Copepod grazing in a subtropical bay: species-specific responses to a midsummer increase in nanoplankton standing stock

Albert Calbet*, Michael R. Landry, Rebecca D. Scheinberg

Department of Oceanography, University of Hawaii at Manoa, 1000 Pope Road, Honolulu, Hawaii 96822, USA

ABSTRACT: Ingestion rates of 4 small copepod species (*Oithona simplex*, *O. nana*, *Acrocalanus inermis* and *Parvocalanus crassirostris*) were investigated in Kaneohe Bay, Hawaii, during a midsummer increase of the pico- and nanoplankton communities. There was no evidence that adult female copepods fed significantly on picoplankton-sized cells. However, all the species responded behaviorally to variations in the concentration (10 to $110 \mu\text{g C l}^{-1}$) and size spectrum (relative increase of cells $>5 \mu\text{m}$) of nanoplankton prey. The copepods generally behaved as opportunistic particle feeders, demonstrating higher consumption rates on the most abundant cells (2 – $5 \mu\text{m}$ nanoplankton); however, autotrophs were usually selected over heterotrophs of similar size. Maximum ingestion rates were similar for the 2 calanoids and *O. nana* (around $120\,000$ cells copepod $^{-1}$ d $^{-1}$) and lower for *O. simplex* (around $40\,000$ cells copepod $^{-1}$ d $^{-1}$), but biomass-specific rates of *O. simplex* equaled those of the other species. At the highest nanoplankton concentrations, the ingestion rates of copepods appeared saturated, daily rations ranging from 100% body C d $^{-1}$ for *A. inermis* to 260% body C d $^{-1}$ for *P. crassirostris*. The differences between ingestion rates measured as cells per copepod per day and those converted to carbon suggested that ingestion might be held below potential by the cumulative handling times of individual prey rather than the physiological constraints of food consumption and digestive processing.

KEY WORDS: Copepod · Ingestion rates · Nanoplankton · *Oithona simplex* · *O. nana* · *Acrocalanus inermis* · *Parvocalanus crassirostris*

INTRODUCTION

Marine planktonic communities comprise a wide variety of organisms from prokaryotes to complex metazoans. Among the latter, copepods are the most abundant and ubiquitous group (Humes 1994, Verity & Smetacek 1996), playing important roles in the transfer of matter and energy from primary producers to higher trophic levels (fish larvae) and in the export of organic matter from the euphotic to deeper layers of the oceans. Most experimental research on copepods has focused on larger species, and routine sampling with relatively coarse mesh nets typically means that smaller species are undersampled or ignored in marine systems (Hopcroft et al. 1998). Although this situation

has begun to be remedied in recent studies (Sabatini & Kiørboe 1994, Roff et al. 1995, Uye & Sano 1998, Hopcroft & Roff 1998, Hopcroft et al. 1998), there is still relatively little known about the trophic function of small copepods in marine ecosystems.

Small copepod species, along with juvenile stages of larger forms, are important as trophic intermediaries between classical and microbial food webs (Roff et al. 1995, Wickham 1995). This role may be specially significant in oligotrophic ecosystems, where pico-sized (0.2 to $2 \mu\text{m}$) auto- and heterotrophic organisms comprise much of the system biomass (Campbell et al. 1994, 1997). On average, copepods feed on prey about a factor of 18 smaller than their linear body dimensions (Hansen et al. 1994). Therefore, smaller copepods are closer than larger copepods to the base of the microbial food web in terms of physical constraints on their feeding mechanisms. Small copepods may also increase the efficiency of trophic transfer by short-circuiting

*Present address: Institut de Ciències del Mar, CSIC, Dept. Biologia Marina i Oceanografia, Ps. Joan de Borbó s/n, 08039 Barcelona, Catalunya, Spain. E-mail: acalbet@icm.csic.es

intermediate levels of protistan predators which tend to feed on prey much closer to their own body size (Hansen et al. 1994).

In the present study, we examine the feeding of small copepods on the ambient nanoplankton community of a subtropical embayment. In order to contribute to a better understanding of the biology and behavior of small copepods in general, we compare experimental results for 4 species: 2 cyclopoids (*Oithona simplex* and *O. nana*) and 2 calanoids (*Acrocalanus inermis* and *Parvocalanus crassirostris*).

