

Feeding response of *Nyctiphanes australis* (Euphausiacea) to various nanoplankton sizes and taxa

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ABSTRACT: Nanoplankton (2 to 20 μm) are a substantial fraction of the plankton in the sea, where they form a potential food source for zooplankton. Monocultures of 12 nanoplankton taxa of different cell size and 1 species of *Thalassiosira* (microplankton) were offered to *Nyctiphanes australis* to determine whether they would be consumed and, if so, determine rates of clearance and ingestion by the euphausiid. *N. australis* ingested very small cells (3.5 to 5.4 μm equivalent spherical diameter) at rates $\leq 5 \times 10^5$ cells h^{-1} . A total of 8 nanoplankton taxa were consumed at rates that provided *N. australis* with its minimum food requirement of 2% body carbon d^{-1} , and so could maintain it when microplankton abundance is low. Our results suggest that *N. australis* can detect and avoid unpalatable food such as the chlorophytes *Dunaliella* and *Nannochloris*, but is susceptible to the toxic dinoflagellate *Alexandrium minutum*.

KEY WORDS: Zooplankton · Nanoplankton · Ingestion rate

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INTRODUCTION

In his classic book, 'The open sea', Alister Hardy (1956) discussed maritime seasons. In particular, he noted that summer is a period of strong thermocline, diminished nutrients and 'surprisingly few' floating plants. In the waters off Otago, SE New Zealand (170° 45' E, 45° 45' S), such a pattern exists between December and February each year (Brewin 1952, Hawke 1989). During this same period, larval and juvenile *Nyctiphanes australis* are generally abundant along the Otago coast. *N. australis* provides a key trophic link in the pelagic foodweb between the primary producers (phytoplankton) and many seabirds, fish and mammals.

During the summer of 1997–98, 95% of the potentially available phytoplankton food particles were <8 μm ESD (equivalent spherical diameter) (G. J. Haywood unpubl. data). This observation raises 2 questions concerning the ability of *Nyctiphanes australis* to utilise this phytoplankton resource: (1) Is *Nyctiphanes*

australis restricted to ingesting phytoplankton >8 μm ESD, thereby leaving the smaller fraction <8 μm ESD because it is too small for *N. australis* to handle? (2) Were the available taxa <8 μm ESD unacceptable to *N. australis* for reasons other than cell size?

The lower size limit for the ingestion of particles by euphausiids is determined by the spacing of setules, the small, hair-like structures on the bristles of the setae on the appendages that form the feeding basket (Jørgensen 1966). For instance, the intersetule distance of *Euphausia superba* and *E. pacifica*, which are also filter-feeding euphausiids, is about 7 μm (Jørgensen 1966). These species can retain nanoplankton of 5 μm diameter (Parsons et al. 1967) and organisms >10 μm with the greatest efficiency (McClatchie & Boyd 1983).

Intersetule distances on the feeding basket of *Nyctiphanes australis* (1 to 7.5 μm) indicate that nanoplankton can be collected (Dalley 1989). This was confirmed by McClatchie et al. (1991), who offered adult *N. australis* 2 diatoms, *Chaetoceros gracilis* and *Thalassiosira weissflogii*, of diameters 5 and 10 to 15 μm ,

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respectively. *C. gracilis* was cleared at higher rates than *T. weissflogii*, but McClatchie et al. (1991) implied that the long siliceous setae may substantially increase the effective size of cells of these species. Long setae may also physically prevent some herbivores like *Euphausia superba* from eating *C. gracilis* (Parsons et al. 1967, Opalinski et al. 1997).

Marchant & Nash (1986), who found large numbers of nanoplanktonic organisms in the gut and faecal material of *Euphausia superba*, pointed out that relatively little attention has been paid to the grazing of krill on nanoplankton. Taking this into account, our study builds on that of McClatchie et al. (1991). We offered *Nyctiphanes australis* a range of nanoplanktonic food of diverse size and taxa (including non-setose nanoplankton) in order to (1) determine which taxa they will eat, (2) establish whether they can eat phytoplankton <8 µm, and (3) propose mechanisms to account for any differences in their ingestion rates of the various nanoplankton taxa.

