

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

II. Drag, efficiency and a comparison with other swimming organisms

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Abstract

Swimming efficiency (the ratio of thrust power required to overcome hydrodynamic drag to net metabolic energy expenditure) was calculated for the vertically migrating euphausiid *Euphausia pacifica* swimming at speeds of 1–20 cm s⁻¹ and at temperatures of 8° and 12 °C. Efficiencies ranged from 0.014 to 2.8% at 8 °C and 0.009 to 1.69% at 12 °C. A comparison with efficiency in fishes 2–3 orders of magnitude larger in weight (efficiency range ~ 10–25%) indicates that locomotion in *E. pacifica* is far less efficient, a probable result of the organism's small size (\bar{x} = 33.5 mg WW) and multiple-paddle mode of propulsion. Net cost of transport of *E. pacifica* is three to six times the cost of a hypothetical value for sockeye salmon. Low swimming efficiencies in zooplankton such as *E. pacifica* are responsible for the underestimation of zooplankton swimming costs. Multiple-paddle propulsion is less efficient than the undulatory mode of fishes.

Introduction

Locomotory efficiency, the ratio of total drag to the metabolic energy used in propulsion, is an excellent means of comparing different propulsive mechanisms and of evaluating the influence of size on locomotory costs. Studies on locomotory efficiency in swimming organisms have primarily focused on teleost fishes greater than 5 cm in length (cf Webb, 1975 a), largely due to the difficulties associated with direct measurement of swimming costs in smaller organisms. It has been assumed that swimming efficiency in crustacean zooplankton (1–30 mm total length) is about 5% (Klyashtorin and Yarzhombek, 1973; Svetlichnyi *et al.*, 1977) for purposes of calculating swimming cost from determinations of dead drag.

The accuracy of swimming costs calculated from the ratio of drag to swimming efficiency depends on the

accuracy of the assumed efficiency. The only available direct measurements of swimming efficiency are in fishes two to three orders of magnitude larger in weight than crustacean zooplankton. The fishes have efficiencies ranging from 10–25% (Webb, 1975 a, b). The large differences in size between zooplankton and fishes (Reynolds numbers: zooplankton ~ 10⁰–10³; fishes ~ 10⁴–10⁷), their very different propulsive mechanisms (undulatory vs paddle propulsion) and the paucity of data describing locomotion in zooplankton suggested a need for further inquiry into the efficiency of zooplankton swimming.

This paper examines the swimming efficiency of zooplankton using *Euphausia pacifica* as an example. The power required to overcome the drag of the individual is obtained from hydrodynamic theory (theoretical drag) and compared to recent measurements of the rates of energy expenditure associated with swimming at various speeds (Torres and Childress, 1983). Four of the most specialized terms used in the paper are defined below. Webb (1975 a) and Vogel (1981) give detailed treatment of hydrodynamics relevant to biologists.

Theoretical drag – the hydrodynamic resistance of a rigid body with the same dimensions as the animal to which it is compared (Webb, 1975 a).

Dead drag – the measured hydrodynamic resistance of a dead animal (cf. Brett, 1963).

Critical swimming speed – the maximum swimming speed able to be sustained for 60 min (Brett, 1964).

Standard Metabolic Rate – the oxygen consumption rate associated with no activity; the ectothermic equivalent of basal metabolic rate (Brett, 1964).

Material and methods

Theoretical drag power was calculated from the standard hydrodynamic equation (Batchelor, 1967)

$$P_D = 1/2 \rho A U^3 C_d,$$

where

P_D = theoretical drag power (ergs s^{-1})

ρ = density of seawater ($g\ cm^{-3}$)

U = swimming speed ($cm\ s^{-1}$)

C_d = drag coefficient

A = cross-sectional area of the animal (cm^2).

Cross-sectional area A was found by measuring the width and depth of ten *Euphausia pacifica* (16.2- to 20.4-mm total length) at the midpoint of the carapace, using micrometer calipers and calculating the area of an equivalent ellipse. A least-squares regression yielded the relationship $A = 3.24 + 0.45\ l$ ($r = 0.65$), where A is cross-sectional area (mm^2) and l is total length in mm. A cross-sectional area of $4.4\ mm^2$ corresponded to the mean total length of animals (17 mm) used to obtain oxygen consumption data (Torres and Childress, 1983); this value was chosen as A .

