

Feeding and metabolism of *Euphausia lucens* (Euphausiacea) in the southern Benguela current

Venetia Stuart

Marine Biology Research Institute, Department of Zoology, University of Cape Town, Rondebosch, 7700, South Africa

ABSTRACT: Feeding and metabolic rates of *Euphausia lucens* (6 to 14 mm total length) were measured in the laboratory at 12.5 °C. Ingestion rates were obtained using diatoms *Thalassiosira weissflogii*, anchovy larvae, *Artemia* nauplii and copepods *Acartia africana* as food. Maximum carbon-specific ingestion rates were equivalent to 21 to 22 % body carbon d⁻¹ feeding on larvae or nauplii, and 11 % d⁻¹ feeding on diatoms. Very few copepods were removed, probably due to their swimming behaviour. Respiration and ammonium excretion rates of a size range of euphausiids were measured, and O:N ratios indicated significant protein catabolism. Minimal respiratory carbon losses could be met by *E. lucens* feeding on diatoms at a cell concentrations of 2.5×10^6 l⁻¹, or carnivorously on fish larvae or copepods at concentrations of 13 and 156 l⁻¹ respectively. These results suggest that euphausiids rely on patchy distributions of food and may only feed carnivorously during chance encounters of prey. Similar results were obtained for the nitrogen budget. The *E. lucens* population in the southern Benguela current has the potential of exerting a considerable predatory impact on newly hatched anchovy larvae in this region.

INTRODUCTION

Euphausia lucens is the dominant euphausiid in the southern Benguela current off the west coast of South Africa (Nepgen 1957), where it constitutes approximately 50 % of the total overall zooplankton biomass (Pillar 1984a). Because of its great abundance, it is found in the diets of organisms ranging from baleen whales (Best 1967) and seabirds, to several species of commercially important fish such as the Cape hakes *Meluccius capensis* and *M. paradoxus* (Botha 1980), snoek *Thyrsites atun* (Nepgen 1979) and anchovy *Engraulis capensis* (King & Macleod 1976).

Little is known of the feeding behaviour and general biology of *Euphausia lucens*, making it difficult to assess its role in the Benguela ecosystem. According to the literature, most euphausiids are omnivorous, consuming both phytoplankton and zooplankton such as copepods and fish larvae (Mauchline & Fisher 1969, Theilacker & Lasker 1974, Ohman 1984, McClatchie 1985). Fish scales have also been recorded in the stomach contents of several euphausiid species, mainly from the genus *Thysanopoda* (Mauchline 1980). *E. lucens* may therefore have a significant impact on the phyto- and zooplankton communities in

the Benguela ecosystem, as well as playing a major role in the transfer of energy to higher trophic levels. Since the distribution of *E. lucens* overlaps with that of many species of fish larvae, they may also contribute significantly to the heavy mortality of early larval stages.

In a study on the vertical distribution of zooplankton, Pillar (1984b) found that during the day, no adult or juvenile *Euphausia lucens* were caught up to the maximum sampling depth of 70 m, whereas after sunset the numbers increased sharply in the region of the thermocline (20 to 30 m), where they remained until sunrise. A typical temperature profile of the area showed surface temperatures of 16.5 °C, a thermocline between 16 and 15 °C, and subthermocline temperatures of 15 to 11 °C for waters from 30 to 100 m. Individuals therefore migrate through a vertical temperature gradient of at least 5 C° a day.

In order to estimate the food requirements of an organism, it is necessary to have measurements of its metabolic rate, and no data are available for *Euphausia lucens*. This study was undertaken to examine the grazing impact of *E. lucens* on the plankton community in the Benguela ecosystem, and to estimate energy transfer through the population.

MATERIALS AND METHODS

Collection and maintenance of euphausiids. Euphausiids were collected after sunset with a 950 μm mesh Bongo net from a depth of 80 m off the west coast of South Africa (33° 48' S, 18° 22' E). The contents of the cod-end were poured into plastic buckets filled with seawater, and all damaged animals and other material siphoned off. Healthy specimens were returned to the laboratory within 3 h of capture, and were placed in 10 l tanks covered with black polythene sheeting (~15 individuals per tank). They were maintained at a temperature of 12.5 °C, and were fed twice a week on a culture of the diatom *Thalassiosira weissflogii*, and newly hatched *Artemia* nauplii. All subsequent handling of specimens was done using a wide-bore pipette. Under these conditions the euphausiids grew and moulted regularly, and could be maintained in the laboratory for several months. The specimens used in the experiments ranged in size from 6 to 14 mm in length, and all experiments were conducted at a temperature of 12.5 °C, which is approximately the mean temperature experienced during the course of their daily vertical migrations (Pillar 1984b).

Size relations. To establish the relation between body length (from the tip of the rostrum to the distal end of the telson) and uropod length, a large number of fresh and formalin-preserved specimens were measured under a dissecting microscope using a calibrated micrometer. Body length and dry weight were also measured on a size range of freshly collected euphausiids, after rinsing briefly in distilled water and drying in an oven at 60 °C for 48 h. Carbon and nitrogen content of these specimens was determined using a Heraeus CHN analyser. Regression equations were calculated interrelating all body size indices, allowing for conversion between the different parameters. After moulting, some euphausiids were sacrificed, and the dry weight and carbon and nitrogen content of the moults and animals were measured separately. The uropods of the moults were also measured, providing an estimate of body size at any stage of experimentation, without injury to the euphausiid.

