Vol. 107: 41–53, 1994 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published April 21

Quantitative analysis of carnivory in the krill *Nyctiphanes australis*, with an examination of the effect of non-preferred phytoplankton alternative prey

Conrad A. Pilditch*, Sam McClatchie**

Portobello Marine Laboratory, University of Otago, Marine Science and Aquaculture Centre, PO Box 56, Dunedin, New Zealand

ABSTRACT: The functional responses of *Nyctiphanes australis* feeding on the copepod *Acartia* spp. (hereafter *Acartia*) at 0.5 to 15 copepods l^{-1} and on the diatom *Chaetoceros gracilis* at 1.7 to 14.8 µg chl *a* l^{-1} were measured to provide the first quantitative information on carnivorous feeding rates for this krill. Predation rates on *Acartia* [0.004 to 0.144 *Acartia* (mg acetone-extracted dry weight, $E_{dw})^{-1}$ h^{-1}] were comparable to those of more carnivorous krill and were up to 32 times higher than grazing rates on *C. gracilis*. Ingestion rates on *C. gracilis* were very low (0.45 to 3.45 ng pigment mg^{-1} E_{dw} h^{-1}), but because of their small size, algae like *C. gracilis* may be suboptimal food for *N. australis*. We used a Holling type III model to describe the predation functional response. A Michaelis-Menten model best described the grazing functional response. *N. australis* ingested *Acartia* at significantly lower rates when algae were present. This effect was independent of algal concentration: ingestion rates of *Acartia* at 3.1, 7.5 and 17.0 µg chl *a* l^{-1} were not significantly different. Parameter estimates showed that the presence of *C. gracilis* reduced the attack rate on, and increased the handling time of, *Acartia*. Presumably the increased time spent processing (capturing, handling, ingesting) *C. gracilis* reduced the time available to search for *Acartia*. Krill ingested pigment faster at high copepod concentrations. Analysis of gut pigment in *N. australis* feeding on *Acartia* alone showed that significant quantities of pigment can be derived from either the stomachs of ingested prey or copepod faeces. The implications of this finding are that herbivorous feeding rates measured *in situ* by the gut fluorescence technique may be biased for omnivorous zooplankton.

KEY WORDS: Krill · Functional response · Carnivory · Alternative prey · Gut pigment · *Nyctiphanes australis*

INTRODUCTION

Euphausiids, or krill, are an important and little-studied component of the pelagic food web in temperate southern hemisphere waters. Euphausiids exhibit a wide range of feeding behaviours (reviewed in Mauchline 1980), and they are able to feed on a variety of plankton ranging in size from nanoplanktonic algae to other adult krill. *Nyctiphanes australis* (Sars 1883) is restricted to southeastern Australian and New Zealand neritic waters (Sheard 1953, Bary 1956), where it periodically swarms in great abundance. *N. australis* is important in the diets of sea birds and commercially exploited fish species (Ritz & Hosie 1982), but there is very little quantitative information on the trophic dynamics of this krill. Similarities between the functional feeding morphology of *N. australis* and *Euphausia superba* led Dalley & McClatchie (1989) to conclude that both krill species capture algae by compression filtration. Based on analysis of its gut contents, *N. australis,*

Present addresses:
*Oceanography Department, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1
**MAF Fisheries South, 45 Filleul St., Private Bag 1926, Dunedin, New Zealand

like most euphausiids, appears to be omnivorous (Mauchline 1980, Ritz et al. 1990). The morphology of the feeding appendages suggests that *N. australis* can filter nanoplankton-sized particles (2 to 20 µm), but it also has a 'mandible resembling that of a predominantly carnivorous krill species' (Dalley & McClatchie 1989). There are few quantitative comparisons of carnivorous and herbivorous feeding by euphausiids on natural foods (Ohman 1984, McClatchie 1985, Price et al. 1988, Stuart & Pillar 1990). These few studies examining feeding of krill on zooplankton and natural algal prey have shown differences between carnivorous and herbivorous feeding rates. Measurements of predation rates on natural zooplankton prey are uncommon for any species of krill.

McClatchie (1988) reviewed the different functional response models which have been applied specifically to euphausiid feeding. The various forms of functional responses were reviewed by Holling (1959a, b), Murdoch & Oaten (1975), Hassell et al. (1976, 1977), Hassell (1978) and Abrams (1982). Many factors have been shown to affect the predation rates of zooplankton and micronekton, including krill. Among the factors which have been investigated are temperature (Kiørboe et al. 1982), predator size (Theilacker & Lasker 1974, Kato et al. 1982, Yen 1983, Simard et al. 1986), prey size (Fowler et al. 1971, Yen 1983, 1985, Greene & Landry 1985, Price et al. 1988), presence of alternative prey (Downing 1981, Landry 1981), predator feeding history (Runge 1980, Ishii 1990, McClatchie et al. 1991), food quality (Head & Harris 1987, Houde & Roman 1987, Cowles et al. 1988) and presence of predator conspecifics (Schultze & Folt 1989). Many of these factors vary from season to season (Runge 1980) and even during one day if significant spatial shifts in prey or predator density occur due to diel vertical migration (Ohman 1990, Stuart & Pillar 1990). This complicates the construction of models describing predation, as well as the extrapolation of laboratory results to nature. Amid this plethora of factors, optimal foraging theory provides some testable hypotheses, and it is in this framework that we will attempt to explain our results.

The aims of this study were to quantify the functional response of *Nyctiphanes australis* to copepod (*Acartia* spp.) and small diatom (*Chaetoceros gracilis*) food. We present these results in the absence of any previous quantitative data on ingestion rates. We examined the effect of non-preferred prey on carnivorous ingestion rates. We also estimated the magnitude of errors which could arise by interpreting pigment in the guts of *N. australis* as being derived from herbivorous feeding, when in fact, the pigment could arise during carnivorous feeding.

METHODS

Herbivory: functional response of *Nyctiphanes australis* grazing on *Chaetoceros gracilis*. *N. australis* were collected by dip net from daytime surface swarms in Otago Harbour, New Zealand (45° 50' S, 170° 37' E) between October 1989 and April 1990. Active adult krill were maintained at 11 ± 0.5 °C in 150 l buckets under dim light (0.4 to 0.5 µE m^{-2} s^{-1}) on a 12 h light:12 h dark cycle. Krill were fed *C. gracilis* ad libitum 2 to 3 times a week and the water in the buckets was replaced with fresh 5 µm filtered seawater (FSW) at least twice a week. *C. gracilis* cultures were grown in f/2 medium (Guillard & Ryther 1962) in 5 l flasks, at 15 °C, on a 16 h light:8 h dark cycle, and kept in suspension by a magnetic stirring bar. Log phase cultures (5 to 9 d after inoculation) were used for all experiments. The krill's maintenance diet was occasionally supplemented with mixed zooplankton collected using a 0.5 m diameter, 202 µm mesh conical net deployed in Otago Harbour.

Krill were maintained in the laboratory for a minimum of 10 d prior to an experiment to allow them to molt, thereby losing any epizoic diatoms attached to the exoskeleton (McClatchie et al. 1990). A small dip net and wide-bore pipette were used to transfer 91 to 110 krill from holding containers to a 60 l polyethylene bucket filled with FSW. Krill were acclimated for 24 h to *Chaetoceros gracilis* under the maintenance conditions at the experimental concentration (1, 3, 5, 8, 11, or 15 µg chl *a* l^{-1}) prior to each experiment. *C. gracilis* was mixed by a magnetic stirring bar enclosed in 1 mm mesh (to prevent damage to krill) and driven by a motor beneath the bucket (McClatchie et al. 1991). The initial algal concentration was maintained throughout the acclimation period and experiment by the method described by McClatchie et al. (1991).

At the end of each acclimation period the water in the 60 l bucket was exchanged twice by siphoning and any dead krill removed; experimental krill density was 1.4 to 1.8 krill l^{-1}. *Chaetoceros gracilis* was added at about 10:30 h to minimize the effects of feeding rhythmicity and all experiments were run for 4 to 6 h. The chl *a* concentration in the water was determined spectrophotometrically (Parsons et al. 1984) from two 250 ml water samples taken at 1 to 1.5 h intervals during the experiment. Water samples were prefiltered through a 100 µm screen to remove faecal material.