MATERIALS AND METHODS

Experiments were conducted during summer and early autumn 1998 (Table 1) at a fixed station (21°25.728'N, 157°46.713'W) in the southern basin of Kaneohe Bay, Oahu, Hawaii, USA. Water was collected at 2 m intervals through the 12 m water column with a 2 l Niskin bottle and gently mixed in a 20 l polycarbonate carboy. The abundance of copepods was assessed using a 0.5 m diameter plankton net with 64 µm mesh hauled vertically from near the bottom to the surface. Samples were quickly preserved in buffered formalin (4% final concentration) for later study. In the laboratory, the species composition of the copepod community was estimated by counting and identifying at least 250 ind. sample⁻¹.

Experimental organisms were also collected by vertical net tows, and the contents of the cod end were poured into an isothermic container. The animals were transported to the laboratory within 30 min of collection and sorted under a dissecting microscope. Depending on the size of the copepods, 12 to 20 adult females of the most abundant species (*Oithona simplex*, 247 µm ± 0.3 SE; *O. nana*, 364 µm ± 2.5 SE; *Acro-*

calanus inermis, 508 µm ± 1.0 SE; and, in Expts 3 and 4, *Parvocalanus crassirostris*, 384 µm ± 0.1 SE) were added to 250 ml polystyrene culture flasks (Corning) filled with bay water prescreened by gentle reverse filtration through a 64 µm mesh in order to remove copepods and other large grazers. These copepod concentrations were higher than those in the ambient environment, but within the range that elicits no crowding effect for the largest species, *A. inermis* (Kimmerer 1984a). Each experiment was prepared with 4 replicate treatment bottles for each species, 4 initials and 4 control bottles without added copepods.

Experimental bottles were incubated *in situ* at 2 m depth for 24 h, the water temperature varying from 26 to 27.5°C during the study. At the beginning and end of each incubation, the water was subsampled for assessment of the pico- and nanoplankton communities. For picoplankton abundances, 2 ml samples were preserved with paraformaldehyde (0.2% final concentration) and stored at -85°C (Vaulot et al. 1989). The samples were thawed and stained with Hoeschst 33342 (1 µg ml⁻¹) according to Monger & Landry (1993) and processed using a Coulter EPIC 753 flow cytometer equipped with two 5 W Argon lasers, MSDS volume-control sampling and Cytomation CICERO software (Campbell et al. 1997). For nanoplankton concentrations (defined for this work as >2 µm protozoans, mostly flagellates, that passed through a 64 µm mesh), 50 ml samples were preserved with alkaline Lugol's fixative (0.005% final concentration), followed by the addition of borate-buffered formalin (2% final concentration) and sodium thiosulfate (0.3% final concentration) (Sherr & Sherr 1993). After fixation, the samples were stained momentarily with proflavin (10 µg ml⁻¹ final concentration) followed by DAPI (2 µg ml⁻¹) and filtered onto 2 µm black polycarbonate membrane filters. The filters were mounted on slides with immer-

Table 1 Initial abundances and net growth rates in controls (n = 4) after 24 h incubations for the different components of the nanoplankton community. Values are expressed as mean ± SE. Het: heterotrophs; Auto: autotrophs

1998		2–5 µm Het	2–5 µm Auto	>5 µm Het	>5 µm Auto	Total
Expt 1 (25 Jun)	Cells ml ⁻¹	3110 ± 102	1150 ± 223	107 ± 4	62 ± 3	4430
	µg C l ⁻¹	5.7	1.8	1.9	2.5	12.0
	Growth rate (d ⁻¹)	0.26 ± 0.141	-0.31 ± 0.226	0.34 ± 0.081	-0.18 ± 0.129	
Expt 2 (29 Jul)	Cells ml ⁻¹	3160 ± 413	3590 ± 186	382 ± 44	633 ± 89	7760
	µg C l ⁻¹	5.5	8.4	5.7	11.0	31.0
	Growth rate (d ⁻¹)	0.44 ± 0.031	0.62 ± 0.054	0.11 ± 0.149	0.25 ± 0.058	
Expt 3 (26 Aug)	Cells ml ⁻¹	5560 ± 823	2800 ± 235	1030 ± 106	990 ± 121	10380
	µg C l ⁻¹	9.6	6.6	15.0	17.0	49.0
	Growth rate (d ⁻¹)	0.75 ± 0.105	0.24 ± 0.051	0.68 ± 0.083	0.25 ± 0.177	
Expt 4 (8 Oct)	Cells ml ⁻¹	9870 ± 840	4500 ± 870	1740 ± 622	1610 ± 153	17720
	µg C l ⁻¹	20.0	11.0	38.0	37.0	110.0
	Growth rate (d ⁻¹)	0.28 ± 0.139	0.95 ± 0.113	-0.002 ± 0.356	0.97 ± 0.041	