Feeding studies. Grazing on phytoplankton cells was investigated using diatoms, since the Benguela is generally a diatom-dominated system (De Decker 1973, Andrews & Hutchings 1980, Olivieri 1983). Similar-sized euphausiids (3 to 6 individuals, depending on size) were placed in 1 l containers filled with 0.45 μm filtered seawater plus a suspension of the diatom *Thalassiosira weissflogii*. Containers were rotated for 5 to 6 h on a plankton wheel (~3 rpm) in dim light. Each experimental container was accompanied by a control (no animals) at the same food concentration, which ranged from 10^3 to 10^4 cells ml^{-1} . Samples were

removed at the beginning and end of each experiment for enumeration of cells on a Coulter Counter (Model TA II) equipped with a 280 μm aperture tube. Ingestion and clearance rates were calculated using the equations of Frost (1972), and were expressed as a function of cell concentration.

Predation by *Euphausia lucens* was investigated using 3 different prey items: newly hatched *Artemia* nauplii (50 to 1000 l^{-1}), copepods *Acartia africana* (20 to 200 l^{-1}), and 1 to 3 d old anchovy larvae (4 to 80 l^{-1}). Although *Artemia* nauplii are not a natural food source for euphausiids, they may nevertheless provide useful information on maximum ingestion rates. Predation experiments were conducted in 500 ml beakers which contained a single euphausiid plus a number of prey which had previously been counted out under a dissecting microscope. After a 16 h feeding period in dim light, the euphausiids were removed, and the remaining prey collected on a 100 μm mesh, stained with Rose Bengal, and counted under a dissecting microscope using a Bogorov tray. Controls were run concurrently

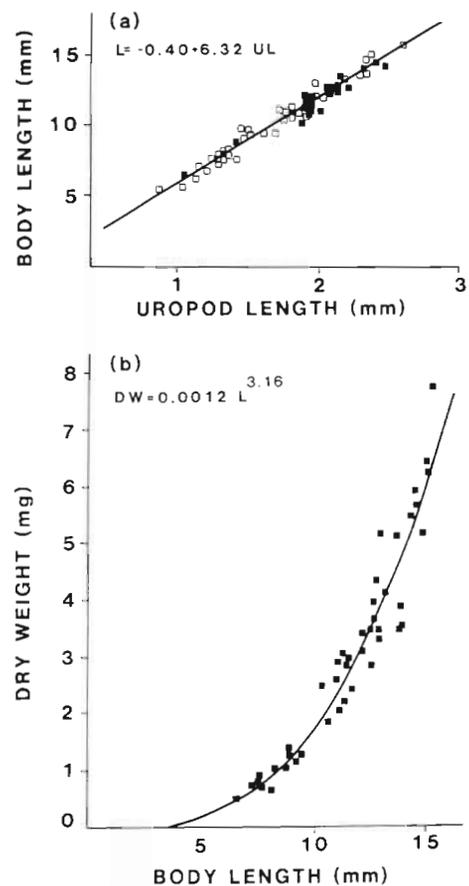


Fig. 1. *Euphausia lucens*. (a) Relation between uropod length (UL) and body length (L) for fresh (■) and formalin-preserved specimens (□); (b) relation between body length and dry weight (DW)

to correct for any counting error. The carbon and nitrogen content of all food items was measured on a Heraeus CHN analyzer, after filtering known numbers of diatoms or prey onto pre-ashed 8 mm GF/C filters, and correcting for blanks.

Data from all feeding studies were fitted by logistic curves, because in 3 out of 4 curves these produced a better fit than the Ivlev curve, using the minimization of the mean square variance as the criterion for goodness of fit (Mullin et al. 1975). The logistic curve also reaches a true asymptote, from which non-subjective critical food concentrations can be estimated, which is useful in a comparative feeding study of this nature.

Metabolism. 'Routine' rates of oxygen consumption were measured on euphausiids after allowing them to equilibrate in filtered seawater for ~2 h. Individual euphausiids were placed in 35 ml respirometry chambers containing filtered seawater (0.45 µm), and the oxygen concentration of the water was recorded before and after a 2 h incubation period using a YSI oxygen probe which was calibrated immediately before use. Control chambers were run concurrently to correct for probe drift, and probe readings were compared to oxygen measurements from Winkler titrations (Parsons et al. 1984), which yielded very similar results in all cases.

An indication of the rate of nitrogen excretion was obtained by measuring ammonium nitrogen, since 80 to 85 % of all nitrogen excreted by euphausiids is in this form (Jawed 1969, Mayzaud 1973). Well-fed speci-

mens were allowed to equilibrate in filtered seawater for 2 h, then individuals were placed in 100 ml beakers with 0.45 µm filtered seawater, which were covered with foil and left for 3 h. Incubation times were kept as short as possible, since Båmstedt (1985) found that incubation time strongly influenced ammonium excretion rates of macrozooplankton. Control beakers (no animals) were run concurrently, and replicate 5 ml samples were taken from each beaker at hourly intervals for an indophenol-blue spectrophotometric determination of ammonium (Koroleff 1976). Ammonium excretion rates were calculated over the 3 h period and were related to specimen size, which was expressed in the form of body nitrogen. The ammonium concentration of several samples taken from the respirometry chambers at the end of the experiments was also measured, so that O:N ratios could be calculated. All experiments were performed on individuals that had recently been collected from the field (~12 h previously) as well as on individuals that had been maintained in the laboratory for ~1 mo, to determine whether long-term laboratory maintenance had any noticeable effects on metabolism.

RESULTS

Clearance and ingestion rates

The relation between body length, uropod length and dry weight of *Euphausia lucens* is shown in Fig. 1. It is apparent from Fig. 1a that preserving specimens in formalin had no effect on the ratio of body length to uropod length. The allometric equations relating carbon and nitrogen content of *E. lucens* to body length and dry weight are shown in Table 1, and were used to make appropriate conversions whenever measurements were not made directly. Carbon represents $40.43 \pm 3.49\%$ (SD) of dry body weight and nitrogen $10.80 \pm 0.71\%$ (SD), while the C:N ratio of whole euphausiids was $3.73:1 \pm 0.24$ (SD). Table 2 shows the approximate size and carbon and nitrogen content of all food items used in the feeding experiments.