MATERIALS AND METHODS

Adult *Nyctiphanes australis* were exposed to 13 species of algae for periods of 2 or 3 d. Monocultures of relatively spherical species of protocistans (Table 1) in the size range of 2 to 20 µm (nanoplankton) were grown in 5 l glass Erlenmeyer flasks in F/2 medium (diatoms) or F/2-Si (flagellates) under a 14:10 h light:dark regime and at a constant 16°C (Guillard & Ryther 1962, Guillard 1975). Algal concentrations were measured before and after exposure to euphausiids. There were 10 replicate containers for each algal food

that was tested: 7 contained euphausiids, 3 lacked euphausiids (controls).

The dense log phase algal cultures were diluted before use in the feeding experiments. To determine the initial chlorophyll *a* (chl *a*) concentration of a culture, 100 ml samples were analysed using the spectrophotometric method of Parsons et al. (1984).

Culture dilutions with sand-filtered seawater were prepared in a clean 80 l plastic cask. The water in the cask was stirred continuously while the 5 l aliquots were removed and transferred into each of 10 white plastic pails in random order. This method ensured that the initial phytoplankton concentrations in the pails were as similar as possible. The pail diameter (275 mm) was considered large enough to avoid 'bottle effects' (Price et al. 1988). We aimed to achieve an initial concentration of chl *a* after dilution of between 5 and 15 µg l⁻¹. A pilot experiment indicated that these concentrations of chl *a* would provide sufficient food, ensuring that approximately 40% would remain at the end of the experiment and feeding could still be detected. The chl *a* concentrations used were expected to remain above the critical mean concentration of ~4 µg l⁻¹ throughout the experiment and enable us to compare the ingestion rates of *Nyctiphanes australis* of the various phytoplankton species (McClatchie et al. 1991).

The average amount of carbon present in *Nyctiphanes australis*, estimated from their average dry biomass and the carbon equivalents outlined in Parsons et al. (1984), was 1.56 ± 0.23 (SD) mg animal⁻¹. Carbon to dry weight ratios for *N. australis* are similar to those of *Euphausia pacifica* (Parsons et al. 1984, James & Wilkinson 1988).

Table 1. Taxonomic name, abbreviation and class (Andersen et al. 1997) of each of the phytoplankton used in the experiments. Taxa listed in order of increasing equivalent spherical diameter (ESD) ±1 SD (µm) of their cells

Phytoplankton	Abbreviation	Class	ESD ± SD
<i>Nannochloris atomus</i> Butcher ^a	<i>Na</i>	Chlorophyceae	3.30 ± 0.68
<i>Phaeocystis pouchetti</i> Langerheim ^b	<i>Pp</i>	Prymnesiophyceae	3.47 ± 0.48
<i>Pavlova lutherii</i> (Droop) Green ^a	<i>Pl</i>	Prymnesiophyceae	4.05 ± 0.65
<i>Isochrysis galbana</i> Parke ^a	<i>Ig</i>	Prymnesiophyceae	4.15 ± 1.10
<i>Chaetoceros muelleri</i> Lemmermann ^a	<i>Cm</i>	Bacillariophyceae	5.37 ± 1.19
<i>Chrysochromulina ericina</i> Parke & Manton ^b	<i>Ce</i>	Prymnesiophyceae	5.74 ± 1.30
<i>Pyramimonas grossi</i> Parke ^b	<i>Pyr</i>	Prasinophyceae	6.69 ± 0.63
<i>Dunaliella tertiolecta</i> Butcher ^a	<i>Dt</i>	Chlorophyceae	8.10 ± 2.15
<i>Rhodomonas lens</i> Pascher et Ruttner ^a	<i>Rl</i>	Cryptophyceae	8.97 ± 0.72
<i>Pseudopedinella pyreforme</i> N. Carter ^b	<i>Pse</i>	Dictyochophyceae	9.21 ± 0.73
<i>Tetraselmis chui</i> Butcher ^a	<i>Tc</i>	Prasinophyceae	10.47 ± 0.53
<i>Alexandrium minutum</i> Halim ^a	<i>Am</i>	Dinophyceae	16.95 ± 1.58
<i>Thalassiosira</i> sp. Cleve ^c	<i>Thal</i>	Bacillariophyceae	25.98 ± 5.90