sion oil and analyzed with a color image-analysis system consisting of a Zeiss epifluorescence microscope with a ZVS 3-chip CCD video camera connected to a computer. The images were processed using Zeiss Image Pro Plus software to facilitate counting and sizing of all heterotrophic and autotrophic organisms. Approximately 300 individuals were enumerated and sized for each sample. We present the results in 2 size fractions; heterotrophs and autotrophs between 2 and 5 μm (hereafter called 2–5 μm Het and 2–5 μm Auto, respectively) and cells larger than 5 μm (>5 μm Het and >5 μm Auto).

Ingestion rates were calculated according to the equations of Frost (1972). The reduction of each prey category during the incubations with grazers relative to the initial concentrations is shown in Table 2. Nanoplankton biovolumes (mostly naked flagellates)

Table 2. Average values and ranges (in parentheses) of % cells reduction of each prey category during the incubations with grazers relative to the initial concentrations. Negative values indicate actual growth compared to initial concentrations

	2–5 μm Het	2–5 μm Auto	>5 μm Het	>5 μm Auto
Expt 1				
<i>A. inermis</i>	66.9 (58, 72)	70.2 (67, 74)	19.6 (–1.0, 38)	63.2 (42, 82)
<i>O. nana</i>	44.4 (32, 60)	57.9 (37, 79)	20.5 (2.6, 38)	60.0 (47, 73)
<i>O. simplex</i>	52.5 (41, 64)	66.5 (53, 74)	–6.4 (–28, 23)	28.9 (20, 38)
Expt 2				
<i>A. inermis</i>	–17.5 (–37, 4.0)	16.8 (–12, 34)	–26.1 (–21, 53)	42.2 (15, 38)
<i>O. nana</i>	5.7 (–14, 15)	19.5 (10, 26)	–26.1 (–49, 16)	42.2 (27, 55)
<i>O. simplex</i>	–12.4 (–43, 22)	6.9 (–48, 27)	–5.1 (–49, 35)	22.4 (4.1, 44)
Expt 3				
<i>A. inermis</i>	–70.1 (–88, –53)	34.6 (–13, 65)	–39.4 (–73, 10)	46.4 (16, 79)
<i>P. crassirostris</i>	–58.5 (–85, –41)	39.6 (34, 44)	–3.5 (–10, 10)	52.3 (31, 75)
<i>O. nana</i>	–67.7 (–109, –35)	8.7 (–15, 19)	–32.3 (–61, –15)	16.7 (–15, 55)
<i>O. simplex</i>	–65.4 (–120, –4.1)	15.6 (2.4, 23)	–16.4 (–97, 49)	9.9 (–55, 46)
Expt 4				
<i>A. inermis</i>	–32.7 (–53, –12)	–97.5 (–130, –75)	10.1 (–11, 36)	–99.6 (–130, –62)
<i>P. crassirostris</i>	–19.0 (–36, –4)	–79.1 (–115, –56)	15.7 (1.4, 28)	–35.5 (–66, –15)
<i>O. nana</i>	–11.3 (–29, 15)	–72.7 (–80, –61)	–14.6 (–33, –5.7)	–52.2 (–80, –25)
<i>O. simplex</i>	–23.2 (–32, –6.3)	–132.4 (–140, –125)	–34.3 (–76, 5.7)	–109.4 (–130, –89)

were converted to cell carbon using a factor of 0.22 $\text{pg C } \mu\text{m}^{-3}$ (Borsheim & Bratbak 1987). Copepod carbon contents (C) were estimated from the dry weight (DW) to length regressions of Hopcroft et al. (1998) and a C/DW ratio of 0.45 (Omori & Ikeda 1984). Selective feeding among the different nanoplankton components was calculated according to Vanderploeg & Scavia's (1979a,b) electivity index (E^*):

$$E_i^* = \frac{W_i - (1/n)}{W_i + (1/n)}$$

where n is the number of kinds of food items and W_i is defined by the equation:

$$W_i = \frac{G_i/X_i}{\sum (G_i/X_i)}$$

where G_i is the amount of food eaten per unit of time (cells copepod $^{-1}$ d $^{-1}$) and X_i is the food concentration. This index, also used previously by Turner & Tester (1989), compares favorably with other indexes as a robust assessment of grazing electivity (Vanderploeg & Scavia 1979b, Lechowicz 1982).