Table 1. *Euphausia lucens*. Relation between body length (L), carbon content (W_c), nitrogen content (W_n) and dry weight (DW) expressed in the form $Y = ax^b$. The number of samples (n) and correlation coefficient (r^2) of each relation is also shown

Variable	Equation	r^2	n
Carbon weight (µg)	$W_c = 0.341 L^{3.28}$	0.92	25
Carbon weight (µg)	$W_c = 369.97 DW^{1.09}$	0.98	25
Nitrogen weight (µg)	$W_n = 0.118 L^{3.17}$	0.94	25
Nitrogen weight (µg)	$W_n = 103.68 DW^{1.04}$	0.98	25

Table 2. Approximate size, mean carbon and nitrogen content and C:N ratios of triplicate samples of algae and prey used in feeding experiments with *Euphausia lucens*. Results have been expressed per cell or individual

Food item	Size (µm)	µg C	µg N	C:N
<i>Thalassiosira weissflogii</i>	10 – 16	1.18×10^{-4}	0.21×10^{-4}	5.73:1
<i>Artemia</i> Day 1	200	1.568	0.292	5.37:1
<i>Artemia</i> Day 3	450	1.065	0.240	4.44:1
<i>Acartia africana</i>	1370	3.20	0.71	4.22:1
Anchovy Day 1	2000	7.85	1.85	4.24:1
Anchovy Day 3	3120	7.06	1.77	3.98:1

Greatly reduced feeding rates were obtained for individuals which moulted during the course of the feeding experiments, thus all ingestion rates have been calculated from results obtained from non-moulting specimens only.

Grazing and clearance rates for *Euphausia lucens* feeding on the diatom *Thalassiosira weissflogii* are illustrated in Fig. 2. Results have been expressed in the form of carbon-specific rates to minimize any size-dependent effects, and cell concentrations have been expressed in terms of carbon, using the values shown in Table 2. Maximum ingestion rates were achieved at a critical concentration of 400 to 500 $\mu\text{g C l}^{-1}$ and represent 100 $\mu\text{g C ingested (mg body carbon)}^{-1} \text{ d}^{-1}$. Euphausiids appear to adjust their clearance rates over a wide range of food concentrations, with a reduction in feeding effort at low cell concentrations.

In order to quantify the relation between body size ($\mu\text{g C}$ or N) and ingestion rate for euphausiids 9 to 14 mm in length, cell concentrations above the critical concentration were used, and the relation can be expressed by the following allometric equations:

$$\text{Ingestion } (\mu\text{g C d}^{-1}) = 0.207 W_c^{0.879} \quad (n = 17; r^2 = 0.59) \quad (1)$$

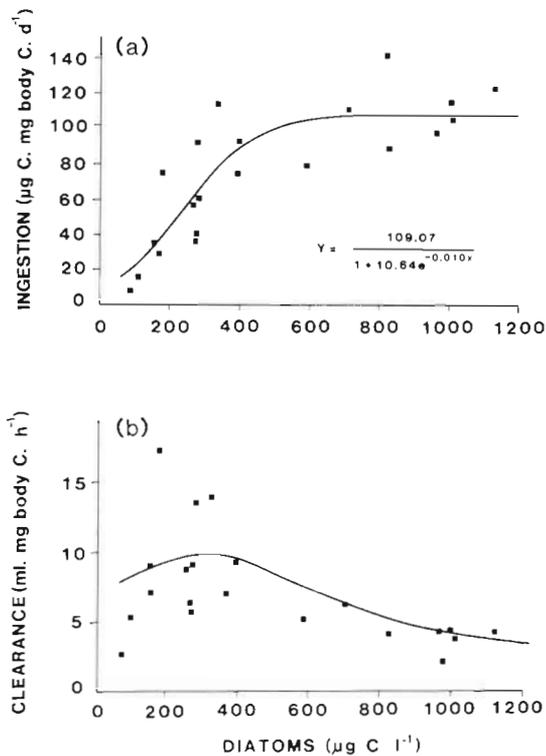


Fig. 2. *Euphausia lucens* (11 mm total length). (a) Carbon-specific ingestion and (b) clearance rates when feeding on the diatom *Thalassiosira weissflogii*. The line for (a) was fitted using a logistic curve, while that for (b) was derived by rearrangement of the ingestion equation in (a)

$$\text{Ingestion } (\mu\text{g N d}^{-1}) = 0.117 W_n^{0.876} \quad (n = 17; r^2 = 0.59) \quad (2)$$

High feeding rates were obtained for euphausiids preying on *Artemia* nauplii and anchovy larvae, with a similar saturation response above a critical prey concentration (Fig. 3). Carbon and nitrogen-specific