Functional response was measured using the gut pigment method (Mackas & Bohrer 1976). At the end of an experiment, 10 samples of 5 krill each (50 individuals) were rinsed thoroughly with FSW to remove adhering algae and analyzed for gut pigment. Reingestion of fluorescent faecal material was not considered a significant source of gut pigment since

during experiments faecal material collected on the protective mesh surrounding the stirring bar and was therefore removed from the water column. A replicate sample size of 5 krill was chosen to reduce the variability in gut pigment due to different feeding rates among individuals (McClatchie et al. 1990). The fluorometer calibration constant and acidification ratio were calculated for log phase *Chaetoceros gracilis* cultures (Parsons et al. 1984). McClatchie et al. (1990) demonstrated that grinding or dissection of the stomachs was unnecessary for full pigment extraction. Background krill fluorescence was measured from triplicate samples of 4 *Nyctiphanes australis* free of epizoic diatoms and starved for 4 d in Whatman GF/C-filtered seawater. Faecal strings produced as krill emptied their guts were removed to prevent reingestion of pigmented material. The acetone-extracted dry weights (E_{dw}) of the individual krill sampled for gut pigment were determined after 48 h at 69 °C.

Ingestion rate (I, ng pigment mg^{-1} E_{dw} h^{-1}) was estimated using the equilibrium rate equation described by Dagg & Grill (1980):

$$I = r\,G/E_{dw}$$

where G = total gut pigment, E_{dw} = mean extracted dry weight of the krill sampled, and r = constant proportion of gut cleared h^{-1} (r^{-1} = gut passage time). For *Nyctiphanes australis* grazing on *Chaetoceros gracilis* at 11 °C, $r = 1.68$ h^{-1} (McClatchie et al. 1991).

The chl *a* and pheophorbide *a* content (the sum of which was assumed to be total pigment, G) were calculated using the equations of Dam & Peterson (1988). To correct for digestive loss of chl *a* we used an average chlorophyll loss of 33% as measured by Dam & Peterson (1988) for copepod grazing. This correction is very approximate because the magnitude of digestive loss varies widely (Penry & Frost 1991).

Chl *a* was assumed to represent the total pigment in the water since log phase cultures were used (Roy et al. 1989). If it is assumed that all gut pigment was once chl *a* the rate of ingested carbon (I_c, ng C mg^{-1} E_{dw} h^{-1}) can be estimated from:

$$I_c = 25.9\,r\,G_m$$

where G_m = amount of gut chlorophyll (i.e. molar equivalent weight of chl *a*; see Dam & Peterson 1988) and 25.9 = carbon to chl *a* ratio for log phase *Chaetoceros gracilis*. Clearance rates (F, ml mg^{-1} E_{dw} h^{-1}) were estimated from:

$$F = I/C$$

where C = phytoplankton concentration (µg chl *a* l^{-1}).

Carnivory: functional response of *Nyctiphanes australis* feeding on *Acartia* spp. and gut pigment derived from carnivory on herbivorous prey. Adult *Acartia* spp. were collected by net in Otago Harbour between February and April 1990. Two species of *Acartia* occur in Otago Harbour, *A. ensifera* and *A. jilletti* (Bradford 1976). These 2 species (henceforth referred to as *Acartia*) dominate copepod populations numerically during summer months (November–February) when *N. australis* is abundant (J. B. Jillett, Portobello Marine Laboratory, pers. comm.). To remove large predators the contents of the cod end were poured gently through a 2 mm mesh sieve immersed in 10 l buckets of 5 µm FSW. On return to the laboratory copepods were further concentrated on an immersed 250 µm mesh sieve, lightly anaesthetized with MS222 (Yen 1982) and sorted under a dissecting microscope. Only apparently healthy adults with undamaged appendages and normal swimming patterns were chosen. No attempt was made to discriminate between the 2 species of *Acartia*, or between males and females, during this study because of their similar morphology and size (0.65 to 0.80 mm prosome length in adult).

Practical difficulties of experimental replication, sorting, and recovering copepods meant that the 60 l containers used for grazing experiments could not be used for carnivory experiments. *Acartia* were placed in 'prey-holding containers' at the experimental density. These were 4 l plastic pails with 2 windows 3 cm wide cut down opposite sides and covered with 100 µm mesh. The containers were immersed in 10 l buckets of 5 µm FSW, and the *Acartia* were fed excess *Chaetoceros gracilis* and allowed 24 h recovery under maintenance conditions. Laboratory-maintained *Nyctiphanes australis* were acclimated in 4 l containers for 24 h to a suspension of small copepods (ca 6 l^{-1}) that was dominated numerically by *Acartia*. Krill density during acclimation was 1.5 krill l^{-1}, adjusted to 1.25 krill l^{-1} for the experiments. Containers were mixed with a magnetic stirring bar enclosed in 100 µm mesh cage (to prevent damage to *Acartia*).

Water in the prey-holding containers was exchanged twice (to remove *Chaetoceros gracilis*) by immersing the containers in FSW and allowing them to drain before transferring *Acartia* to the experimental container. Acclimated krill were added close to 10:30 h; the experiment duration was 5.3 to 6.3 h; other conditions were as above. Each initial copepod density (0.5, 1, 2, 4, 8, 15 *Acartia* l^{-1}) was replicated 7 or 8 times. At the end of each experiment krill were removed with a wide-bore pipette, rinsed with FSW and analyzed for gut pigment to quantify the amount of gut pigment derived during carnivorous feeding. The individual extracted dry weight of the krill was determined. After the krill had been removed, water from each container was gently poured through a 100 µm mesh sieve and the remaining copepods counted under a dissecting microscope. Occasionally, 2 × 2.5 l water samples were

analyzed spectrophotometrically for chl *a* to ensure that chlorophyll levels in the water were very low, and so would not provide an additional source of pigment in the guts of the krill. Experiments were undertaken to ensure that *Acartia* lost from containers were due to krill predation and that krill were feeding on living prey. The number of *Acartia* lost due to handling methods was determined from 20 containers holding 0.5 to 15 *Acartia* l^{-1} but no krill.

To measure the natural mortality and that due to handling, 6 control containers were stocked with 7.5 *Acartia* l^{-1}. After the acclimation and experimental procedure *Acartia* were transferred to a solution of neutral red. Living copepods stain a dark red while dead ones stain transparent brown (Crippen & Perrier 1974). A known mixture of living and heat-killed *Acartia* was stained to ensure that living and dead *Acartia* could be discriminated accurately.

Weight specific ingestion rates (*Acartia* mg^{-1} E_{dw} h^{-1}), corrected for the proportion of copepods recovered from the control vessels, were converted to ingested carbon using the mean carbon content of *Acartia* (3.25 µg). Ingestion rates were plotted against the initial concentration of *Acartia* (McClatchie & Lewis 1986).

As predation rates are affected by prey size (Fowler et al. 1971, Price et al. 1988), dry weights and lengths were determined every 2 to 3 wk for a sample of *Acartia* sorted for use in experiments. The prosome length of 17 to 20 lightly anaesthetized *Acartia* was measured. A total of 17 to 20 samples of 10 individuals were washed in distilled water, dried at 69 °C for 48 h and weighed.

Carbon was chosen as a common currency to compare ingestion rates of *Nyctiphanes australis* feeding on *Acartia* with those feeding on *Chaetoceros gracilis*. To measure algal carbon 3 culture flasks containing 4 l of f/2 medium were inoculated with 100 ml of *C. gracilis* in log phase growth. At 10:30 h (approximate start time of predation experiments) on Days 5 through 9, inclusive, a 2 l culture sample was taken at random from a flask and analyzed for chl *a* and carbon. The chl *a* concentration was estimated spectrophotometrically from 3 × 10 ml culture samples. *Acartia* were analyzed monthly from February to May 1990 for carbon.

Effect of alternative prey. Laboratory-maintained *Nyctiphanes australis* were acclimated in 4 l pails for 24 h simultaneously to a suspension of small copepods (largely *Acartia* at ca 6 l^{-1}) and *Chaetoceros gracilis* at an initial concentration of approximately 4 µg chl *a* l^{-1}. Figs. 1a & 2 suggest that ingestion rates at these prey concentrations are below the maximum and therefore clearance rates were expected to be maximal.