The density, ρ , of seawater at temperatures of 8° and $12^\circ C$ and a salinity of 34‰ S came from tables of the US Navy Hydrographic Office (La Fond, 1951); values were 1.0265 and $1.0258\ g\ cm^{-3}$, respectively. These values of temperature and salinity were used to obtain the viscosity (Sverdrup *et al.*, 1942) and kinematic viscosity of the seawater, 0.014 ($8^\circ C$) and 0.013 ($12^\circ C$) stokes.

Drag coefficient (C_d) was calculated using the equation for drag coefficient of a sphere (White, 1974).

$$C_d = \frac{24}{Re} + \frac{6}{1 + Re^{1/2}} + 0.4,$$

where

$$Re = \frac{UL}{\nu},$$

where

U = swimming velocity ($cm\ s^{-1}$)

L = total length (1.7 cm)

ν = kinematic viscosity of the seawater.

Reynolds numbers (Re) ranged from 121 to 2616 for *Euphausia pacifica* swimming at speeds between 1 and $20\ cm\ s^{-1}$ (Table 1). Drag coefficient (C_d) for a sphere was specifically chosen to maximize values for theoretical drag power (P_D). Empirically determined drag coefficients are available for the dead drag of *E. superba* (Kils, 1979), a congener three times the length of *E. pacifica*. Values for C_d and theoretical drag power using Kils (1979) data are reported in Table 1 for purposes of comparison.

Swimming efficiency (η_{aerob}) was calculated from the ratio of theoretical drag power (P_D) at a given swimming speed to the metabolic power (P_{aerob}) required for swimming at that speed. Thus

$$\eta_{aerob} = \frac{P_D}{P_{aerob}} \times 100.$$

The oxygen available for propulsion at any speed was calculated as the difference between that consumed at that speed and the standard rate. Values used were those from

Table 1. *Euphausia pacifica*. Reynold's numbers (Re), drag coefficients (C_d), drag power (P_D), metabolic power (P_{aerob}) and efficiencies for *E. pacifica* at 8° and $12^\circ C$ and swimming speeds (U) between 1 and $20\ cm\ s^{-1}$

(cm s^{-1})	Re (8°)	Re (12°)	C_d (sphere) 8°	C_d (sphere) 12°	C_d (<i>E. superba</i>)	P_D 8° sphere (ergs s^{-1})	P_D 12° sphere (ergs s^{-1})	P_D (<i>E. superba</i>) (ergs s^{-1})	P_{aerob} 8° (ergs s^{-1})	P_{aerob} 12° (ergs s^{-1})	Efficiency (%)			
											8° sphere	12° sphere	$8^\circ E. superba$	$12^\circ E. superba$
1	121.4	130.8	1.097	1.066	0.745	0.025	0.024	0.017	168.1	280.1	0.014	0.009	0.010	0.006
2	242.8	261.5	0.861	0.841	0.618	0.156	0.152	0.112	336.2	560.2	0.046	0.027	0.033	0.019
3	364.3	392.3	0.765	0.750	0.555	0.467	0.458	0.339	504.3	840.3	0.093	0.054	0.067	0.040
4	485.7	523.1	0.710	0.697	0.512	1.03	1.01	0.741	672.3	1120	0.153	0.090	0.110	0.066
5	607.1	653.8	0.674	0.663	0.480	1.90	1.87	1.36	840.4	1400	0.226	0.134	0.162	0.097
6	728.6	784.6	0.647	0.637	0.458	3.16	3.11	2.24	1008	1680	0.313	0.185	0.222	0.133
7	850.0	915.4	0.627	0.618	0.440	4.86	4.79	3.41	1176	1960	0.413	0.244	0.290	0.174
8	971.4	1046	0.611	0.603	0.425	7.07	6.97	4.92	1344	2240	0.526	0.311	0.366	0.220
9	1093	1176	0.598	0.590	0.410	9.85	9.72	6.75	1512	2521	0.651	0.386	0.446	0.268
10	1214	1308	0.587	0.580	0.400	13.3	13.1	9.04	1680	2801	0.790	0.468	0.538	0.323
11	1336	1439	0.578	0.571	0.390	17.4	17.2	11.7	1849	3082	0.941	0.557	0.634	0.381
12	1457	1570	0.570	0.563	0.381	22.3	22.0	14.9	2017	3362	1.10	0.654	0.738	0.443
13	1579	1700	0.563	0.556	0.373	28.0	27.6	18.5	2185	3642	1.28	0.758	0.848	0.509
14	1700	1831	0.556	0.550	0.366	34.5	34.1	22.7	2353	3922	1.47	0.870	0.965	0.579
15	1821	1962	0.550	0.545	0.358	42.0	41.6	27.3	2521	4202	1.66	0.989	1.08	0.650
16	1943	2093	0.545	0.540	0.353	50.5	50.0	32.7	2689	4482	1.88	1.12	1.22	0.729
17	2064	2224	0.541	0.535	0.347	60.1	59.4	38.5	2857	4762	2.10	1.24	1.35	0.809
18	2186	2354	0.537	0.531	0.342	70.8	70.0	45.1	3026	5042	2.34	1.39	1.49	0.894
19	2307	2485	0.532	0.528	0.337	82.5	81.8	52.2	3194	5322	2.58	1.53	1.63	0.982
20	2429	2616	0.529	0.524	0.331	95.6	94.7	59.8	3362	5602	2.84	1.69	1.78	1.07