^aPortobello Marine Laboratory, University of Otago, culture collection
^bIsolated from Blueskin Bay, Otago, by O. B. Bojo
^cIsolated from Blueskin Bay, Otago, by G. J. Haywood

Cell concentration. The contents of the pails were always stirred before they were sampled to ensure a uniform distribution of particles. More frequent sampling might have unduly disturbed the animals. Aliquots (250 ml) were taken from each of the 3 'control' pails at the start of the experiment and from all 10 containers after 48 or 72 h. Cells were counted by an Elzone model 180XY particle counter and by microscope (direct counts of Lugol's preserved samples) in a 1 ml capacity Sedgewick Rafter tray. A minimum of 200 cells was counted to validate the Elzone counter.

***Nyctiphanes australis*.** Adult *N. australis* (16 to 18 mm in length) were collected from 10 km offshore and transported to the laboratory in 20 l pails. Healthy animals were maintained in the laboratory, 20 per pail, at 12°C, under a 14:10 h light:dark regime and a diet of *Thalassiosira* sp.

For the experiments, 5 animals were transferred to each pail using a scoop net to avoid the addition of extra water or food. A small aerator in every pail circulated the water. Experiments were carried out at 12°C, the same temperature as the source of the animals, in a controlled temperature facility and in total darkness to minimise phytoplankton growth. Experiments started and ended in the afternoon and lasted for 48 or 72 h.

Feeding rate calculations. Grazing coefficients, clearance rates and ingestion rates of *Nyctiphanes australis* were calculated according to Marin et al. (1986, 1987; see their Table 7). Based on these recommendations, initial concentration rather than mean concentration was used in the calculation of ingestion rates. Ingestion rates, clearance rates, cell concentrations and volumes were analysed using the Systat 5 software package (Wilkinson 1989). The acceptance level used throughout was 95 % ($p \leq 0.05$).

RESULTS

Cells

The ESD frequencies of the various phytoplankton taxa were normally distributed about mean values ranging from 3 (*Nannochloris atomus*) to 27 μm (*Thalassiosira* sp.) (Table 1).

Initial cell concentrations varied among phytoplankton taxa by up to 2 orders of magnitude, as more small cells than large cells were required to obtain a chl a concentration in the range 5 to 15 $\mu\text{g l}^{-1}$. An average percentage of 51.7 ± 6.1 (SD) of the cells (compared to the cell concentration of the controls) remained at the end of the experiments. *Nyctiphanes australis* cleared more *Thalassiosira* sp. cells than expected, however, so that only 22% remained at the end of the experiment.

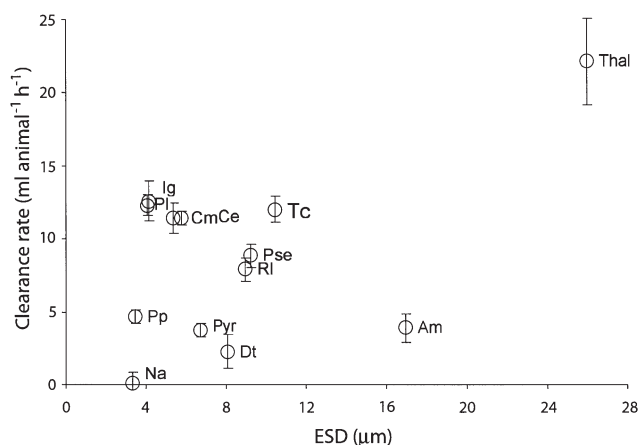


Fig. 1. *Nyctiphanes australis*. Clearance rates (\pm SE) of phytoplankton cells plotted as a function of the cell ESD (μm) of the taxa used (see Table 1 for abbreviations). Order x-axis: Na, Pp, Pl, Ig, Cm, Ce, Pyr, Dt, Rl, Pse, Tc, Am, Thal

For 2 phytoplankton taxa (*Nannochloris atomus* and *Dunaliella tertiolecta*), the cell concentrations in treatments exposed to *Nyctiphanes australis* were not significantly different from the controls. At the end of 72 h exposure to *Alexandrium minutum*, 40% of the *N. australis* were dead or dying.