Acartia were transferred to the experimental container as described above and *Chaetoceros gracilis* was added. The protected stirring bar maintained *C. gracilis* in suspension at a satisfactory level; sedimentation of *C. gracilis* as measured by a decrease in fluorescence was 1.3% h^{-1}. The volume of *C. gracilis* culture to add was determined from 2 × 10 ml culture samples analyzed spectrophotometrically. Water samples, 2 × 250 ml, were taken from a control container (no *Acartia* or krill) at the start of an experiment and analyzed spectrophotometrically to determine the initial chl *a* concentration. Acclimated krill were added close to 10:30 h. The experiment ended after 5 to 6 h with the removal of krill which were analyzed for gut pigment. Extracted dry weights of the individual krill were determined. The remaining copepods were collected on a 100 µm mesh screen and counted.

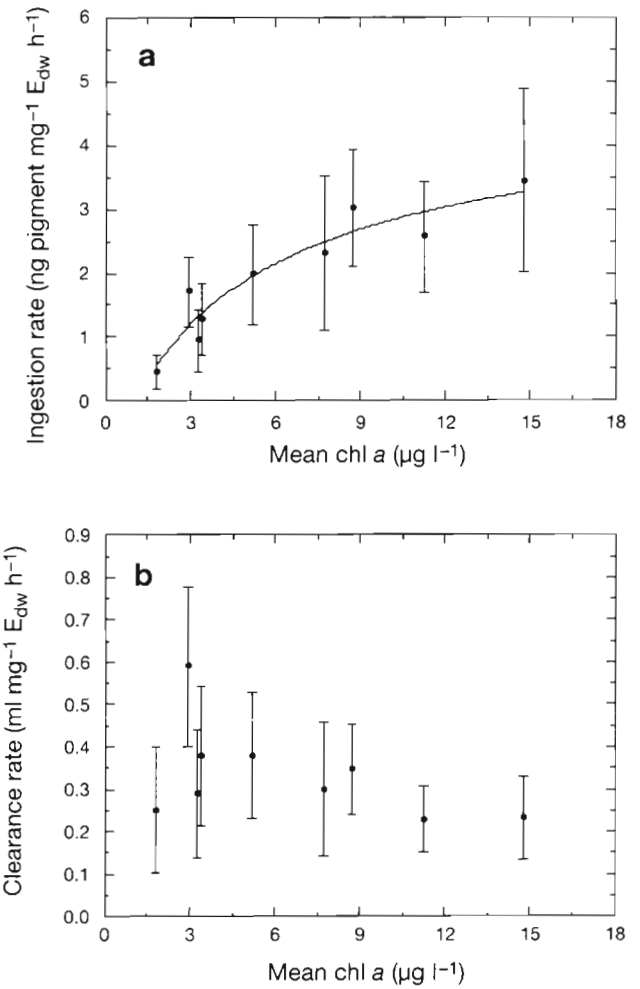

Fig. 1. (a) Ingestion rates and (b) clearance rates of *Nyctiphanes australis* grazing on *Chaetoceros gracilis* vs mean chl *a* concentration. The fitted curve in (a) is the Michaelis-Menten model: $y = 4.26\ (x - 1.00)/[5.73 + (x - 1.00)]$; see text for explanation. Data are means of 10 replicate samples (± 1 SD) of 5 krill each. The mean acetone-extracted dry weight of the krill sampled was 3.8 ± 1.1 mg (± 1 SD, n = 630)

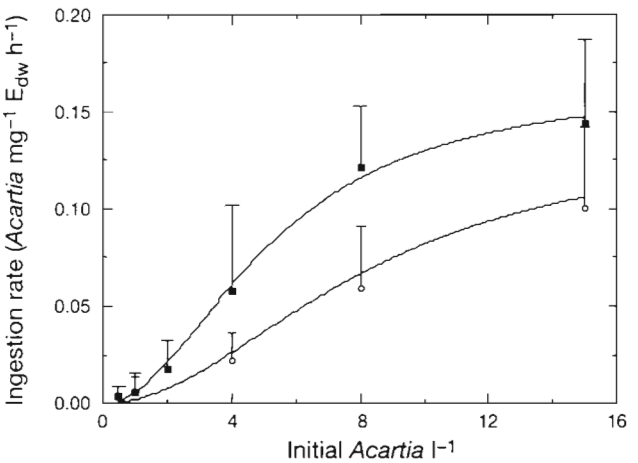

Fig. 2. Functional response curve for ingestion rate of *Nyctiphanes australis* feeding on *Acartia* vs initial *Acartia* concentration in the absence (■) and presence (○) of *Chaetoceros gracilis*. A Holling type III model is fitted to both data sets, for ■: $y = 0.006x^2/[1+0.006(6.03x^2)]$, and for ○: $y = 0.002x^2/[1+0.002(7.20x^2)]$; see text for explanation. Data in the absence of *C. gracilis* are means of 7 or 8 replicate experiments (± 1 SD), and the mean acetone-extracted dry weight per krill was 3.7 ± 1.1 mg (±1 SD, n = 223). Data in the presence of *C. gracilis* are means of grouped data for ingestion rates on *Acartia* at 3.14, 7.52 and 17.03 µg chl *a* l^{-1} (± 1 SD). In mixed prey experiments mean acetone-extracted dry weight per krill was 3.4 ± 0.8 mg (±1 SD, n = 411). 1-way SDs are shown for clarity

The prey combinations chosen were based on the location of the initial slope, slope break, and asymptotic levels of the single prey functional response curves (see Figs. 1a & 2). Initial phytoplankton concentrations were 3, 7 and 17 µg chl *a* l^{-1} and initial copepod concentrations were 1, 4, 8 and 15 l^{-1}. Each combination was replicated 7 or 8 times.

RESULTS

Herbivory: functional response of *Nyctiphanes australis* feeding on *Chaetoceros gracilis*

The functional response of *Nyctiphanes australis* feeding on *Chaetoceros gracilis* is shown in Fig. 1. Ingestion rates varied significantly with chl *a* concentration ($p < 0.001$, Jonckheere test for ordered alternatives; Siegal & Castellan 1988) from 0.45 ± 0.27 ng pigment mg^{-1} E_{dw} h^{-1} (mean ± 1 SD, n = 10 replicates) at 1.8 µg chl *a* l^{-1} to 3.45 ± 1.45 ng pigment mg^{-1} E_{dw} h^{-1} at 14.8 µg chl *a* l^{-1}. Ingestion rates appear to saturate at chl *a* concentrations > ca 8 µg l^{-1}. Variability in ingestion rates among replicate samples was high, with the coefficient of variation (CV) ranging from 32 to 60%. Clearance rates were very low ranging from 0.25 ± 0.15 ml mg^{-1} E_{dw} h^{-1} at 1.8 µg chl *a* l^{-1} to 0.59 ± 0.19 ml mg^{-1} E_{dw} h^{-1} at 2.9 µg chl *a* l^{-1}. Clearance rates were reduced at lower chl *a* concentrations, maximal at 3 to 5 µg chl *a* l^{-1} then declined gradually (Fig. 1b).

LOWESS, a locally weighted robust regression smoothing procedure, was used to provide an objective fit that summarized trends in the data (Wilkinson 1989). A LOWESS fit to the data presented in Fig. 1a (not shown) suggested ingestion rate increased at a decreasing rate with chl *a* concentration. Holling type II, Michaelis-Menten and Ivlev models have been used to quantify the feeding behaviour of other zooplankton species exhibiting this form of functional response (reviewed in McClatchie 1988). These models were fitted to the data using nonlinear least squares analysis (SYSTAT, MODEL procedure with the Quasi-Newton method; Wilkinson 1989) to estimate parameters, parameter errors, and residual sum of squares (RSS). It is statistically invalid to apply tests of significance (*F*-tests) to nonlinear models (Draper & Smith 1981) so that the RSS was used to determine the most appropriate model. All the models had similar RSS values (ranging from 68.8 to 69.6) indicating small differences in fit. The RSS value was lowest for the Michaelis-Menten model (68.8, Fig. 1a) suggesting that this model fitted the data best. That is

$$I = 4.26\,(C - 1.00)/[5.73 + (C - 1.00)]$$

where 4.26 = maximum ingestion rate (ng pigment mg^{-1} E_{dw} h^{-1}); C = chl *a* concentration (µg l^{-1}), 1.00 = chl *a* concentration at which $I = 0$; and 5.73 = half-saturation constant. Examination of the partial correlation matrices showed that the half saturation constant was highly positively correlated (0.97) with the maximum ingestion rate. Highly correlated parameters ($> |0.9|$) mean that the values of the parameters cannot be uniquely determined (Draper & Smith 1981).

Carnivory: functional response of *Nyctiphanes australis* feeding on *Acartia* spp.