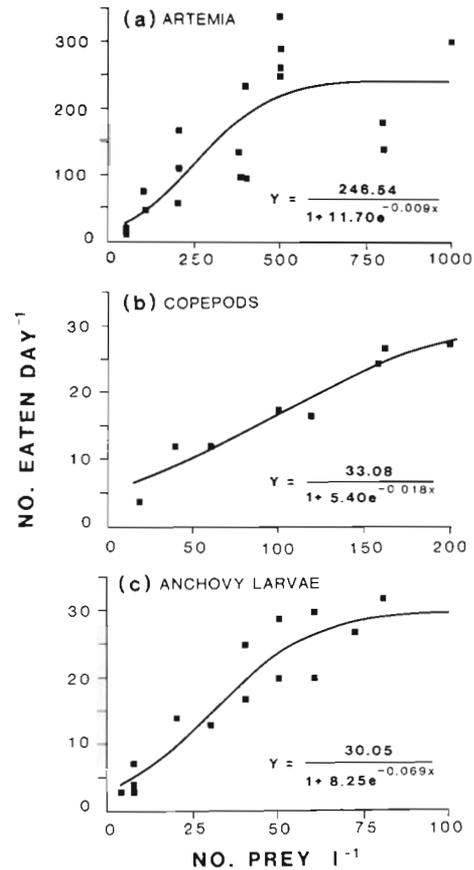


Fig. 3. *Euphausia lucens* (11 mm total length). Predation rates feeding on (a) *Artemia* nauplii, (b) adult copepods (*Acartia africana*) and (c) anchovy larvae, as a function of prey concentration. All lines were fitted using a logistic curve

ingestion rates for all food items were calculated using the appropriate values from Table 2, and are illustrated in Fig. 4. It is apparent that *Euphausia lucens* is able to obtain a substantially greater ration from *Artemia* nauplii and anchovy larvae than from diatoms or copepods. Lower ingestion rates on diatoms may be attributed to a reduced retention efficiency for these relatively small cells. In preliminary feeding experiments, ingestion rates were not measurable when diatoms 4 to 5 μm in diameter (*Thalassiosira pseudonana*) were fed to *E. lucens*, indicating that small cells are not efficiently retained by the filtering mesh of the food basket.

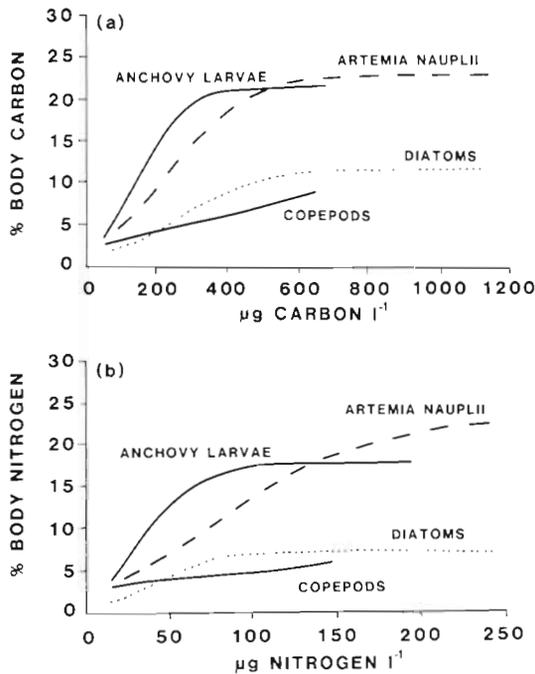


Fig. 4. *Euphausia lucens* (11 mm total length). (a) Carbon- and (b) nitrogen-specific ingestion rates when feeding on *Artemia* nauplii, anchovy larvae, copepods *Acartia africana* and the diatom *Thalassiosira weissflogii*

Metabolism

'Routine' rates of oxygen consumption for *Euphausia lucens* of different sizes are shown in Fig. 5, and can be expressed by the allometric equation:

$$\mu\text{l O}_2 \text{ h}^{-1} = 2.687 \text{ DW}^{0.845} \quad (n = 40; r^2 = 0.83) \quad (3)$$

From Fig. 5 it can be seen that long term laboratory maintenance of euphausiids did not have any noticeable effects on their metabolism.

Nitrogen excretion rates for different sized euphausiids are shown in Fig. 6, and can be described by the allometric equation:

$$\mu\text{g N h}^{-1} = 0.255 \text{ DW}^{0.748} \quad (n = 28; r^2 = 0.70) \quad (4)$$

As in the case of respiration, long-term laboratory maintenance had no significant effects on nitrogen excretion rates. An indication of the proportion of protein catabolized relative to carbohydrate and lipid can be obtained by means of the O:N ratio, calculated by atomic equivalents. The mean O:N ratio for freshly collected individuals was 10.30 ± 2.16 (SD), which was not significantly different ($p > 0.05$) from that of laboratory-maintained individuals, where the O:N ratio was 11.28 ± 1.90 (SD), signifying considerable protein catabolism in both cases (Conover & Corner 1968).

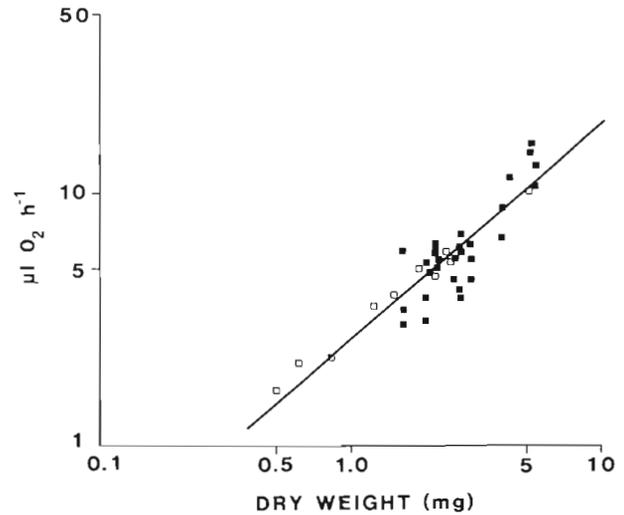


Fig. 5. *Euphausia lucens*. Relation between respiration rate ($\mu\text{l O}_2 \text{ h}^{-1}$) and body weight (mg dry weight) at 12.5°C. Data for freshly collected euphausiids (■), as well as for specimens maintained in the laboratory for ~1 mo (□) are shown, and the line represents the allometric equation that best fits all data points

Euphausiids in the length range 10 to 12 mm moulted regularly every 4 to 5 d, resulting in a loss of approximately 2.57% of the body carbon and 0.92% of the body nitrogen. The moults were rapidly colonized by bacteria and numerous large ciliates soon after they had been discarded, and were completely broken down by these microorganisms within a few days.