Cell clearance rates by *Nyctiphanes australis* ranged from 0.13 $\text{ml animal}^{-1} \text{h}^{-1}$ (*Nannochloris atomus*) to 22.03 $\text{ml animal}^{-1} \text{h}^{-1}$ (*Thalassiosira* sp.) and were not related linearly to the cell concentration (regression $F = 2.35$, $p = 0.153$), or to the size of the cell (regression $F = 3.71$, $p = 0.081$; Fig. 1, Tables 1 & 2).

Ingestion rates of cells were not directly related linearly to cell concentration (regression $F = 0.50$, $p = 0.496$) or the size of phytoplankton cells ($F = 3.65$, $p = 0.083$; Table 2, Fig. 2). If *Thalassiosira* sp. (microplankton) is excluded, ingestion rates are related to cell size ($F = 5.81$, $p = 0.037$).

Nyctiphanes australis ingested more cells $< 8 \mu\text{m}$ ESD than cells $> 8 \mu\text{m}$ ESD (t -test, $t_{2 \text{ tail}} = 2.699$, $p = 0.021$; Table 2).

Carbon

The rate of carbon ingested was independent of the concentration of phytoplankton carbon in the pails ($F = 0.95$, $p = 0.351$; Fig. 3) and the size of the cells ($F = 4.23$, $p = 0.064$; Fig. 3). Carbon ingested by *Nyctiphanes australis* ranged from 0.08 $\mu\text{g C animal}^{-1} \text{h}^{-1}$ (*Nannochloris atomus*) to 6.31 $\mu\text{g C animal}^{-1} \text{h}^{-1}$ (*Thalassiosira* sp.), or between 0.13% (*N. atomus*) and 9.69% (*Thalassiosira* sp.) of *N. australis*' body carbon per day (Fig. 4, Table 2). There was no difference between the ingestion rate ($\mu\text{g C animal}^{-1} \text{h}^{-1}$) of cells $< 8 \mu\text{m}$ or $> 8 \mu\text{m}$ ESD (t -test $t_{2 \text{ tail}} = 1.315$, $p = 0.192$).

Table 2. Carbon content ($\mu\text{g cell}^{-1}$), concentrations (mg C l^{-1}), clearance ($\text{ml animal}^{-1} \text{h}^{-1}$) and ingestion rates ($10^3 \text{ cells} \pm \text{SE animal}^{-1} \text{h}^{-1}$, $\mu\text{g C animal}^{-1} \text{h}^{-1}$) of adult *Nyctiphanes australis* for the phytoplankton taxa (see Table 1 for abbreviations.) For standard errors (SE) of most rates, see Figs. 1–4. Calculations based on cell concentrations measured by electronic particle counter. C_0 = initial concentration, C_{tc} = concentration at time t in control container, C_t = concentration at time t in experimental container, CR = clearance rate, I = ingestion rate (Marin et al. 1986, 1987), % (% body carbon d^{-1}) = carbon ingested:krill body carbon, * = concentrations of *Nannochloris atomus* and *Dunaliella tertiolecta* in treatments with and without euphausiids, which did not differ significantly