Over the experimental period the mean prosome length of all *Acartia* was 0.79 ± 0.06 mm (± 1 SD, n = 108). The mean dry weight of 1 *Acartia* was 7.4 µg estimated from 108 samples of 10 individuals. Copepods could be recovered from control containers with 99% efficiency (± 1.9%, ± 1 SD, n = 20). Mortality due to handling was 0.6%. These results indicated that prey missing from experimental containers or dying during the experiment were consumed or attacked by krill, and that variations in feeding rates could not have been due to changes in the size of *Acartia*.

Ingestion rates varied significantly with *Acartia* concentration (Fig. 2; $p < 0.001$, Jonckheere test for ordered alternatives; Siegal & Castellan 1988) from

0.004 ± 0.005 *Acartia* mg^{-1} E_{dw} h^{-1} (mean ± 1 SD, n = 8) at 0.5 *Acartia* l^{-1} to 0.144 ± 0.043 *Acartia* mg^{-1} E_{dw} h^{-1} at 15 *Acartia* l^{-1}. Variation among replicate containers was high, with a CV ranging from 26 to 150%. At *Acartia* concentrations >4 l^{-1} ingestion rates rose at a decreasing rate and appear to saturate above 8 *Acartia* l^{-1}.

A LOWESS fit to the data (not shown) described a sigmoid curve consistent with a Holling type III model. The Holling type III model was fitted to the data (Fig. 2),

$$I = 0.006\ P^2/(1 + 0.006 \times 6.034\ P^2)$$

where 0.006 = instantaneous attack rate (l mg^{-1} E_{dw} h^{-1}), P = *Acartia* concentration (l^{-1}), and 6.034 = handling time per prey item (mg E_{dw} h *Acartia*$^{-1}$). The attack rate and handling time were not highly correlated (0.59), thus unique estimates of the parameters were determined. Examination of the residuals showed a pattern of increasing variance at higher *Acartia* concentrations. Transforming the independent variable may stabilize the variance, but it complicates interpretation of the models (McClatchie 1986).

Carbon contents of prey were used as the common currency to compare feeding rates. The mean carbon to chl *a* ratio for *Chaetoceros gracilis* during log phase growth was 25.9 ± 2.7 (mean ± 1 SD, n = 5). Carbon as a percentage of dry weight was 14.1 to 19.3% with a mean (± 1 SD) of 16.8 ± 2.0%. These values fall between the ranges cited for other species of diatoms (Parsons et al. 1961). The carbon content of adult *Acartia* ranged from 38.6 to 46.3% of the dry weight. Given a mean dry weight of 7.4 µg, an *Acartia* contained 3.6 µg of carbon. These values were comparable to those for *A. ensifera* collected in the Cape Farewell-Taranaki Bight of New Zealand (James & Wilkinson 1988). The highest mean ingestion rate on *C. gracilis* was 123 ng C mg^{-1} E_{dw} h^{-1} at 383 µg C l^{-1}, which was 3.8 times lower than the maximum mean ingestion rate on *Acartia* (470 ng C mg^{-1} E_{dw} h^{-1} at 48 µg C l^{-1}). At carbon concentrations of 50 µg C l^{-1} the carbon that krill ingested from *Acartia* was 32 times higher than that obtained by grazing on *C. gracilis*.

Gut pigment derived during carnivorous feeding

At similar carbon concentrations the mean amount of krill gut pigment ingested during carnivorous feeding was 4 times higher than that obtained from krill grazing on *Chaetoceros gracilis* (Fig. 3). A significant positive linear relationship existed between the amount of gut pigment in krill and the *Acartia* concentration ($p < 0.01$, $r^2 = 0.275$). The y-intercept was significantly different from zero ($p < 0.001$) and probably represents gut pigment derived from feeding during acclimation. Since *Acartia* had been fed to excess on *C. gracilis* during acclimation, krill gut pigment was most likely derived from *C. gracilis* in the guts of the *Acartia* or from faeces produced by *Acartia* during acclimation and the experiment. Chl *a* concentration in the experimental containers was very low (<0.27 µg l^{-1}) and the algae which were present were even smaller than *C. gracilis* (<5 µm), so that they could not have been a significant source of krill gut fluorescence. The background fluorescence of *Acartia* was considered insignificant because *Acartia* are 500 times smaller (by dry weight) than *Nyctiphanes australis* and the background fluorescence of *N. australis* was only 2 to 17% of the measured fluorescence. Pigment in the guts of copepod prey or copepod faecal material can be an important component of the gut pigment in the krill, which has previously been interpreted to represent herbivorous feeding.

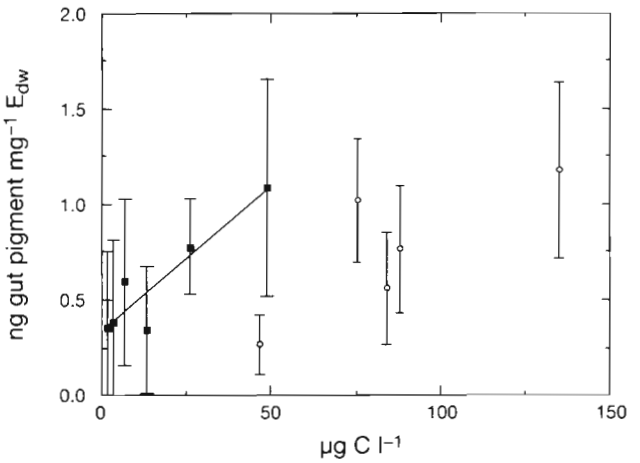

Fig. 3. Amount of gut pigment derived from *Nyctiphanes australis* feeding on *Chaetoceros gracilis* (○) compared to the gut pigment derived during feeding on *Acartia* (■) vs carbon concentration. Gut pigment derived from carnivorous feeding is positively related to *Acartia* concentration ($y = 0.015x + 0.345$, $p < 0.05$, $r^2 = 0.275$). *C. gracilis* data are means of 10 replicate samples of 5 krill (±1 SD), *Acartia* data are means of 7 or 8 replicate experiments where no replicate samples were possible (see 'Methods') (±1 SD)

Effect of alternative prey

Like the single prey functional response, ingestion rates on *Acartia* in the presence of *Chaetoceros gracilis* were highly variable among replicate containers (CVs for single prey were 26 to 150% vs 2-prey CVs of 28 to 130%). *Acartia* ingestion rates (I_A) were $\log_e$ transformed to stabilize the variance (Zar 1984) and 2-way analysis of variance was used to determine the effect of initial *C. gracilis* concentration and initial *Acartia* concentration on I_A. The mean I_A was signifi-

Table 1. *Nyctiphanes australis*. Comparison of ingestion rates at different concentrations of *Chaetoceros gracilis* and *Acartia* using 2-way analysis of variance. Data were $\log_e$ transformed before analysis. Horizontal lines join ingestion rates that are not significantly different in a Tukey test at $p < 0.05$

Dependent variable: ingestion rate of *N. australis* on *Acartia*

Independent variables	df	*F*	$p > F$
Initial *C. gracilis* concentration	3	11.94	0.0001
Initial *Acartia* concentration	3	70.47	0.0001
Interaction	9	1.09	0.06

Effect of *Acartia* concentration on the ingestion rates of *Acartia* by *N. australis*

	Acartia concentration (*Acartia* l^{-1})			
	1	4	8	15
Mean ingestion rate (*Acartia* mg^{-1} E_{dw} h^{-1})	0.01	0.03	0.07	0.11
Tukey test ($p < 0.05$)	——	——	——	——

Effect of *C. gracilis* concentration on the ingestion rates of *Acartia* by *N. australis*

	C. gracilis concentration (µg chl *a* l^{-1})			
	0	3.14	7.52	17.03
Mean ingestion rate (*Acartia* mg^{-1} E_{dw} h^{-1})	0.08	0.05	0.05	0.04
Tukey test ($p < 0.05$)	——	————		

cantly affected by *C. gracilis* concentration ($p < 0.001$; Table 1). There was no significant interaction effect ($p > 0.05$; Table 1) between *C. gracilis* concentration and *Acartia* concentration. Mean I_A increased significantly with increasing *Acartia* concentration ($p < 0.05$, Tukey test; Table 1). A significant change in mean I_A could be detected only as a function of the presence or absence, and not concentration, of *C. gracilis* ($p < 0.05$, Tukey test; Table 1).