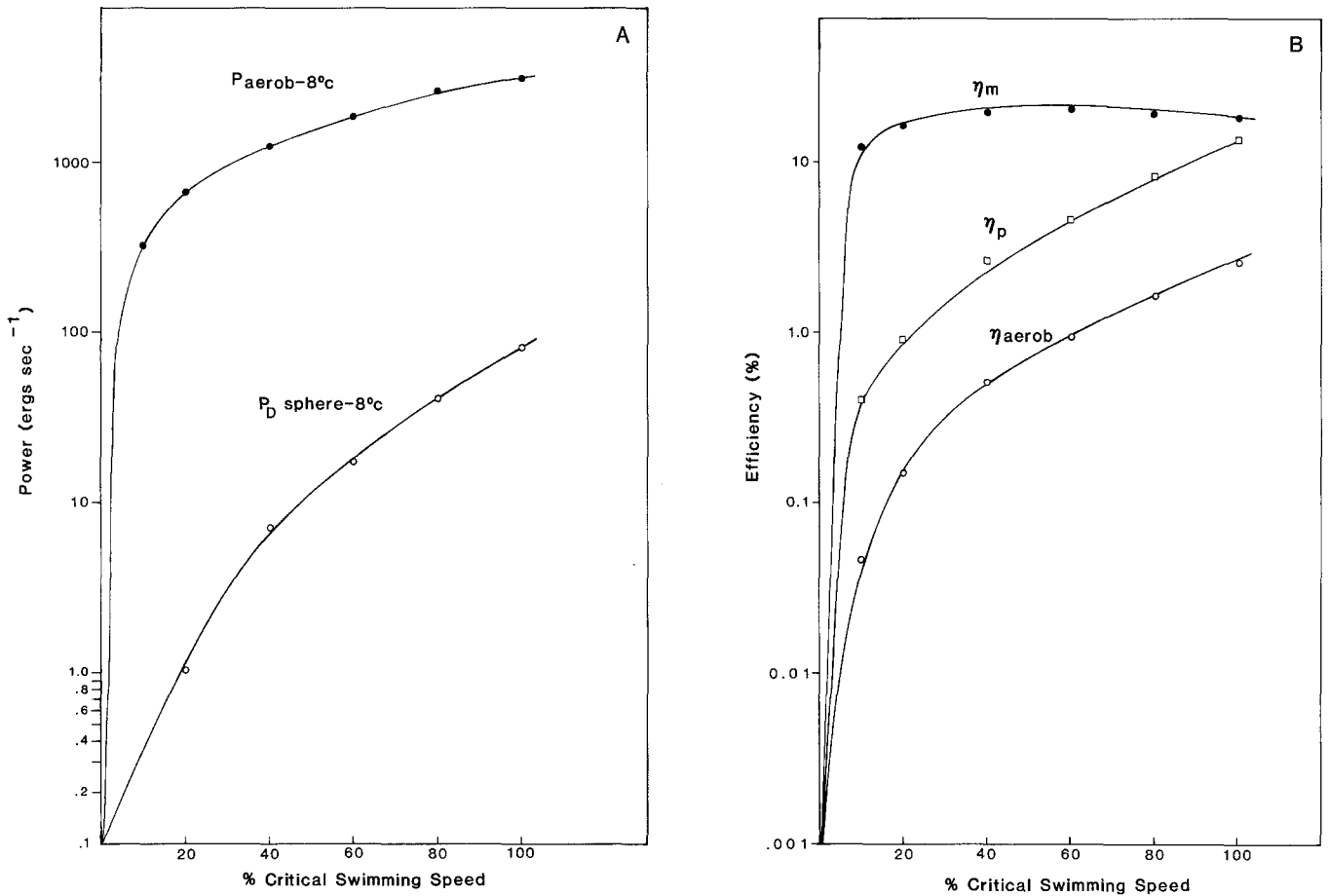


Fig. 1. Summary of the relationships between metabolic power (P_{aerob}) and theoretical drag power (P_D sphere), and between aerobic efficiency, muscular efficiency and propellor efficiency expressed as a percentage of critical swimming speed. (A) Closed circles represent metabolic power available for propulsion as a function of percent U_{crit} ; open circles represent the theoretical drag power calculated as explained in text. (B) Closed circles represent muscle efficiency based on the assumption that crustacean muscles behave in the same way as vertebrate muscle systems with maximum power output occurring at U_{crit} . Aerobic efficiency values (open circles) are taken from Table 1. Propellor efficiency (open squares) has been calculated from the relationship between muscular efficiency and aerobic efficiency as explained in text

Figs. 1 and 2 (8 °C, 1 ATM, CMT and 12 °C, 1 ATM, CMT) in Torres and Childress (1983). Thus, oxygen available for propulsion was calculated as $y=0.012 x$ [$y=\mu l O_2 mg DW^{-1} h^{-1}$; x =swimming speed ($m h^{-1}$) $DW=6.9 mg$] at 8 °C and $y=0.020 x$ at 12 °C. Metabolic power was calculated assuming an oxy-calorific equivalent of $2.0 \times 10^5 ergs s^{-1} \mu l O_2^{-1}$ (Webb, 1975 a).

Propulsive efficiency (η_p) was calculated from the relationship between muscular efficiency (η_m) and total swimming efficiency (η_{aerob}):

$$\eta_{aerob} = \eta_m \times \eta_p.$$