	Carbon	C_0	C_{tc}	C_t	CR	I (cells)	I (C)	I (%)
Na	4.40	0.649	0.736	0.730*	0.13	18.5 ± 21	0.08	0.13
Pp	5.02	0.293	0.163	0.113	4.70	274 ± 26	1.38	2.11
Pl	7.50	0.315	0.294	0.110	12.56	528 ± 57	3.96	6.08
Ig	7.99	0.207	0.184	0.061	12.31	367 ± 20	2.93	4.50
Cm	10.59	0.189	0.158	0.063	11.44	204 ± 19	2.16	3.31
Ce	18.55	0.241	0.216	0.091	11.42	148 ± 6.2	2.75	4.22
Pyr	27.61	0.173	0.077	0.045	3.75	23.4 ± 3.1	0.65	0.99
Dt	44.08	0.376	0.352	0.293*	2.27	19.4 ± 11	0.85	1.31
Rl	59.16	0.352	0.162	0.069	7.93	47 ± 4.9	2.79	4.28
Pse	63.36	0.077	0.056	0.028	8.87	10.7 ± 0.1	0.68	1.04
Tc	88.4	0.175	0.153	0.057	11.58	23.8 ± 1.8	2.02	3.11
Am	309.05	0.270	0.168	0.108	3.90	3.4 ± 0.8	1.05	1.62
Thal	381.85	0.285	0.326	0.066	22.03	16.5 ± 0.4	6.31	9.69

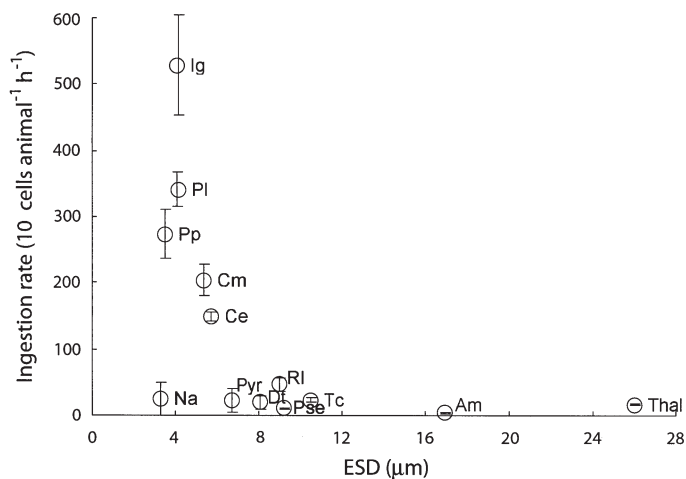


Fig. 2. *Nyctiphanes australis*. Ingestion rate ($\text{cells animal}^{-1} \text{h}^{-1}$) plotted as a function of the ESD (μm) of the cells consumed (see Table 1 for abbreviations). Order x-axis: Na, Pp, Pl, Ig, Cm, Ce, Pyr, Dt, Rl, Pse, Tc, Am, Thal

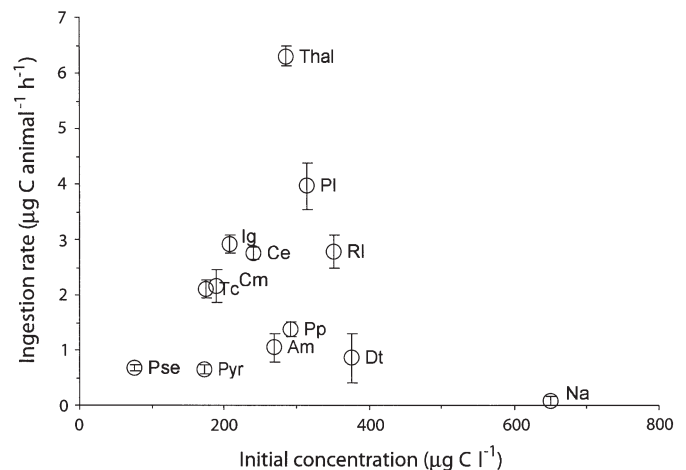


Fig. 3. *Nyctiphanes australis*. Ingestion rates ($\mu\text{g C animal}^{-1} \text{h}^{-1}$) of cells plotted as a function of the initial cell concentration ($\mu\text{g C l}^{-1}$) (see Table 1 for abbreviations). Order x-axis: Pse, Pyr, Tc, Cm, Am, Ig, Ce, Thal, Pl, Rl, Dt, Na

DISCUSSION

Ingestion rates

The results of these experiments establish that *Nyctiphanes australis* can consume several taxa in the nanoplankton range of 2 to 20 μm . When presented with small cells ($<8 \mu\text{m}$ ESD), *N. australis* increased its ingestion rate to attain an intake of carbon comparable to that of a diet of cells $>8 \mu\text{m}$.