I_A values were grouped and the functional response modelled. A LOWESS fit suggested a linear or a Holling type III functional response. The residual RSS value for the type III model was slightly lower than for a linear regression (0.059 vs 0.060) suggesting that the type III response provides a better description of the data than a linear response. For both models examination of the residuals showed a pattern of increasing variance at higher *Acartia* concentrations; however, as explained above, transformation of the dependent variable complicates interpretation of the model so transformation was avoided. A Holling type III model also provided the best description of the functional response of *Nyctiphanes australis* feeding on *Acartia* in the absence of *Chaetoceros gracilis*. For both data sets parameter values for the type III model were uniquely determined (parameter correlations $< |0.9|$) thus comparable. In the presence of *C. gracilis* the attack rate on *Acartia* was decreased from 0.006 to 0.002 l mg^{-1} E_{dw} h^{-1}, and the handling time increased from 6.034 to 7.196 mg E_{dw} h *Acartia*$^{-1}$. The effect of decreased attack rate and increased handling time on the functional response can be seen in Fig. 2: a much lower rate of increase in the ingestion rate on *Acartia* in the presence of *C. gracilis*.

Ingestion rates on *Chaetoceros gracilis* (I_C) in the presence of *Acartia* were highly variable among replicate containers (CV = 29 to 130%). I_C data were $\log_e$ transformed to stabilize the variance (Zar 1984), and 2-way analysis of variance was used to determine the effect of *C. gracilis* concentration and *Acartia* concentration on I_C. Ingestion rate was significantly affected by *Acartia* concentration ($p < 0.001$; Table 2). There was a significant interactive effect ($p < 0.001$; Table 2) between concentrations of the diatom and copepod on I_C. Mean I_C increased with increasing *C. gracilis* concen-

Table 2. *Nyctiphanes australis*. Comparison of ingestion rates of krill feeding on *Chaetoceros gracilis* at different concentrations of *C. gracilis* and *Acartia* using a 2-way analysis of variance. Data were $\log_e$ transformed before analysis. Horizontal lines join ingestion rates that are not significantly different in a Tukey test at $p < 0.05$

Dependent variable: ingestion rate of *N. australis* on *C. gracilis*

Independent variables	df	*F*	$p > F$
Initial *C. gracilis* concentration	2	7.46	0.001
Initial *Acartia* concentration	3	17.06	0.0001
Interaction	6	4.93	0.001

Effect of *C. gracilis* concentration on the ingestion rates of *C. gracilis* by *N. australis*

	C. gracilis concentration (µg chl *a* l^{-1})		
	3.14	7.52	17.03
Mean ingestion rate (ng pigment mg^{-1} E_{dw} h^{-1})	1.00	1.34	2.46
Tukey test ($p < 0.05$)	————		——

Effect of *Acartia* concentration on the ingestion rates of *C. gracilis* by *N. australis*

	Acartia concentration (*Acartia* l^{-1})			
	1	4	8	15
Mean ingestion rate (ng pigment mg^{-1} E_{dw} h^{-1})	1.49	1.07	1.28	2.44
Tukey test ($p < 0.05$)	————			——

tration (Table 2), and a Tukey test revealed I_C at 17.03 µg chl *a* l^{-1} was significantly higher ($p < 0.05$) than ingestion rates at 7.52 and 3.14 µg chl *a* l^{-1}. A comparison between I_C at different concentrations of *Acartia* showed ingestion rates were significantly higher ($p < 0.05$, Tukey test; Table 2) at 15 *Acartia* l^{-1} than at 1, 4 and 8 *Acartia* l^{-1}. No attempt was made to model the functional response of *Nyctiphanes australis* grazing on *C. gracilis* in the mixed experiments since 3 points would not provide a reasonable definition.

DISCUSSION

Previous authors (Yen 1983, Spitze 1985) compared model parameters as a method of detecting changes in the functional response as environmental factors are changed. However for the Michaelis-Menten and type II models the high correlations between parameters preclude uniquely determining parameter values. For these models, the functional response curves should not be compared using their non-unique parameter values.

Results from this study suggest that grazing rates saturate at high chl *a* concentrations. This result contrasts with the functional response of *Nyctiphanes australis* feeding on *Chaetoceros gracilis* determined by McClatchie et al. (1991) using the controlled dilution of *in vivo* fluorescence method. A linear model best described their data, and ingestion rates did not saturate at concentrations as high as 34 µg chl *a* l^{-1}. McClatchie et al.'s (1991) functional response experiments were conducted under identical conditions to ours, except that the temperature was 15 °C instead of 11 °C. The implication is that the form of the functional response varies with temperature. An alternative explanation lies in the different way in which the functional response was measured (but see McClatchie et al. 1991 for a comparison of methods).

The form of the functional response was a type II for *Nyctiphanes australis* feeding on *Chaetoceros gracilis* and a type III for *N. australis* feeding on *Acartia*. Hassell (1978) summarized studies showing that the functional response of a predator can vary with prey type (i.e. prey morphology, chemical composition or mobility). *Acartia* are probably encountered by *N. australis* less frequently while feeding than *C. gracilis* since they are numerically less abundant. This difference in encounter rates has been observed in other predators, and produced changes from a type II to a type III functional response (Hassell 1978, Abrams 1982). Mauchline (1980) stated that euphausiids feed carnivorously by 'encounter feeding', i.e. they capture zooplankton only if the zooplankton bump into the krill's feeding appendages during normal filtering motions. Lasker (1966), in contrast, suggested that *Euphausia pacifica* 'actively hunted' *Artemia* nauplii, since clearance rates were much higher than those observed for algal food. Predators that actively search for prey often generate type III functional responses as they learn to concentrate on more abundant prey (Holling 1965, Hassell 1978). We cannot therefore determine whether the change in functional response is a result of different search modes or is due to a change in encounter rate.

The volume of the experimental container may also have affected the form of the functional response because we measured the *Nyctiphanes australis/Chaetoceros gracilis* functional response in 60 l containers and the *N. australis/Acartia* functional response in 4 l containers. Price et al. (1988) observed that the form of the functional response did not change for *Euphausia superba* feeding on copepods in 50 l and 5 l containers although ingestion rates were lower in small containers. In carnivory experiments the prey were not replaced as they were consumed. Non-replacement may influence the form of the functional response, although experiments were run over relatively short time intervals and the mean prey depletion at each *Acartia* concentration did not exceed 20 to 44 %.

Ohman (1984) measured a type II response for *Euphausia pacifica* feeding carnivorously on *Pseudocalanus* spp., and a type III response for *E. pacifica* feeding herbivorously on *Thalassiosira angstii*. This is the reverse of our observations for *Nyctiphanes australis* where carnivorous feeding produced a type III response and herbivorous feeding a type II response. In both cases the type III response was associated with the prey species that was consumed at a higher rate. It appears that the functional response of krill is not rigid and stereotypic but changes with prey type. Abrams (1982) argued that functional responses measured in the laboratory may differ from those in the field because of the difficulty of experimentally reproducing factors such as predation pressure, which influences foraging time and the availability of numerous prey types. This suggests caution when extrapolating laboratory functional responses to the field.

The intersetule meshes on the feeding basket of *Nyctiphanes australis* are exceptionally fine compared to those of other krill. Consequently *N. australis* should be capable of exploiting nanoplankton-sized (2 to 20 µm) particles (Dalley & McClatchie 1989). *N. australis* is capable of grazing phytoplankton as small as *Chatoceros gracilis*, but results of this study and McClatchie et al. (1991) indicated ingestion and clearance rates on this cell are low. The morphology of *C. gracilis* (see Fig. 13b in McClatchie et al. 1991)

suggests this diatom may not be a very nutritious cell. Ingestion rates appear to saturate at chl *a* concentrations >5 to 8 µg l^{-1}, but rates are so low they cannot possibly represent the physiological maximum defined by the gut volume and gut passage time.

The low and variable grazing rates measured in this study may be a result of the gut pigment method. Two major sources of error pertain to this study: (1) degradation of pigment to nonfluorescing forms (Conover et al. 1986, Lopez et al. 1988, Penry & Frost 1991); and (2) accurate estimation of gut clearance rate constant (Dam & Peterson 1988, Penry & Frost 1990).

In laboratory experiments the extent of chl *a* degradation by copepods is variable (0 to 92%) (Lopez et al. 1988, Peterson et al. 1990), yet differences in experimental procedure make comparisons difficult. Overall, an average chl *a* loss of 33% has been observed in copepods, a value we used to correct pheophorbide concentrations in the absence of chlorophyll destruction values for *Nyctiphanes australis*. Recent work suggests that pigment destruction is not constant but varies as a function of trophic history and, to a lesser extent, food concentration (Mayzaud & Razouls 1992).

