing swimming speed during the migration. Thus, for the equation $y = bx + a$, which describes all six curves, the term $b = 0.014$ and remains constant. The effects of temperature are expressed only in the term a, the y intercept, or standard metabolic rate. The mean value for the influence of temperature on standard rate from Figs. 1–4 was used ($Q_{10} = 2.17$) for calculation of the effects of temperature during the migration.

Our calculations indicate that a migration of the type considered through a thermal profile like that of Santa Barbara Basin, would result in an expenditure of 0.19 cal (41.1 μl oxygen assuming an oxycaloric equivalent of 4.63 Kcal l^{-1} O_2; Brett and Groves, 1979) for an individual *Euphausia pacifica* of 6.9 mg DW, the mean weight of individuals used in this study. The total energy expended per day by a migrating *Euphausia pacifica* may be calculated by adding the total energy expended during migration to the energy expended by spending 9 h at both 12° and 8 °C, using the routine rates measured in this study. The result is 1.07 cal (231.2 μl O_2) per day expended on metabolism for an individual of 6.9 mg DW. This is about equal to what would be expended by spending 24 h at 12 °C: 1.06 cal or 228.4 μl O_2 per day. Thus, for the case examined here, the energy expended in swimming to the surface and back to daytime depth (35.6% of the total) is sufficient to remove any energetic benefit that might have accrued by spending days in the cooler waters typical of the greater depth in the water column (cf. McLaren, 1963).

It must be stressed that the thermal characteristics of the water column in different areas of the world's oceans will exert considerable influence on both the energy expended in migration and the energy that would be expended by spending 24 h at surface temperature. In the Antarctic, where the water at a depth of 300 m is often warmer than that at the surface (Jacobs and Amos, 1967), it is probable that a substantial energy loss would be incurred by migration. In contrast, in the central Pacific where the temperature difference between the surface and a depth of 500 m is 16 °C (Scripps Institute of Oceanography, 1963) a substantial benefit would probably ensue. Further conclusions regarding the energetics of vertical migration await studies of the type described here on migrators from different locations.

Any future consideration of the energetics of vertically migrating zooplankton should include the energy expended during the migration itself. Increasing swimming speed results in greatly increasing oxygen consumption in euphausiids, shrimp, and fishes, making the act of vertical migration expensive for all scattering layer organisms.

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