We calculated that the average assimilation rate of *Nyctiphanes australis* is $40 \mu\text{g C d}^{-1}$ or 2% body carbon

d^{-1} . This is based on the carbon budget of Ritz et al. (1990) in which 2.82 mg of carbon was assimilated by *N. australis* for moulting and respiration during growth from 9.5 to 15 mm in length. This growth takes approximately 70 d (Ritz & Hosie 1982). Boyd et al. (1984) used a similar calculation to estimate that a 45 mm long *Euphausia pacifica* requires about $100 \mu\text{g C d}^{-1}$ or 2.3% body carbon d^{-1} (plus additional food for reproduction and growth) to meet its basic requirements.

Of the diets in our study, 8 provided *Nyctiphanes australis* with the minimum food requirement of 2% body carbon d^{-1} (Table 2, Fig. 4). These 8 taxa of phyto-

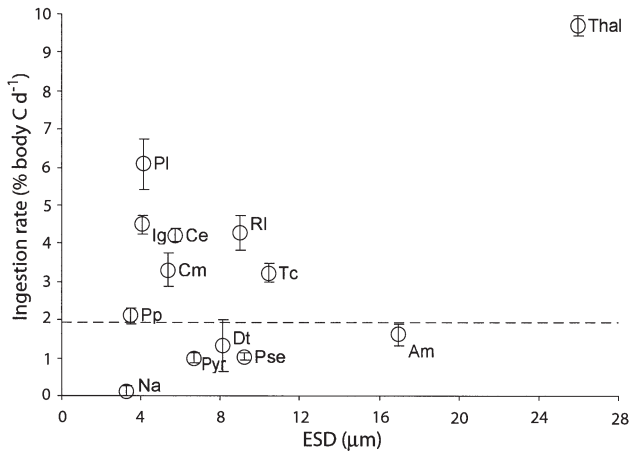


Fig. 4. *Nyctiphanes australis*. Ingestion rate (% body carbon $d^{-1} \pm SE$) as a function of cell ESD (μm). Dotted line represents an estimated minimum food requirement of 2% body carbon d^{-1} (see Table 1 for abbreviations). Order x-axis: Na, Pp, PI, Ig, Cm, Ce, Pyr, Dt, RI, Pse, Tc, Am, Thal

plankton range in cell size from 3.5 to 26 μm ESD. They were ingested at rates that averaged 72.3 ± 13.0 (SE) μg C animal d^{-1} , which is consistent with the daily carbon requirement of $73.6 \mu g d^{-1}$ estimated by Ritz et al. (1990). Atkinson & Snyder (1997) report a positive relationship between carbon availability and ration for *Euphausia superba*, but we found no such relationship for *N. australis* within a range of approximately 75 to 750 μg C l^{-1} available carbon. *N. australis* ingested *Nannochloris atomus*, *Pyramimonas grossi*, *Dunaliella tertiolecta*, *Pseudopedinella pyreforme* and *Alexandrium minutum* at lower rates than were necessary to satisfy minimum daily food requirements.

Nyctiphanes australis ingested the dinoflagellate *Alexandrium minutum* cells at the low rate of 3.4×10^3 cells animal $^{-1} h^{-1}$ or $25.3 \mu g$ C animal $^{-1} d^{-1}$, not sufficient for the minimum daily carbon requirement for *N. australis*. As the stomach contents of *N. australis* periodically contain numerous dinoflagellates (G. J. Haywood pers. obs.), we expected *A. minutum* to be ingested at high rates. *A. minutum* produces paralytic shellfish poison (Hallegraeff et al. 1995) and the poor survival rate of animals exposed to *A. minutum* in our study suggests that *N. australis* may be susceptible to the toxin. However, we did not expect *A. minutum* to be ingested at a low rate by *N. australis* because the euphausiid *Thysanoessa raschii* ingested toxic clones of *Gonyaulax tamarensis* (*Alexandrium tamarensis*) at the same rate as non-toxic clones, the only difference between clones being a 'fluctuation' in the clearance rate of the toxic species (McClatchie 1988). Since ingestion of *A. minutum* by *N. australis* in our study was minimal and some animals survived, it is possible that they might be able to detect and avoid eating the toxin-bearing cells.