The gut clearance rate constant used in this study was determined by McClatchie et al. (1991) from the decline in gut fluorescence of *Nyctiphanes australis* (prefed on *Chaetoceros gracilis*) in filtered seawater. This method is thought to be conservative, overestimating throughput times thus minimizing estimates of food processing rates by approximately 20% (Kiørboe et al. 1985, Kiørboe & Tiselius 1987, Ellis & Small 1989). However, Penry & Frost (1990) suggest the direction of the error is a function of species, experimental conditions and the method for calculating the evacuation rate. McClatchie et al. (1991) measured grazing rates of *N. australis* on *C. gracilis* by the removal of chlorophyll under identical conditions to ours. A comparison with their results suggests that gut pigment rates are underestimated by a factor of 15.

The gut pigment method was used by McClatchie et al. (1991) to estimate *in situ* feeding rates of *Nyctiphanes australis*. *In situ* ingestion rates ranged from 53 to 271 ng pigment $krill^{-1}$ h^{-1}, which were 10 to 900 times higher than rates measured in laboratory functional response experiments at the same temperature (11 °C) and chl *a* concentration (1.8 µg l^{-1}). McClatchie et al. (1991) did not examine krill from the field for epizoic diatoms. Consequently *in situ* rates may have been overestimated by 2 to 5 times (McClatchie et al. 1990). Krill used in laboratory experiments had shed epizoic diatoms by molting.

Low grazing rates in the laboratory may be due to small cell size, unsuitable algal species or laboratory conditions. McClatchie et al. (1991) suggested that the effect of laboratory conditions is minimal in experiments conducted in large containers where krill were acclimated for several weeks in the laboratory. The krill density in our experiments was 1.4 to 1.8 krill l^{-1}. Morris et al. (1983) noted a 6-fold increase in the clearance rates of *Euphausia superba* at densities <0.5 krill l^{-1}. Studies on the feeding behaviour of copepods have shown that the nutritional state of the algal species affects ingestion rates (Houde & Roman 1987, Cowles et al. 1988). As the *Chaetoceros gracilis* cultures used in experiments were always in log phase growth and considered to be in healthy condition, it is unlikely that *Nyctiphanes australis* reduced its feeding rates in response to senescent or poor quality algae. Analyses of the stomach contents of preserved *N. australis* have shown that *in situ*, they ingest a wide range of living and dead items including diatoms (Dalley & McClatchie 1989, Ritz et al. 1990), so there is no reason to suspect that *C. gracilis* is an unsuitable prey species. Small cell size is the most likely factor limiting ingestion rate of algae in this study. Although the spines of *C. gracilis* span ca 80 µm the cell frustule is small, and the spines may lead the krill to reject cells even though they are easily captured. Low ingestion rates indicate that small cells such as *C. gracilis* are suboptimal prey and *N. australis* gains much of its ration from larger algal species or carnivorous feeding.

In contrast to the fine setulation of the feeding basket, *Nyctiphanes australis* has a mandible resembling that of a predominantly carnivorous krill (Dalley & McClatchie 1989). Results show that ingestion rates were 32 times higher on *Acartia* than on *Chaetoceros gracilis* at similar carbon concentrations. There are no other reported carnivorous feeding rates for *N. australis*, and comparisons with other species of krill are difficult due to differences in body size, prey types and experimental conditions. McClatchie (1985) reported ingestion rates of 0.7 to 1.1 copepods $krill^{-1}$ h^{-1} at concentrations of 5 to 15 copepods l^{-1} for the predominantly carnivorous euphausiid *Meganyctiphanes norvegica*. At similar copepod concentrations ingestion rates of *N. australis* were 0.2 to 0.7 *Acartia* $krill^{-1}$ h^{-1}. *M. norvegica* at 30 mm in length is approximately twice the size of *N. australis*. Ingestion rates of the predominantly herbivorous krill *Euphausia pacifica* (20 mm in length) preying on the copepod *Pseudocalanus* sp. (Ohman 1984) were 10 to 20 times lower than the rates we measured for *N. australis* at similar prey concentrations. We conclude that feeding rates on *Acartia* are comparable to those of more carnivorous krill but the gut pigment ingestion rates of *N. australis* in the field show it is also an effective phytoplankton feeder (McClatchie et al. 1991).

Ingestion rates may be underestimated to the extent that *Nyctiphanes australis* injured, but did not fully ingest, their prey. Ohman (1984) reported that

Euphausia pacifica inflicted injuries (mainly to the urosomes, antennules and swimming legs) to 22% of the *Pseudocalanus* used in experiments while Price et al. (1988) noted <1% of copepods that were recovered from predation experiments with *E. superba* were injured. Although injuries were not quantified, *Acartia* that were recovered from our predation experiments did not appear to have significant injuries, which suggests that *N. australis* generally consume all of their prey. We consider that body parts ingested after an unsuccessful attack would not contribute significantly towards the ration of *N. australis*.

Detectable ingestion rates were measured at all chl *a* concentrations examined. Whether ingestion ceases at chl *a* concentrations >0 cannot be answered without extrapolation to concentrations lower than those we measured (1.7 µg chl *a* l^{-1}). McClatchie et al. (1991) measured feeding rates of *Nyctiphanes australis* on *Chaetoceros gracilis* at concentrations of 0.4 µg chl *a* l^{-1} and their data also suggest that ingestion would not cease at chl *a* concentrations >0. There is also no evidence to suggest that feeding stops at low *Acartia* concentrations. These results are consistent with other observations of copepod and euphausiid feeding behaviour which show that feeding and swimming rates are reduced at low phytoplankton concentrations, but do not cease altogether (Frost 1975, Kiørboe et al. 1982, Frost et al. 1983, Hamner 1988, McClatchie 1988).

A decrease in feeding effort on *Chaetoceros gracilis* (measured as clearance rate) at low chl *a* concentrations is consistent with the theoretical predictions of optimal foraging behaviour of suspension-feeding zooplankton (Lam & Frost 1976, Lehman 1976). When the energetic return per unit foraging time is sufficiently reduced, the optimum behaviour is to reduce the cost of feeding by decreasing the effort. Clearance rates on *C. gracilis* also appear to decrease at high chl *a* concentrations. This is commonly explained by a decrease in feeding effort (Hughes 1980), but Ohman (1984) suggested that the time spent capturing and processing algal prey at high concentrations may measurably reduce the total time available for searching for food.

The prey concentrations over which the functional responses were determined in this study (1.7 to 14.8 µg chl *a* l^{-1} and 0.5 to 15 *Acartia* l^{-1}) are higher than 'typical' phytoplankton (0.8 to 2 µg chl *a* l^{-1}; Kawachi 1990) and copepod (0.01 to 1 copepod l^{-1}; Jillett 1976) concentrations observed in Otago Harbour during summer when *Nyctiphanes australis* is abundant. However if, as suggested by previous workers (McClatchie 1986, Price et al. 1988, Price 1989), krill maintain themselves in regions of higher than average prey concentrations, the functional response measurements at higher prey concentrations made in this study are pertinent.

The classic effect of high concentrations of alternative food is to lower the entire functional response (Holling 1959a, Marten 1973, Oaten & Murdoch 1975, Goss-Custard 1977). *Chaetoceros gracilis* had this effect on the functional response of *Nyctiphanes australis* feeding on *Acartia*. It is possible that the reduced attack rate and increased handling time for *Acartia* in the presence of *C. gracilis* are a result of the time spent processing (capturing, handling, ingesting) *C. gracilis* retained on the filter basket, thus reducing the time available to search and capture *Acartia*. However, it is also possible that *N. australis* may filter significantly larger quantities of *C. gracilis* but, for some reason (e.g. palatability), rejects cells before ingestion. This would have a marked effect on the time available for the capture of *Acartia*. Hamner (1988) observed bolus rejection in *Euphausia superba* when the bolus became too large to manipulate or when the animal was satiated. It is unlikely that *N. australis* becomes satiated with *C. gracilis* since the feeding rates that we measured were well below the physiological maximum defined by gut volume and gut passage time.