RESULTS

Plankton community composition

Temporal variations in nanoplankton concentration and growth rates (Frost 1972) during the experimental period are shown in Table 1 and Fig. 1a. The general trend was characterized by an increase in abundance (4430 cells ml^{-1} in June to 17700 cells ml^{-1} in October) and biomass (10 to 110 $\mu\text{g C l}^{-1}$) of nanoplankton through the summer and the beginning of autumn. Although 2–5 μm organisms numerically dominated the nanoplankton, especially at the beginning of the experimental period (96% of the total abundance), >5 μm cells increased in relative contribution to the community starting in July (Expt 2) and reaching a maximum (20% of total abundance) during August–October (Expts 3 and 4). This increase of larger cells was more apparent in terms of carbon, with the biomass of >5 μm cells 2.5 times higher than 2–5 μm cells by the end of the study (8 October). For the different components of the nanoplankton, abundances increased by a factor of 2 for 2–5 μm Het, 4 for 2–5 μm Auto, 16 for >5 μm Het and 25 for >5 μm Auto.

The copepod community was primarily dominated by *Oithona simplex* (mean = 55% of total abundances for all experiments) (Fig. 1b). *Acro-*

Fig. 1. (a) Average concentration of autotrophic (Auto) and heterotrophic (Het) nanoplankton in the control bottles taking into account the initial and final cell concentration and assuming an exponential growth rate (Frost 1972). (b) Copepod abundances (copepodites + adults) of the most common species (*Acrocalanus inermis*, *Parvocalanus crassirostris*, *Oithona nana*, and *O. simplex*) during the experimental period

calanus inermis and *O. nana* each contributed 17% on average to the summer community. However, *Parvocalanus crassirostris* increased in abundance in early autumn, becoming the second most common species in the bay (19% of total abundance) by the time of the final experiment.

Ingestion rates and patterns of food selection

There was no evidence that adult female copepods fed significantly on picoplankton-sized cells (clearance rates equal to zero), probably because the cells were too small to be handled efficiently. Nanoplanktonic organisms, on the other hand, were ingested at high rates by all of the species. Maximum rates of 1.2×10^5 cells copepod⁻¹ d⁻¹ were measured for *Parvocalanus crassirostris* and *Oithona nana* (Expt 4), while *O. simplex* consumed nanoplankton at the lowest absolute rate ($p < 0.05$ for all the experiments except when compared with *O. nana* in Expt 3, Student's *t*-test, Fig. 2). When converted to biomass-specific rates, however, *O. simplex* exhibited similar or higher (Expts 1 and 2) ingestion rates than those of the other species (Fig. 3).

Fig. 2. Ingestion rates (cells copepod⁻¹ d⁻¹) of small copepod species feeding on nanoplankton prey in Kaneohe Bay. Vertical bars show standard errors of 4 replicates

Fig. 3. Specific ingestion rates (cells µg C⁻¹ d⁻¹) of small copepod species feeding on nanoplankton prey in Kaneohe Bay. Vertical bars show standard errors of 4 replicates

In contrast, *Acrocalanus inermis*, the largest species in the study, displayed the lowest biomass-specific consumption rates (although not statistically significant), always below 1.2×10^5 cells µg C⁻¹ d⁻¹. Biomass-specific ingestion rate of *P. crassirostris* (Expts 3 and 4) exceeded those of the other species, reaching values of 3.5×10^5 cells µg C⁻¹ d⁻¹ in Expt 4.