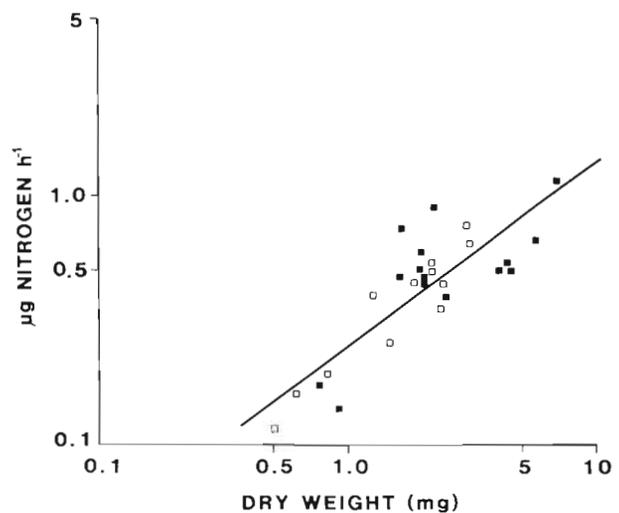


Fig. 6. *Euphausia lucens*. Relation between excretion rate ($\mu\text{g N h}^{-1}$) and body size (mg DW) at 12.5°C. Data for freshly collected euphausiids (■), as well as for specimens maintained in the laboratory for ~1 mo (□) are shown, and the line represents the allometric equation that best fits all data points

DISCUSSION

Ingestion of food particles by *Euphausia lucens* at increasing food concentrations appears to follow the asymptotic functional response curve observed in copepods (Frost 1972) as well as in other euphausiid species (Ohman 1984, Boyd et al. 1984). According to Yen (1983), saturation of feeding occurs as a function of handling time, gut capacity and gut passage time. Carbon-specific ingestion rates varied with the type of food consumed and were maximal for *Artemia* nauplii and anchovy larvae (21 to 22 % body carbon). Nitrogen-specific ingestion rates followed the same trends, but were somewhat lower in all cases. Consumption of *Artemia* nauplii may be abnormally high because they are sluggish swimmers with a limited escape response, and are therefore easily captured. In the field, crustacean nauplii may be important in the diet of *E. lucens*, although it is likely that they are consumed at a slower rate.

Maximum ingestion rates were achieved at a critical carbon concentration of $450 \mu\text{g C l}^{-1}$ for diatoms and $350 \mu\text{g C l}^{-1}$ for anchovy larvae, which are comparable to the values obtained for *Euphausia pacifica* and *Euphausia superba* on various diets (Ross 1979, Boyd et al. 1984). The lower critical concentration for anchovy larvae may be attributed to the size of the food items, since larger particles are more easily captured (Frost 1972). A relatively small carbon ration (7 to 8 % body carbon) was obtained for the intermediate sized copepods, probably due to their faster swimming speed and well-developed escape response, indicating that particle size is not the only factor affecting the rate of ingestion. Similarly, Yen (1985) concluded that although size was an important determinant of dietary selectivity in the carnivorous copepod *Euchaeta elongata*, species-specific behavioural differences, such as the intermittent darting movements of the prey *Acartia clausii*, can also influence feeding rates.

Diatoms provided a maximum carbon-specific ration of $11 \% \text{ d}^{-1}$, or approximately half of that obtained for anchovy larvae and *Artemia* nauplii, suggesting that for *Euphausia lucens*, carnivory provides greater energy returns than herbivory. It should be borne in mind, however, that the size of cells used in the experiments may not be filtered and ingested by *E. lucens* at maximum efficiencies, since it has been shown that particles less than $12 \mu\text{m}$ are retained with a reduced efficiency by *Euphausia superba* (McClatchie & Boyd 1983, Boyd et al. 1984). Unfortunately this could not be tested in the present study due to lack of suitably sized cells. It has also been demonstrated that krill preferentially consume large phytoplankton cells (Holm-Hansen & Huntley 1984) and that maximum clearance rates are directly proportional to the calculated spherical

radius squared of the cells (Quetin & Ross 1985). In contrast to the above findings, Ohman (1984) concluded that *Euphausia pacifica* attains a substantially greater ration from diatoms than from other prey, although these results are not directly comparable since prey concentrations were much lower (max. $158 \mu\text{g C l}^{-1}$) and larger diatoms were used in the experiments ($33.5 \mu\text{m}$ in diameter).

Greater carbon ingestion rates for carnivorously feeding *Euphausia lucens* may be offset by the energetic costs of capturing the prey. Although there is little evidence to suggest that euphausiids actively hunt their prey (Berkes 1975), it is likely that some form of active predation occurs, since they all possess large image-forming compound eyes adapted to seeing at low light intensities (Mauchline & Fisher 1969). Also Lasker (1966) found that more *Artemia* nauplii were eaten by *Euphausia pacifica* than if the catching techniques had simply involved random swimming and filtering of the water. No estimates of the metabolic costs of feeding in euphausiids are available, although preliminary results of Ikeda (1984) indicate that during feeding (on phytoplankton cells), the total metabolic activity of *Euphausia superba* is nearly twice the measured metabolic rates, due to the costs of biochemical assimilation and increased activity when feeding. Whether there is a further increase in metabolism during carnivorous feeding is still unknown, although Torres & Childress (1983) have recorded an approximate 3-fold increase in the oxygen consumption rate of *E. pacifica* due to increased locomotory activity alone.