Values for muscular efficiency were obtained from the data of Hill (1950) using the method of Webb (1971 b), fitting Hill's data by letting maximum muscle efficiency be reached at the critical swimming speed. A theoretical value for critical swimming speed (U_{crit} ; maximum sustainable swimming speed) of *Euphausia pacifica* was calculated from the equation relating size to critical swimming speed in sockeye salmon (Brett and Glass, 1973): $\log Y = 1.1289 + 0.6345 \log x$ [Y =speed ($cm s^{-1}$)

and x =total length (1.7 cm)]. This resulted in a critical swimming speed of $18.8 cm s^{-1}$ for *E. pacifica*.

The minimum cost of transport is most often used for comparison of relative swimming costs. This is obtained from the plateau area of exponential speed vs oxygen consumption curves. The linear relationship of oxygen consumption to swimming speed in *Euphausia pacifica* precludes this type of analysis. Instead, cost of transport was calculated from the oxygen available for propulsion at 75% of a species' critical swimming speed (U_{crit}) from the literature cited in the legend of Fig. 3. This figure (75% U_{crit}) approximates the value for peak muscular efficiency during swimming; (Webb, 1971 b) and is easily compared with previous literature on cost of transport (Tucker, 1970; Schmidt-Nielsen, 1972; Beamish, 1978). When a value for U_{crit} was not available, mean swimming speed was used; data collected at 15 °C were used when possible. Thus:

cost of transport ($cal g^{-1} km^{-1}$) =

$$\frac{cal g^{-1} h^{-1} (75\% U_{crit}) - cal g^{-1} h^{-1} (std rate)}{Km h^{-1} (75\% U_{crit})}$$