Although several studies have examined the effect of phytoplankton on the carnivorous feeding rates of marine copepods, no single general relationship has emerged. Studies suggest, however, that phytoplankton effects tend to be consistent within some genera. Carnivorous feeding rates of both *Calanus finmarchicus* (Anraku & Omori 1963) and *Calanus pacificus* (Landry 1981) decline as phytoplankton concentration increases. In contrast, carnivorous feeding rates of *Centropages hamatus* (Anraku & Omori 1963) and *Centropages furcatus* (Paffenhöfer & Knowles 1980) are unaffected by phytoplankton as are those of *Temora stylifera* (Paffenhöfer & Knowles 1980). These species are more carnivorous than *C. finmarchicus* and *C. pacificus*. Conflicting results for *Acartia tonsa* (Anraku & Omori 1963, Lonsdale et al. 1979) prohibit generalization about the effect of phytoplankton on the carnivorous feeding rates of this species. There is less information about the effect of phytoplankton on the carnivorous feeding rates of euphausiids. Price et al. (1988) observed a significant increase in the ingestion rates on copepods by *Euphausia superba* in the presence of phytoplankton. Stuart & Pillar (1990) suggest that, *in situ*, *E. lucens* will stop feeding on copepods when there is sufficient phytoplankton. Our results show that feeding on copepods by *Nyctiphanes australis* is depressed in the presence of small diatoms.

The fact that *Nyctiphanes australis* feed at higher rates on *Acartia* was not surprising given the much higher carbon per prey unit of these copepods compared to very small diatoms. We have no data from which we can assess the costs of carnivorous feeding relative to herbivory. Optimal foraging theory predicts

decreased feeding rate on energetically less valuable prey in the presence of increasing concentrations of energetically more valuable prey (Pyke et al. 1977). In contrast to this prediction, our data suggest increased rates of feeding on the algae *Chaetoceros gracilis* in the presence of high concentrations of *Acartia*. This could be explained by incidental capture of algae during carnivorous feeding, since *N. australis* has an extremely fine-meshed feeding basket. The problem is that we cannot distinguish such feeding from increased gut pigment derived from krill feeding on fluorescent faecal material and/or *Acartia*, which themselves are full of chlorophyll. In mixed prey experiments the effect would be enhanced because *Acartia* are able to feed continuously on *C. gracilis* until they are captured by *N. australis*. However, the functional response of *Acartia* is depressed in the presence of the algae, and this shows that some time is being allocated to handling the small diatoms. We do not know whether this time is being used for ingestion or rejection of the algae. Holling (1965) defined handling time as the time spent pursuing, subduing and eating prey. The *N. australis*/*Acartia* functional response was obtained by averaging the number of *Acartia* consumed at different prey densities during a 6 h period. The handling times from these functional response curves are very long, on the order of 1.5 h *Acartia*$^{-1}$, which indicates that the krill are not feeding continuously on *Acartia*, and they may in fact obtain their required carbon ration quite quickly. Handling time is a misnomer in this case. Our data demonstrate an interference effect on the ingestion of an optimal prey item (the copepods) by a suboptimal prey (the algae), which, although yielding little nutriment, nevertheless take time to deal with.

Acknowledgements. We thank Bev Dickson, Les Neilson and Colin Adam for their assistance in the collection of zooplankton, Brian Niven and Bryan Manly who helped with data analysis, and Carolyn Burns and John Jillett for comments on an early draft of the manuscript. The constructive criticism of 3 anonymous reviewers contributed to interpretation of the results and the clarity of the manuscript.

LITERATURE CITED

Abrams, P. A. (1982). Functional response of optimal foragers. Am. Nat. 20: 382–390

Anraku, M., Omori, M. (1963). Preliminary survey of the relationship between the feeding habit and the structure of the mouth-parts of marine copepods. Limnol. Oceanogr. 8: 116–126

Bary, B. M. (1956). Notes on ecology, systematics and development of some Mysidarea and Euphausiacea (Crustacea) from New Zealand. Pacif. Sci. 10: 431–461

Bradford, J. M. (1976). Partial revision of the *Acartia* subgenus *Acartiura* (Copepoda: Calanoida: Acartiidae). N.Z. J. mar. Freshwat. Res. 10: 159–202

Conover, R. J., Durvasula, R., Roy, S., Wang, R. (1986). Probable loss of chlorophyll derived pigments during passage through the gut of zooplankton, and some of the consequences. Limnol. Oceanogr. 31: 878–887

Cowles, T. J., Olson, R. J., Chisholm, S. W. (1988). Food selection by copepods: discrimination on the basis of food quality. Mar. Biol. 100: 41–49

Crippen, R. W., Perrier, J. L. (1974). The use of neutral red and Evans blue for live-dead determinations of marine plankton. Stain Technol. 49: 97–104

Dagg, M. J., Grill, D. W. (1980). Natural feeding rates of *Centropages typicus* females in the New York Bight. Limnol. Oceanogr. 25: 597–609

Dalley, D. E., McClatchie, S. (1989). Functional feeding morphology of the euphausiid *Nyctiphanes australis*. Mar. Biol. 101: 195–203

Dam, H. G., Peterson, W. T (1988). The effect of temperature on the gut clearance rate constant of planktonic copepods. J. exp. mar. Biol. Ecol. 123: 1–14

Downing, J. A. (1981). *In situ* foraging responses of three species of littoral cladocerans. Ecol. Monogr. 51: 85–103

Draper, N. R., Smith, H. (1981). Applied regression analysis. Wiley, New York

Ellis, S. G., Small, L. F. (1989). Comparison of gut-evacuation rates of feeding and non-feeding *Calanus marshallae*. Mar. Biol. 103: 175–181

Fowler, S. W., Benayoun, G., Small, L. F. (1971). Experimental studies on the feeding, growth and assimilation in a Mediterranean euphausiid. Thalassia Jugosl. 7: 35–47

Frost, B. W. (1975). A threshold feeding behaviour in *Calanus pacificus*. Limnol. Oceanogr. 20: 263–266

Frost, B. W., Landry, M. R., Hassett, R. P. (1983). Feeding behaviour of large calanoid copepods *Neocalanus cristatus* and *N. plumchrus* from the subarctic Pacific Ocean. Deep Sea Res. 30: 1–13

Goss-Custard, J. D. (1977). The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. J. Anim. Ecol. 46: 1–19

Greene, C. H., Landry, M. R. (1985). Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata*. Ecology 66: 1408–1416

Guillard, R. R. L., Ryther, J. H. (1962). Studies of marine planktonic diatoms. I. *Cyastella mana* Hustedt and *Neloxuli confesvacea* Clive. Can. J. Microbiol. 8: 229–239

Hamner, W. M. (1988). Biomechanics of filter feeding in the Antarctic krill *Euphausia superba*: review of past work and new observations. J. Crust. Biol. 8: 149–163

Hassell, M. P. (1978). The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton

Hassell, M. P., Lawton, J. H., Beddington, J. R. (1976). The components of arthropod predation I. The prey death rate. J. Anim. Ecol. 45: 135–164

Hassell, M. P., Lawton, J. H., Beddington, J. R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids. J. Anim. Ecol. 46: 249–262

Head, E. J. H., Harris, L. R. (1987). Copepod feeding patterns before and during a spring bloom in Bedford Basin, Nova Scotia. Mar. Ecol. Prog. Ser. 40: 221–230

Holling, C. S. (1959a). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91: 293–320

Holling, C. S. (1959b). Some characteristics of simple types of predation and parasitism. Can. Entomol. 91: 385–398

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. Mem. entomol. Soc. Can. 45: 1–60