Measured routine metabolic and excretion rates for *Euphausia lucens* are comparable to those of *Euphausia pacifica* at the same temperature (Ross 1982) and no long-term laboratory maintenance effects were apparent (see Fig. 5 & 6). Nitrogen excretion and the decomposition of moults and faeces produced by *E. lucens* in the Benguela ecosystem may be important in the regeneration of nutrients for phytoplankton production (see Bidigare et al. 1981, Båmstedt 1985), especially during the course of their daily vertical migrations to the phytoplankton-rich surface waters (Pillar 1984b). Using the data for ingestion rates on different food sources, it is possible to calculate the minimum food concentration at which respiratory costs and nitrogen requirements are met by the assimilated ration. The results for *Artemia* nauplii have been omitted since they do not constitute a natural food source.

The rate of oxygen consumption for a standard-sized individual of 11 mm body length (2.32 mg) is $131.53 \mu\text{l O}_2 \text{ d}^{-1}$ (from Eq. 3), which is equivalent to $56.38 \mu\text{g C d}^{-1}$, (or 6.4 % body carbon) using a respiratory quotient of 0.8 for protein metabolism (Prosser 1973). The rate of carbon assimilation at different food

levels was calculated from the product of carbon ingestion (estimated from Fig. 3a), and assimilation efficiency (84 %, after Lasker 1966), and is presented in Table 3. Loss of carbon through respiration was subtracted from these results, in order to determine the minimum food levels required to meet respiratory costs.

The same procedure may be followed to estimate the minimum nitrogen requirements for an 11 mm euphausiid, which excretes $11.46 \mu\text{g N d}^{-1}$ (calculated from Eq. 4), or 4.8 % body nitrogen d^{-1} . Nitrogen ingestion rates at different food levels were estimated from Fig. 4b, and assimilated nitrogen was calculated assuming a nitrogen assimilation efficiency of 86 % (Ross 1979). These results are shown in Table 4.

Clearly, in dilute food suspensions, *Euphausia lucens* can never meet the costs of metabolism, regardless of the type of food consumed. Likewise, Kato et al. (1982) found that the Antarctic krill could not ingest enough carbon from seawater with low phytoplankton

concentrations to compensate for carbon lost through metabolism, suggesting that patchy concentrations of food have to be exploited in the field to meet carbon and nitrogen requirements. Mullin & Brooks (1976) have demonstrated that small-scale distributions in phytoplankton were responsible for the fact that the copepod *Calanus pacificus* could not ingest sufficient cells to equal respiration at many points sampled during 2 cruises in April and June.

It is also apparent from Table 3 that a diet of copepods alone can only meet respiratory and excretory costs at extremely high concentrations, which are rarely encountered in the field. Copepods are therefore likely to be consumed only during chance encounters to supplement their diet, and never relied upon as a sole food source. This is consistent with gut content analyses of *Euphausia lucens*, which were described to contain phytoplankton cells and traces of copepod remains (Nepgen 1957).

Phytoplankton concentrations of $300 \mu\text{g C l}^{-1}$

Table 3. *Euphausia lucens*. Rate of carbon assimilation ($\mu\text{g C d}^{-1}$) for an 11 mm specimen feeding on diatoms (D), anchovy larvae (L) and copepods (C), calculated from the sum of the ingestion rate (estimated from Fig. 3a) and the carbon assimilation efficiency (84 %, after Lasker 1966). Assimilation minus respiration ($\mu\text{g C d}^{-1}$) for each food source is shown, as well as the approximate density of cells or prey needed to meet the carbon requirements

Food conc. $\mu\text{g C l}^{-1}$	Assimilation			Assimilation - respiration		
	D	L	C	D	L	C
0	0	0	0	-56.4	-56.4	-56.4
100	16.8	43.9	23.6	-39.5	-12.5	-32.8
200	31.5	104.6	31.5	-24.9	+48.2	-24.9
300	45.6	141.7	36.0	-10.7	+85.3	-20.4
400	64.1	155.2	43.9	+7.7	+98.8	-12.5
500	74.2	157.4	51.7	+17.8	+101.1	-4.6
600	80.9	157.4	58.5	+24.5	+101.1	+2.1
No. l^{-1}				2.5×10^6	13	156

Table 4. *Euphausia lucens*. Rate of nitrogen assimilation ($\mu\text{g N d}^{-1}$) for an 11 mm specimen feeding on diatoms (D), anchovy larvae (L) and copepods (C), calculated from the sum of the ingestion rate (estimated from Fig. 3b) and the nitrogen assimilation efficiency (86 %, after Ross 1979). Assimilation minus nitrogen excretion ($\mu\text{g N d}^{-1}$) is shown, as well as the approximate density of cells or prey needed to satisfy the nitrogen requirements

Food conc. $\mu\text{g N l}^{-1}$	Assimilation			Assimilation - respiration		
	D	L	C	D	L	C
0	0	0	0	-11.5	-11.5	-11.5
20	3.2	9.8	7.2	-8.3	-1.6	-4.3
40	6.7	22.0	8.0	-4.7	+10.5	-3.5
60	9.8	30.3	8.9	-1.6	+18.8	-2.5
80	13.1	34.2	9.9	+1.7	+22.7	-1.6
100	14.1	36.2	10.6	+2.6	+24.8	-0.9
120	14.7	36.2	11.8	+3.3	+24.8	+0.4
No. l^{-1}				2.9×10^6	11	131

required to meet the metabolic costs of an 11 mm *Euphausia lucens* are commonly found in the southern Benguela region when phytoplankton blooms develop following upwelling, although average values for oceanic and shelf water may be somewhat lower, in the region of $80 \mu\text{g C l}^{-1}$ (Andrews & Hutchings 1980, Barlow 1982). It is likely that lower phytoplankton concentrations may be sufficient when larger cells are present. Fish larvae are required at a comparatively low carbon concentration of $100 \mu\text{g l}^{-1}$, which is equivalent to 13 larvae l^{-1} . Densities of this order of magnitude are never recorded in the field (Shelton 1984), although it should be borne in mind that net hauls used to estimate zooplankton numbers are integrated over considerable depth ranges, and cannot accurately assess the density of organisms which have a patchy distribution. The high prey concentrations needed to meet respiratory demands may be attributable, in part, to stress-induced increases in metabolism in the relatively small respirometry chambers.