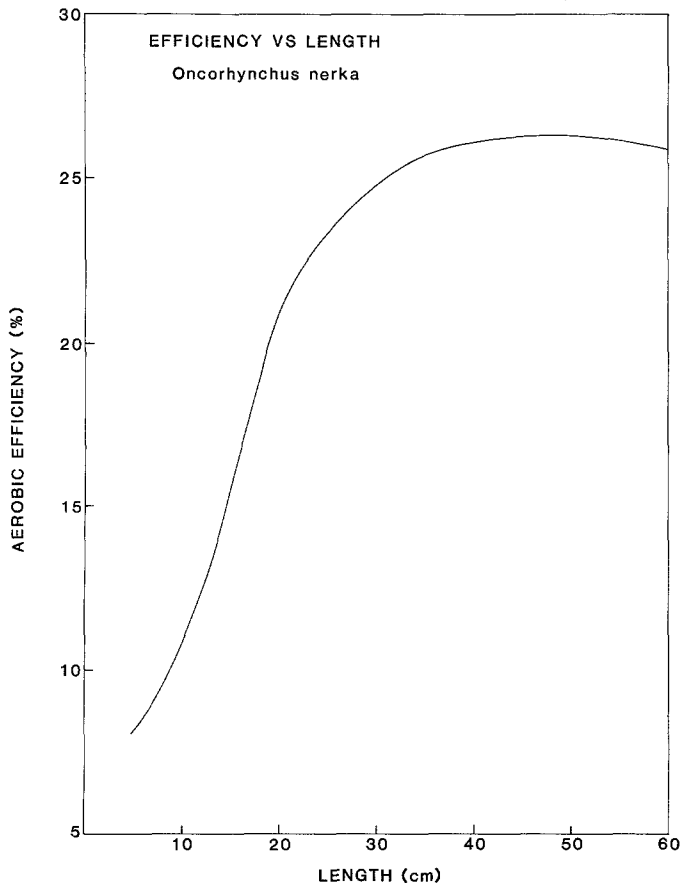


Fig. 2. *Oncorhynchus nerka*. Overall efficiency as a function of length for sockeye salmon at 15 °C. Figure redrawn from Webb, 1975a

Results and discussion

Swimming efficiency

Swimming efficiency in *Euphausia pacifica* varies from 0.014% (1 cm s⁻¹) to 2.85% (20 cm s⁻¹) at 8 °C and from 0.009% to 1.69% at 12 °C (Table 1). In contrast, swimming efficiency in teleost fishes varies from 10% in *Cymatogaster aggregata* (Embiotocidae, Webb, 1975 b) to 26% in *Oncorhynchus nerka* (Salmonidae, Webb, 1975 a) when swimming at critical speeds. Physiological determinations of muscular efficiency indicate that the maximum expected overall efficiency is about 25% (Hill, 1950). Large streamlined fishes with high propulsive efficiency, e.g. *O. nerka* (sockeye salmon), approach this ideal figure, whereas smaller fishes and fishes with oscillatory fin-propulsive mechanisms such as pectoral fin propulsion (e.g. *C. aggregata*) exhibit lower overall efficiencies.

Swimming efficiency is at least one order of magnitude lower in *Euphausia pacifica* than that expected on the basis of similar studies on fishes. There are two possible sources of error that might cause the observed low efficiencies in *E. pacifica*: (1) the empirically determined cost of swimming is too high [see Torres and Childress, 1983]; (2) theoretical drag as calculated is too low.

Swimming metabolism

There are no data directly comparable to that reported in Torres and Childress (1983). However, studies have