The presence of *Nyctiphanes australis* did not cause a significant change in the number of *Nannochloris atomus* cells and we have no evidence that *N. australis* ate *N. atomus* (Figs. 1–4). Possible explanations for the euphausiid's failure to ingest this alga are that the spacing of the setae and setules on the food-gathering limbs (pereopods) of *N. australis* ($\sim 7 \mu m$, Fig. 1A,B; Dalley & McClatchie 1989) might be too wide to retain *N. atomus*, or that *N. atomus* might have chemical or physical properties that cause it to be an unpalatable food, or that *N. australis* was not motivated to eat.

The size and frequency distribution of *Phaeocystis pouchetti*, which is ingested, overlap with those of *Nannochloris atomus*, which is not ingested (Table 1), so there is no evidence that cell size alone determined why *N. atomus* was not ingested.

Dunaliella tertiolecta was poorly ingested by *Nyctiphanes australis* and *Euphausia superba* (Lasker 1966). Poor growth and survival of crustaceans (a copepod and the larvae of a brachyuran crab) on chlorophytes such as *D. tertiolecta* and *Nannochloris atomus* (Koski et al. 1998, Lehto et al. 1998) have been attributed to a deficiency of some of the essential polyunsaturated fatty acids (Støttrup & Jensen 1990, Brown et al. 1997) or sterols (Klein Breteler et al. 1999). An alternative proposition is that chlorophytes are unpalatable, indigestible, or insufficiently nutritious to be eaten (Anderson 1978, Sarokin & Carpenter 1982, Porra 1990, Hart 1994, Caers et al. 1998, Koski et al. 1998, Lehto et al. 1998). We conclude that some inadequacy or unpleasant attribute of the chlorophyte cells deterred *N. australis* from eating them.

Pyramimonas grossi and *Pseudopedinella pyreforme* concentrations may have fallen below the critical concentration during the experiments (Boyd et al. 1984), or there may be some unpleasant property of these cells which accounts for their low ingestion rate by *N. australis*.

Clearance rates

Ritz et al. (1990) estimated a 'filtering rate' of $6.76 ml$ animal $^{-1} h^{-1}$ from the stomach fluorescence of adult *Nyctiphanes australis* collected in Storm Bay, Tasmania. This rate falls in the range of clearance rates of 8.73 ± 5.75 (SD) ml animal $^{-1} h^{-1}$ that we measured for 13 taxa of phytoplankton and supports our conclusion that the feeding behaviour of *N. australis* in our study was similar to that in its natural environment.

Chaetoceros muelleri is sufficiently similar in size and morphology to *C. gracilis* for the clearance rates of these 2 species by *Nyctiphanes australis* to be compared. *N. australis* cleared *C. muelleri* in our study at 11.4 ± 1.1 (SE) ml animal $^{-1} h^{-1}$, which is close to a rate

of 8 to 12 ml animal⁻¹ h⁻¹ for *C. gracilis* (McClatchie et al. 1991). Both species of *Chaetoceros* have setae that are presumed to make them easier to handle and ingest than other taxa. However, the ESD of *C. muel-leri* and that of non-setose *Chrysochromulina ericina* are similar (Table 1) as are their clearance and ingestion rates by *N. australis* (Table 2), suggesting that setae per se did not make a difference.