Since *Euphausia lucens* is able to consume large numbers of anchovy larvae in the laboratory (see Fig. 3c), it is interesting to examine the potential predation pressure of euphausiids on these stocks, although it should be borne in mind that there is still no evidence for *E. lucens* feeding on anchovy larvae in the field. Pillar (unpubl. data) obtained a mean annual dry mass for *E. lucens* of $4.8 \text{ g per } 10 \text{ m}^2$ (equivalent to $1.94 \text{ g C per } 10 \text{ m}^2$) for an area encompassing the sampling site of the present study. This biomass of euphausiids would only have to ingest 1% of their body carbon per day in the form of anchovy larvae to consume approximately 2500 larvae per 10 m^2 (using the carbon conversion values given in Table 2). Since the density of anchovy larvae in this area ranges from 1 to $> 10\,000$ per 10 m^2 (Shannon et al. 1984), it is possible that the euphausiid population could contribute significantly to the mortality of early larval stages, especially if a feeding school of euphausiids encountered a dense patch of fish larvae. The distribution of *E. lucens* also overlaps with that of numerous other species of fish larvae such as round herring and lantern fish (Crawford 1980, Davis et al. 1981) which may also be affected by euphausiid predation. Further studies on the distribution, abundance and density of local aggregations of prey, as well as gut contents of euphausiids in this area, are necessary before one can evaluate the actual extent of such predation.

In conclusion, it appears that *Euphausia lucens* is an opportunistic omnivore in the southern Benguela ecosystem, capable of consuming a wide variety of food items. Studies on the larval growth and development of *E. lucens* have demonstrated that a mixed algal (*Tetraselmis chuii*) and animal (*Artemia* nauplii) diet produced better growth in the larvae than did pure

algal or animal diets (Pillar 1984c), indicating that omnivory is beneficial to these euphausiids. Since *E. lucens* is a migrant species, it is probable that its diet may change from a carnivorous diet at depth to a herbivorous diet at the surface. The success of *E. lucens* in the Benguela ecosystem may be both due to its ability to exploit many different types of food, as well as to undergo daily vertical migrations, which provide a continual variation in the food supply.

Acknowledgements. I thank Prof. J. G. Field, Dr. S. Nicol and 2 anonymous referees for critical comments on the manuscript. I am also grateful to S. C. Pillar from the Sea Fisheries Research Institute for his help in collecting euphausiids and setting up experiments, and Dr. C. Brownell for providing anchovy larvae and copepods. This study was funded by a research grant from the Council for Scientific and Industrial Research for the Benguela Ecology Program.

LITERATURE CITED

- Andrews, W. R. H., Hutchings, L. (1980). Upwelling in the southern Benguela current. *Prog. Oceanogr.* 9: 1–81
- Båmstedt, U. (1985). Seasonal excretion rates of macrozooplankton from the Swedish west coast. *Limnol. Oceanogr.* 30: 607–617
- Barlow, R. G. (1982). Phytoplankton ecology in the southern Benguela current. III. Dynamics of a bloom. *J. exp. mar. Biol. Ecol.* 63: 239–248
- Berkes, F. (1975). Some aspects of feeding mechanisms of euphausiid crustaceans. *Crustaceana* 29: 266–270
- Best, P. B. (1967). Distribution and feeding habits of baleen whales off the Cape Province. *Investl Rep. Div. Sea Fish. S. Afr.* 57: 1–44
- Bidigare, R. R., Johnson, M. A., Guffy, J. D., Biggs, D. C. (1981). Nutrient chemistry of ammonium in Antarctic surface waters. *Antarct. J. U.S.* 16: 168–170
- Botha, L. (1980). The biology of the Cape hakes *Meluccius capensis* (Cast.) and *M. paradoxus* (Franca) in the Cape of Good Hope area. Ph. D. thesis, Univ. of Stellenbosch
- Boyd, C. M., Heyraud, M., Boyd, C. N. (1984). Feeding behaviour of krill. *J. Crust. Biol.* 4 (Spec. No. 1): 123–141
- Conover, R. J., Corner, E. D. S. (1968). Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. *J. mar. biol. Ass. U.K.* 45: 49–75
- Crawford, R. J. M. (1980). Seasonal patterns in South Africa's West Cape purse-seine fishery. *J. Fish Biol.* 16: 649–664
- Davies, S. L., Newman, G. C., Shelton, P. A. (1981). A review of the South African multispecies fishery in ICSEAF Division 1.6 in 1980. *Colln. scient. Pap. int. Commn. S.E. Atlant. Fish.* 8: 51–74
- De Decker, A. H. B. (1973). Agulhas bank plankton. In: Zeitzschel, B. (ed.) *Ecological studies*, Vol. 3, Analysis and synthesis. Springer-Verlag, Berlin, p. 189–219
- Frost, B. W. (1972). Effects of size and concentration of food particles on the feeding behaviour of the planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 17: 805–815
- Holm-Hansen, O., Huntley, M. (1984). Feeding requirements of krill in relation to food sources. *J. Crust. Biol.* 4 (Spec. No. 1): 156–173
- Ikeda, T. (1984). Sequences in metabolic rates and elemental composition (C, N, P) during the development of