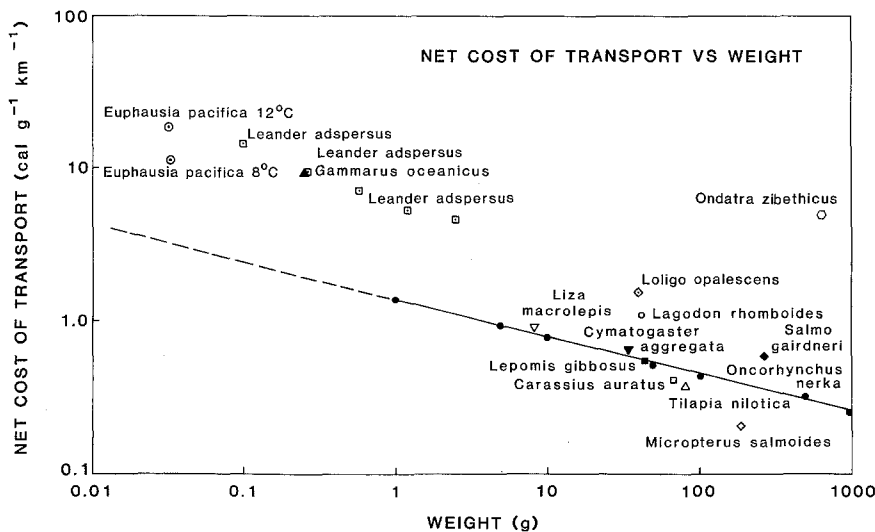


Fig. 3. Net cost of transport as a function of weight for twelve swimming species (after Schmidt-Nielsen, 1972; Beamish, 1978). Cost was calculated at 75% of critical swimming speed if data were available; if not, averaged swimming speed was used. Temperature chosen for calculation was 15 °C or that closest to 15 °C. The solid line represents a regression of cost of transport vs weight for *Oncorhynchus nerka* between 1 and 1 000 g from data in Brett and Glass, 1973 (equation: $y = 1.416 W^{-0.25}$, y = net cost of transport (cal g⁻¹ km⁻¹) w = weight (g) $r = 0.99$). The dashed line is an extrapolation of the solid line into weight values typical of zooplankton species, for purposes of comparison. Data from the following papers were used to construct this graph: *Carassius auratus*, Smit *et al.*, 1971; *Cymatogaster aggregata*, Webb, 1975 b; *Euphausia pacifica*, Torres and Childress, 1983; *Gammarus oceanicus*, Halcrow and Boyd, 1967; *Lagodon rhomboides*, Wohlschlag *et al.*, 1968; *Leander adspersus*, Ivlev, 1963; *Lepomis gibbosus*, Brett and Sutherland, 1965; *Liza macrolepis*, Kutty, 1969; *Loligo opalescens*, O'Dor, 1982; *Micropterus salmoides*, Beamish, 1970; *Ondatra zibethicus* (muskrat) Fish, 1982; *Salmo gairdneri*, Webb, 1971 b; *Tilapia nilotica*, Farmer and Beamish, 1969

reported routine metabolic rates for *Euphausia pacifica* at 10 °C: 0.79 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$, (Paranjape, 1967); 1.28 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$, (Small *et al.*, 1966); 1.31 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$, (Small and Hebard, 1967); 1.34 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$, (Pearcy *et al.*, 1969); 1.47 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$, (Lasker, 1966); and 1.65 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$, (Pearcy and Small, 1968). In comparison, averaging the routine rates at 8° and 12 °C in Torres and Childress (1983) produces a figure of 1.18 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$, at the low end of the range (0.79–1.65 $\mu\text{l O}_2 \text{ mg DW}^{-1} \text{ h}^{-1}$) for routine rate in *E. pacifica*. Thus, while the slope of the oxygen consumption vs swimming speed relationship cannot be directly addressed, the data are quite comparable to those available. It should be noted that the data need to be in error by an order of magnitude to account for the very low efficiency in *E. pacifica*, which is clearly not the case.

Drag

Calculations of theoretical drag intentionally maximized drag values by using the drag coefficient of a sphere. Reynolds numbers for *Euphausia pacifica* (range 121–2616) are in the range where inertial forces exceed viscous forces in determining total drag. At these Reynolds numbers the sphere may be considered a bluff body, a conformation that yields little or no hydrodynamic advantage such as that conferred by a fusiform shape. For comparison, drag coefficients and total drag power are presented in Table 1, using values obtained from Kils' (1979) study on *E. superba*. Those figures are approximately 70% of those obtained using Cd of a sphere. Further confirmation is afforded by a comparison of theoretical drag in a sockeye salmon extrapolated to the size of *E. pacifica* and swimming at critical speed (data from Brett and Glass, 1973; Webb, 1975 a). Thrust power (drag power) generated would be 56.0 ergs s^{-1} for a 1.7-cm sockeye salmon swimming at 18.8 cm s^{-1} compared to a value of 78.4 ergs s^{-1} for *E. pacifica* swimming at the same velocity using the Cd of a sphere, and 48.7 ergs s^{-1} using the Cd of *E. superba*. Thus, the best data available for comparison strongly indicate that the calculated values for total drag power presented in Table 1 are in the high end of the expected range for *E. pacifica*. The relationship between drag power (P_D) and metabolic power available for propulsion (P_{aerob}) as a function of critical swimming speed for *E. pacifica* are graphically represented in Fig. 1A.

The above discussion indicates that the overall swimming efficiency of *Euphausia pacifica* is not subject to major error and therefore is quite low when compared to that of larger swimming organisms. Overall swimming efficiency (η_{aerob}) is the product of the efficiency of the muscles used in propulsion and the efficiency of the multiple-paddle propulsive system itself (η_p) (see methods; Webb, 1971 b). No data are available on the efficiency of crustacean muscle, so it must be assumed that changes in efficiency are related to shortening speed as in

the higher vertebrates (Hill, 1950). Swimming speed is directly related to muscle shortening speeds; therefore the diagram in Hill (1950) can be used to construct a curve relating muscle efficiency to swimming speed by assuming that maximal power output will occur at *E. pacifica*'s theoretical U_{crit} (Fig. 1 B; after Webb, 1971 b). Propulsive efficiency can then be deduced from the relationship of overall efficiency (η_{aerob}) to muscular efficiency (η_m), (Fig. 1 b). These calculations suggest that propeller efficiency (η_p) varies between 0.9% at 20% U_{crit} to 14% at 100% U_{crit} . Thus, the most likely explanation for the observed low overall swimming efficiency in *E. pacifica* is the low efficiency of the multiple-paddle propulsive system.