Houde, S. E. L., Roman, M. R. (1987). Effects of food quality

on the functional response of the copepod *Acartia tonsa*. Mar. Ecol. Prog. Ser. 40: 69–77
Hughes, R. N. (1980). Optimal foraging theory in the marine context. Oceanogr. mar. Biol. A. Rev. 18: 423–438
Ishii, H. (1990). *In situ* feeding rhythms of herbivorous copepods, and the effect of starvation. Mar. Biol. 105: 91–98
James, M. R., Wilkinson, V. H. (1988). Biomass, carbon ingestion and ammonia excretion by zooplankton associated with an upwelling plume in western Cook Strait, New Zealand. N.Z. J. mar. Freshwat. Res. 22: 249–257
Jillett, J. B. (1976). Zooplankton associations off Otago Peninsula, south-eastern New Zealand, related to different water masses. N.Z. J. mar. Freshwat. Res. 10: 543–557
Kato, M., Segawa, S., Tanoue, E., Murano, M. (1982). Filtering and ingestion rates of the Antarctic krill, *Euphausia superba* Dana. Trans. Tokyo Univ. Fish. 5: 167–175
Kawachi, R. (1990). Diurnal variation in feeding activity of the krill *Nyctiphanes australis*. M.Sc. thesis, University of Otago
Kiørboe, T., Møhlenberg, F., Nicolajsen, H. (1982). Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food concentration and temperature. Ophelia 21: 181–194
Kiørboe, T., Møhlenberg, F., Riisgård, H. U. (1985). *In situ* feeding rates of planktonic copepods: a comparison of four methods. J. exp. mar. Biol. Ecol. 88: 67–81
Kiørboe, T., Tiselius, P. T (1987). Gut clearance and pigment destruction in a herbivorous copepod, *Acartia tonsa*, and the determination of *in situ* grazing rates. J. Plankton Res. 9: 525–534
Lam, R. K., Frost, B. W. (1976). Model of copepod filtering response to changes in size and concentration of food. Limnol. Oceanogr. 21: 490–500
Landry, M. R. (1981). Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. Mar. Biol. 65: 77–82
Lasker, R. (1966). Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. J. Fish. Res. Bd Can. 23: 1291–1317
Lehman, J. T (1976). The filter-feeder as a optimal forager, and the predicted shapes of feeding curves. Limnol. Oceanogr. 21: 501–516
Lonsdale, D. J., Henile, D. R., Siegfried, C. (1979). Carnivorous feeding behaviour of the adult calanoid copepod *Acartia tonsa*. J. exp. mar. Biol. Ecol. 36: 235–248
Lopez, M. D. G., Huntley, M. E., Sykes, P. F. (1988). Pigment destruction by *Calanus pacificus*: impact on the estimation of water column fluxes. J. Plankton Res. 10: 715–734
Mackas, D. L., Bohrer, R. (1976). Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. J. exp. mar. Biol. Ecol. 25: 77–85
Marten, G. C. (1973). An optimization equation for predation. Ecology 54: 92–101
Mauchline, J. (1980). The biology of mysids and euphausiids. Adv. mar. Biol. 18
Mayzaud, P., Razouls, S. (1992). Degradation of gut pigment during feeding by a subantarctic copepod: importance of feeding history and digestive acclimation. Limnol. Oceanogr. 37: 393–409
McClatchie, S. (1985). Feeding behaviour in *Meganyctiphanes norvegica* (M. Sars) (Crustacea: Euphausiacea). J. exp. mar. Biol. Ecol. 86: 271–284
McClatchie, S. (1986). Time-series feeding rates of the euphausiid *Thysanoessa raschii* in a temporally patchy food environment. Limnol. Oceanogr. 31: 469–477
McClatchie, S. (1988). Functional response of the euphausiid *Thysanoessa raschii* grazing on small diatoms and toxic dinoflagellates. J. mar. Res. 46: 631–646
McClatchie, S., Jaquiery, P., Kawachi, R., Pilditch, C. (1991). Grazing rates of *Nyctiphanes australis* (Euphausiacea) in the laboratory and Otago Harbour, New Zealand, measured using three independent methods. Cont. Shelf Res. 11: 1–22
McClatchie, S., Kawachi, R., Dalley, D. E. (1990). Epizoic diatoms on the euphausiid *Nyctiphanes australis*: consequences for gut pigment analysis of whole animals. Mar. Biol. 104: 227–232
McClatchie, S., Lewis, M. R. (1986). Limitations of grazing rate equations: the case for time series measurements. Mar. Biol. 92: 135–140
Morris, D. J., Ward, P., Clarke, A. (1983). Some aspects of the feeding in the Antarctic krill, *Euphausia superba*. Polar Biol. 2: 21–26
Murdoch, W. W., Oaten, A. (1975). Predation and population stability. Adv. ecol. Res. 9: 2–131
Oaten, A., Murdoch, W. W. (1975). Switching, functional response, and stability in predator-prey systems. Am. Nat. 109: 299–318
Ohman, M. D. (1984). Omnivory by *Euphausia pacifica*: the role of copepod prey. Mar. Ecol. Prog. Ser. 19: 125–131
Ohman, M. D. (1990). The demographic benefits of diel vertical migration by zooplankton. Ecol. Monogr. 60: 257–281
Paffenhöfer, G.-A., Knowles, S. C. (1980). Omnivorousness in marine planktonic copepods. J. Plankton Res. 2: 355–365
Parsons, T. R., Maita, Y., Lalli, C. M. (1984). A manual of chemical and biological methods for sea water analysis. Pergamon Press, Oxford
Parsons, T. R., Stephens, K., Strickland, J. D. H. (1961). On the chemical composition of eleven species of marine phytoplankters. J. Fish. Res. Bd Can. 18: 1001–1016
Penry, D. L., Frost, B. W. (1990). Re-evaluation of the gut-fullness (gut fluorescence) method for inferring ingestion rates of suspension-feeding copepds. Limnol. Oceanogr. 35: 1207–1214
Penry, D. L., Frost, B. W. (1991). Chlorophyll *a* degradation by *Calanus pacificus*: dependence on ingestion rate and digestive acclimation to food resources. Limnol. Oceanogr. 36: 147–149
Peterson, W., Painting, S., Barlow, R. (1990). Feeding rates of *Calanoides carinatus*: a comparison of five methods including evaluation of the gut fluorescence method. Mar. Ecol. Prog. Ser. 63: 85–92
Price, H. J. (1989). Swimming behaviour of krill in response to algal patches: a mesocosm study. Limnol. Oceanogr. 34: 649–659
Price, H. J., Boyd, K. R., Boyd, C. M. (1988). Omnivorous feeding behaviour of the Antarctic krill *Euphausia superba*. Mar. Biol. 97: 67–77
Pyke, G. H., Pulliam, H. R., Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137–154
Ritz, D. A., Hosie, G. W. (1982). Production of the euphausiid *Nyctiphanes australis* in Storm Bay, South-eastern Tasmania. Mar. Biol. 68: 103–108
Ritz, D. A., Hosie, G. W., Kirkwood, R. J. (1990). Diet of *Nyctiphanes australis* Sars (Crustacea: Euphausiacea). Aust. J. mar. Freshwat. Res. 41: 365–374
Roy, S., Harris, R. P., Poulet, S. A. (1989). Inefficient feeding by *Calanus helgolandicus* and *Temora longicornis* on *Coscinodiscus wailesii*: quantitative estimation using chlorophyll-type pigments and effects on dissolved free amino acids. Mar. Ecol. Prog. Ser. 52: 145–153
Runge, J. A. (1980). Effects of hunger and season on the feeding behaviour of *Calanus pacificus*. Limnol. Oceanogr. 25: 134–145

Sars, G. O. (1883). Report on the Schizopoda collected by H.M.S. Challenger during the years 1873–76. Rep. scient. Results Voyage H.M.S. Challenger 13: 1–228

Schultze, P. C., Folt, C. L. (1989). Effects of conspecifics and phytoplankton on predation rates of omnivorous copepods *Epischura lacustris* and *Epischura nordenskioldi*. Limnol. Oceanogr. 34: 444–450

Sheard, K. (1953). Taxonomy, distribution and development of Euphausiacea (Crustacea). Rep. Brit. N.Z. Antarctic Res. Exped. Ser. B 8: 1–72

Siegal, S., Castellan, N. J. Jr (1988). Nonparametric statistics for the behavioural sciences, 2nd edn. McGraw-Hill, New York

Simard, Y., Lacroix, G., Legendre, L. (1986). Diel vertical migrations and nocturnal feeding of a dense coastal krill scattering layer (*Thysanoessa raschi* and *Meganyctiphanes norvegica*) in stratified surface waters. Mar. Biol. 91: 93–105

Spitze, K. (1985). Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. Ecology 66: 938–949

Stuart, V., Pillar, S. C. (1990). Diel grazing patterns of all ontogenetic stages of *Euphausia lucens* and *in situ* predation rates on copepods in the southern Benguela upwelling region. Mar. Ecol. Prog. Ser. 64: 227–241

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, New York

Wilkinson, L. (1989). SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL

Yen, J. (1982). Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. J. exp. mar. Biol. Ecol. 63: 105–117

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. 79: 9–77

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

Zar, J. H. (1984). Biostatistical analysis, 2nd edn. Prentice Hall, Englewood Cliffs, NJ

This article was submitted to the editor

Manuscript first received: February 1, 1993
Revised version accepted: January 5, 1994