- Euphausia superba* DANA and estimated food requirements during its lifespan. *J. Crust. Biol.* 4 (Spec. No. 1): 273–284
- Jawed, M. (1969). Body nitrogen and nitrogenous excretion in *Neomysis rayii* Murdoch and *Euphausia pacifica* Hansen. *Limnol. Oceanogr.* 14: 748–754
- Kato, M., Sewaga, S., Tanoue, E., Murano, M. (1982). Filtering and ingestion rates of the Antarctic krill, *Euphausia superba* DANA. *Trans. Tokyo Univ. of Fish.* 5: 167–175
- King, D. P. F., Macleod, P. R. (1976). Comparison of the food and the filtering mechanism of the pilchard, *Sardinops ocellata*, and the anchovy *Engraulis capensis*, off South West Africa, 1971–1972. *Investl Rep. Sea Fish. Brch S. Afr.* 111: 1–29
- Koroleff, F. (1976). Determination of ammonia. In: Grasshof, K. (ed.) *Methods of seawater analysis*. Verlag Chemie, Weinheim, p. 126–133
- Lasker, R. (1966). Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. *J. Fish. Res. Bd Can.* 23: 1291–1317
- Mauchline, J. (1980). The biology of mysids and euphausiids. *Adv. mar. Biol.* 18: 1–681
- Mauchline, J., Fisher, L. R. (1969). The biology of the euphausiids. *Adv. mar. Biol.* 7: 1–454
- Mayzaud, P. (1973). Respiration and nitrogen excretion of zooplankton II. Studies on the metabolic characteristics of starved animals. *Mar. Biol.* 21: 19–28
- McClatchie, S. (1985). Feeding behaviour in *Meganycitiphanes norvegica* (M. Sars) (Crustacea: Euphausiacea). *J. exp. mar. Biol. Ecol.* 86: 271–284
- McClatchie, S., Boyd, C. M. (1983). Morphological study of sieve efficiencies and mandibular surfaces in the Antarctic krill, *Euphausia superba*. *Can. J. Fish. Aquat. Sci.* 40: 955–967
- Mullin, M. M., Stewart, E. F., Fuglister, F. J. (1975). Ingestion by planktonic grazers as a function of concentration of food. *Limnol. Oceanogr.* 20: 259–262
- Mullin, M. M., Brooks, E. R. (1976). Some consequences of distributional heterogeneity of phytoplankton and zooplankton. *Limnol. Oceanogr.* 21: 784–796
- Nepgen, C. S. de V. (1957). The euphausiids of the west coast of South Africa. *Investl Rep. Div. Fish. Un. S. Afr.* 28: 1–30
- Nepgen, C. S. de V. (1979). The food of the snoek, *Thyrsites atun*. *Fish. Bull. S. Afr.* 11: 39–42
- Ohman, M. D. (1984). Omnivory by *Euphausia pacifica*: the role of copepod prey. *Mar. Ecol. Prog. Ser.* 19: 125–131
- Olivieri, E. T. (1983). A description of the hydrography and phytoplankton communities in the upwelled waters of the Cape Peninsula, South Africa, September 1972 – February 1973. *S. Afr. J. mar. Sci.* 1: 199–229
- Parsons, T., Maita, Y., Lalli, C. (1984). *A manual of chemical and biological methods for seawater analysis*. Pergamon Press, Oxford
- Pillar, S. C. (1984a). A comparison of the performance of four zooplankton samplers. *S. Afr. J. mar. Sci.* 2: 1–18
- Pillar, S. C. (1984b). Diel variations in the vertical distribution of some common zooplankton species off the west coast of South Africa. *S. Afr. J. mar. Sci.* 2: 71–80
- Pillar, S. C. (1984c). Laboratory studies on the larval growth and development of *Euphausia lucens* (Euphausiacea). *S. Afr. J. mar. Sci.* 2: 43–48
- Prosser, C. L. (1973). *Comparative animal physiology*. W. B. Saunders Co., Philadelphia
- Quetin, L. B., Ross, R. M. (1985). Feeding by antarctic krill, *Euphausia superba*: does size matter? In: Siegfried, W. R., Condy, P. R., Laws, R. M. (ed.) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, p. 372–377
- Ross, R. M. (1979). Carbon and nitrogen budgets over the life of *Euphausia pacifica*. Ph. D. thesis, Univ. of Washington
- Ross, R. M. (1982). Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. *Mar. Biol.* 68: 1–13
- Shelton, P. (1984). Notes on the spawning of anchovy during the summer of 1982–3. *S. Afr. J. Sci.* 80: 69–71
- Shannon, L. V., Hutchings, L., Bailey, G. W., Shelton, P. A. (1984). Spatial and temporal distribution of chlorophyll in South African waters as deduced from ship and satellite measurements, and their implications for pelagic fisheries. *S. Afr. J. mar. Sci.* 2: 109–130
- Theilacker, G. H., Lasker, R. (1974). Laboratory studies of predation by euphausiid shrimps on fish larvae. In: Blaxter, J. H. S. (ed.) *The early life history of fish*. Springer-Verlag, New York, p. 287–299
- Torres, J. J., Childress, J. J. (1983). Relation of oxygen consumption to swimming speed in *Euphausia pacifica* I. Effects of temperature and pressure. *Mar. Biol.* 74: 79–86
- Yen, J. (1983). Effects of prey concentration, prey size, predator life stage, predator starvation and season on predation rates of the carnivorous copepod *Euchaeta elongata*. *Mar. Biol.* 75: 69–77
- Yen, J. (1985). Selective predation by the carnivorous marine copepod *Euchaeta elongata*: Laboratory measurements of predation rates verified by field observations of temporal and spatial feeding patterns. *Limnol. Oceanogr.* 30: 577–597