A clear-cut mechanistic explanation for the observed low propulsive efficiency is lacking. However, there are several reported trends in size vs efficiency and in size vs metabolism that partially explain the results presented here. First, a theoretical treatment by Webb (1975 a) suggests that overall efficiency declines precipitously with decreasing size in the best studied swimming species: *Oncorhynchus nerka*, the sockeye salmon (Fig. 2, redrawn from Webb, 1975 a). In this species, propulsive efficiency at U_{crit} declines from a figure of 24% (approximately ideal) for individuals 25 cm in length to 8.1% in 5-cm salmon. The present explanation for the observed decline is an inadequate model for evaluating total drag in smaller fishes (< 25 cm), resulting in underestimated drag values and therefore low efficiency (Webb, 1975 a). However, physiological considerations must also be brought to bear, notably the very well documented trend of increasing weight-specific metabolism with decreasing size. Figure 3 represents the net costs of transport for several species of teleost fishes swimming at 75% U_{crit} (see 'Material and methods'). The line in Fig. 3 is a regression of net cost of transport vs weight for *O. nerka*, the only species for which data are available over a 4 orders-of-magnitude range in weight (Schmidt-Nielsen, 1972). The slope of the line is -0.25 [$y = 1.416 W^{-0.25}$; $y = \text{net cost of transport (cal g}^{-1} \text{ h}^{-1})$ $W = \text{weight (g)}$ $r = 0.99$], indicating that the apparently universal relationship between metabolism and size (see Prosser, 1973) applies as well to the metabolism associated with higher swimming speeds as it does to standard and routine metabolism. A slope of -0.25 for weight-specific metabolism vs size is equivalent to a slope ("b-value") of 0.75 in the classic allometric equation $m = aW^b$ describing metabolism (m) vs weight (W) in plant and animal species. Virtually all species studied in this regard show a "b-value" of approximately 0.75 for the relationship of standard or routine metabolism vs weight (see Prosser, 1973) indicating a dependence intermediate between surface area (0.66) and weight (1.00). In contrast, if the relationship of total drag power vs weight is examined in a similar manner for *O. nerka*, the slope of the line is 1.15 [$d = 2802 W^{1.15}$ where $d = \text{total drag ergs s}^{-1}$ and $W = \text{weight (g)}$ $r = 0.99\%$]. This indicates that drag increases at a more rapid rate with increasing size than does metabolic rate. This does not explain low

efficiencies in smaller organisms in a mechanistic sense. It does point out that, while it costs proportionately more energy to run a smaller organism, it costs proportionately less for smaller organisms to overcome hydrodynamic resistance by the medium. The resulting ratio yields the observed low efficiencies.

Cost of transport

A comparison of net cost of transport (cf. Tucker, 1970; Schmidt-Nielsen, 1972; Beamish, 1978) is also an excellent means of conceptualizing relative swimming costs among organisms using different propulsive mechanisms (Fig. 3). It has been noted (Schmidt-Nielsen, 1972; Beamish, 1978) that the net cost of transport in several fish species, when plotted against weight, more-or-less follows the line described by net cost of transport vs weight in *Onco-rhynchus nerka* (see discussion above). That is, at any given weight the net cost of transport in fish species is neither greater than twice nor less than one-half the equivalent value for *O. nerka*. This is strong testament to the similarity of energetic costs of propulsion in fishes, most of which utilize an undulatory propulsive mechanism. The jet propulsion employed by the pelagic squid *Loligo opalescens* (O'Dor, 1982) is somewhat more costly than that of fishes, with a value for net cost of transport approximately 3 times that of *O. nerka*. Similarly, if the curve describing net cost of transport vs weight in *O. nerka* is extrapolated into the weight range of *Euphausia pacifica*, cost of transport for *E. pacifica* at 8 °C is approximately 3.5 times and at 12 °C approximately 5.8 times that of *O. nerka*. This suggests that the multiple-paddle propulsive system employed by most pelagic Crustacea is much less efficient than the undulatory propulsion used by most fishes, even when size is taken into consideration. Ivlev's (1963) work on the cost of swimming in the decapod *Leander adspersus* (Fig. 3) corroborates that suggestion. He collected data over a size range of 0.1 to 2.5 g, overlapping the lower weight range in Fig. 3. Values for net cost of transport in *L. adspersus* are approximately 4 times that of *O. nerka* at the same weight. Halcrow and Boyd (1967) provided further information on cost of swimming in multiple-paddle propulsive systems; their values for the gammarid amphipod *Gammarus oceanicus* are approximately 5 times the equivalent value for *O. nerka* (Fig. 3). If a line is fitted to describe the relationship of cost of transport vs weight in swimming Crustacea using all data in Fig. 3, the result is $m = 6.26 W^{-0.28}$ ($m = \text{cost of transport, cal g}^{-1} \text{ km}^{-1}$, $W = \text{weight, g}$, $r = 0.94$). The slope (-0.28) is very similar to that obtained for sockeye salmon (-0.25) but the proportionality constant (6.3) is 4.4 times that obtained for *O. nerka* (1.42). Thus it seems that the paddle-propulsion employed by Crustacea is less efficient than the undulatory mode of fishes.