Studies of feeding by calanoid copepods on protozoa have indicated linear relationships between clearance rates and cell size, although escape behaviours of some protozoa are also important (Burns & Gilbert 1993). The rates at which *Platymonas subcordiformis* (now *Tetraselmis subcordiformis*), *Gonyaulax polyhedra* (*Lingulodinium polyhedra*), *Thalassiosira fluviatilis* (*Thalassiosira weissflogii*) and *Dunaliella tertiolecta* were cleared by *Euphausia superba* (mean clearance rates: 25, 14.6, 4.1, 2.4 ml animal⁻¹ h⁻¹; diameters: 10–15, 30–45, 10–20, 5–10 µm, respectively) were not related to size (Lasker 1966). However, the clearance rates of *Euphausia superba* for cells <20 µm were significantly lower than those for larger cells (Meyer & El-Sayed 1983) and clearance rates of 3 species of diatom and a prymnesiophyte (cell sizes 4 to 40 µm ESD) were related to cell size (Quetin & Ross 1985). For the 12 species of nanoplankton in our study, excluding *Thalassiosira* sp., clearance rates of *Nyctiphanes australis* were not related to taxa cell size ($F = 0.14$, $p = 0.716$). However, the rate at which *N. australis* cleared *Thalassiosira* sp. (microplankton) was greater than the rate at which it cleared nanoplankton and is consistent with the findings of Meyer & El-Sayed (1983).

Ingestion of phytoplankton by euphausiids is influenced by phytoplankton species and concentration, water temperature and euphausiid size (McClatchie 1986, 1988, Price et al. 1988, McClatchie et al. 1991, Stuart & Huggett 1992). The mean daily ration of carbon ingested by *Nyctiphanes australis* exposed to 13 different taxa was 3.24% (range 0.13 to 9.69%) body carbon. This percentage and range of carbon is similar to estimates of 0.15 to 9% body carbon d⁻¹ for *Euphausia superba* (Boyd et al. 1984, Pakhomov et al. 1997, Perissinotto et al. 1997). In our study, the carbon derived by *N. australis* from the diatom *Thalassiosira* sp. (9.69 ± 0.26 [SE]% body carbon d⁻¹) was substantially greater than the carbon derived from any of the 12 nanoplankton taxa (mean 2.70 ± 0.51 [SE]% body carbon d⁻¹). The low percentage carbon derived from nanoplankton ($\leq 6\%$) implies that whereas diets of mixed nanoplankton would supply sufficient energy to maintain a population of *N. australis* of 9.5 to 15 mm length, microplankton would be necessary in the diet for reproduction to occur.

Nyctiphanes australis consumed more small cells than large cells in the range 2 to 20 µm, to ingest

approximately the same amount of carbon (Fig. 4). This result suggests that *N. australis* adjusts its consumption of small cells to achieve the same food intake as it does on diets of larger cells. The process by which euphausiids collect food items from the water to form a bolus in their food basket (Mauchline 1980, Antezana et al. 1982, Hamner 1988, G. J. Haywood pers. obs.) may account for the higher rates of ingestion of small cells and clearance rates that are not related to cell size. Bolus size, rather than the functional size (presence of setae) or shape of the cells being consumed, may determine the rate of food intake. It is possible that electrostatic charge on cell surfaces may assist euphausiids to harvest cells ~4 µm ESD (Kils 1983, Campbell et al. 1997, Hammer et al. 1999), or that sticky transparent exopolymer particles (TEP) (Alldredge et al. 1993) exuded by phytoplankton may assist euphausiids by aggregating nanoplankton-sized particles into clusters (Passow & Alldredge 1999).

In summary, *Nyctiphanes australis* was not restricted to ingesting phytoplankton >8 µm ESD. Ingestion rates indicate that *N. australis* is well adapted to feeding on food in the 3.5 to 8 µm ESD size range and would survive, but may not grow well or reproduce on a diet of nanoplankton.

Some phytoplankton taxa are not eaten by *Nyctiphanes australis* for reasons other than cell size. Since *N. australis* feed discriminately and can clearly handle small cells efficiently, it is plausible that they contributed to the dominance of cells <8 µm ESD off the Otago coast in the summer of 1997–98, by selectively grazing palatable species of phytoplankton.

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