A precise description of the relationship between drag and efficiency in small (1–30 mm), swimming Crustacea requires studies similar to those by Brett (1963, 1964) and

Webb (1971 a, b). The best data available strongly suggest the following conclusions. First, efficiency in small, swimming Crustacea as typified by *Euphausia pacifica* is quite low; therefore low values for total drag do not imply low swimming costs. Second, the observed low efficiencies in small Crustacea may be partially explained by the well documented relationship of size vs metabolism and by the observed relationship of size vs total drag. Third, it is quite probable that multiple-paddle propulsive systems are only 20–30% as efficient as the undulatory propulsive mechanisms employed by teleosts.

Low overall efficiency in the propulsive system of *Euphausia pacifica* is not an unexpected conclusion if it is considered in the context of the species' natural history. *E. pacifica* is classically considered a filter feeder (Mauchline and Fisher, 1969) or encounter feeder (Berkes, 1975). As such its locomotory system must satisfy the fourfold requirements for hovering, high maneuverability, and rapid acceleration and deceleration. Those requirements must be balanced against the species' need for what is essentially rectilinear locomotion during its diel migration of 200 to 400 m. Among fishes, the most similar propulsive mode to that of the multiple-paddle system of euphausiids and other pelagic Crustacea is the low efficiency (10%; Webb, 1975 b) labriform or pectoral fin swimming of demersal and reef-dwelling fishes. Pectoral fin propulsion is considered to be an adaptation for both maneuverability and efficient slow speed swimming (Marshall, 1966; Blake, 1979). Pectoral fin swimmers revert to caudal fin propulsion when moving at high speed (Webb, 1975 b; Blake, 1979). Pelagic Crustacea do not have the option of switching propulsive modes. The multiple-paddle propulsive system based on drag must suffice for high and low speed swimming in addition to allowing excellent maneuverability. The locomotory system of euphausiids must compromise between the two tasks.

Ultimately, the question remains as to what the influence of low swimming efficiency is on the overall energy consumption of *Euphausia pacifica*. The data of Ross (1979) indicate that the ingestion rate of an individual *E. pacifica* of 6.9 mg DW (mean DW of individuals used in the present study) at 8 °C is 2.5 cal d⁻¹. Net cost of transport for a 6.9 mg DW individual to swim 1 000 m at 3 cm s⁻¹ is 0.38 cal or 15% of its daily ration. Total cost of transport for 1 000 m is 0.57 cal or 23% of daily ingested energy. A distance of 1 000 m is 58 824 body lengths. Thus, the energetic cost of swimming is not excessive despite the low swimming efficiency.

The effective immediate environment, or ambit, of a zooplankton (Hauray *et al.*, 1978) is ultimately determined by a balance between its cost of transport and need for forage. As such, cost of swimming is an important factor in shaping its life history. It is hoped that future considerations of zooplankton energetics will consider the cost of transport in smaller swimming organisms.

Acknowledgements. The author would like to thank Dr. P. W. Webb, Dr. J. J. Childress, Dr. S. L. Vargo, and Ms. L.

M. Bell for advice, encouragement, and critical review of the manuscript. Dr. J. J. Childress contributed the measurements of *Euphausia pacifica* necessary for calculation of cross-sectional area. The research reported here was supported by discretionary monies awarded to the author by the Department of Marine Science, University of South Florida. This paper is dedicated to Mr. Walt Bone, an extraordinary teacher and superb human being.

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