Ingestion rates for the different components of the nanoplankton (Fig. 4) indicated that 2–5 µm Het were the main prey consumed in Expts 1 and 3, while 2–5 µm Auto were the most consumed prey in Expts 2 and 4. Based on average concentrations of the different food items during the incubations (Fig. 1a), it is apparent that all of the copepod species behaved as opportunistic feeders, consuming more of the cells that were available at the highest concentrations. Despite the copepods' tendency to feed on the most abundant prey, electivity indices were significantly higher ($p < 0.02$ in all cases, Kruskal-Wallis nonparametric test) for autotrophs compared to heterotrophic prey (Fig. 5). However, within autotrophic and heterotrophic categories separately, electivity indices did not differ significantly for 2–5 µm and >5 µm cells, and no size-dependent patterns of prey selection were evident.

Saturation of feeding

The functional response relationships for *Acrocalanus inermis* and both *Oithona* species suggest saturated grazing rates at nanoplankton concentrations greater than 10 000 cells ml^{-1} (Fig. 6a). Although ingestion rates increased slightly above this cell concentration, no significant differences were found between rates at the more elevated concentrations ($>30\,000$ cells ml^{-1}) and those at the next highest levels ($\sim 10\,000$ cells ml^{-1}). The maximum response to changes in food concentration, displayed by *O. nana*, showed only a factor of 1.4 increase in cells ingested per copepod for a 5-fold increase in nanoplankton abundance. However, in terms of carbon consumed, the increase in ingestion at higher food concentration was substantial (Fig. 6b). For example, *O. nana* displayed biomass-specific ingestion rates 2.7 times higher when food concentration (as $\mu\text{g C l}^{-1}$) increased by a

Fig. 4. Ingestion rates (cells copepod $^{-1}$ d $^{-1}$) of small copepod species on the different components of the nanoplankton community in Kaneohe Bay (see 'Results'). Vertical bars show standard errors of 4 replicates

Fig. 5. Electivity indices for the different components of the nanoplankton prey consumed by 4 copepod species in Kaneohe Bay. Indexes were calculated according to Vanderploeg & Scavia (1979a,b). Average nanoplankton concentrations were calculated according to Frost (1972). Error bars show standard errors of 4 replicates

Fig. 6. (a) Ingestion rates (cells copepod⁻¹ d⁻¹) versus nanoplankton concentration (cells ml⁻¹) for *Acrocalanus inermis* (●), *Parvocalanus crassirostris* (○), *Oithona nana* (■) and *O. simplex* (□). (b) Biomass-specific ingestion rates (μg C ingested μg C copepod biomass⁻¹ d⁻¹) versus nanoplankton concentration (μg C l⁻¹) calculated according to Frost (1972). Error bars show standard errors of 4 replicates

factor of 2.5. Similar responses were also evident in the daily rations of the copepods, which ranged from <30% body C d⁻¹ for all species in the first experiment to about 100% d⁻¹ for *A. inermis* and 200% d⁻¹ for the other species in Expt 4 (Fig. 7). Following the patterns of prey abundances, most of the biomass consumed in Expts 1 and 3 was in the form of heterotrophic prey, and in Expts 2 and 4 most was associated with autotrophs. By the last experiment, >5 μm prey accounted for most of the biomass consumed.

DISCUSSION

The plankton community of Kaneohe Bay

Kaneohe Bay, a subtropical embayment on the northeastern coast of Oahu, Hawaii, was the site of a sewage

outfall from the 1950s to 1977. The subsequent diversion of the outfall to a deep-water site initiated a gradual return toward mesotrophy in the bay (Smith et al. 1981, Taguchi & Laws 1989, Laws & Allen 1996), including a shift to dominance of smaller cells in the planktonic community (Taguchi & Laws 1989, Laws & Allen 1996). In the southeast sector of the bay, chlorophyll *a* concentrations have declined over 1 order of magnitude after the diversion, from ~5 μg l⁻¹ in 1975 (Taguchi & Laws 1989) to 0.3–0.5 μg l⁻¹ in 1992 (Laws & Allen 1996). These changes in the concentration and size distribution of the primary producers have resulted in lower copepod abundance relative to previous studies of the bay (Newbury & Bartholomew 1976); however, the species composition is quite similar to previous reports. For example, the dominant species described in 1976 were *Acrocalanus inermis*, *Oithona simplex* and *O. nana* (Hirota & Szyper 1976, Newbury & Bartholomew 1976). Two main differences between the present and the previous communities are the current dominance of cyclopoids over calanoids and the presence of an additional co-dominant species, *Parvocalanus crassirostris*. It is notable that the same species present in 1976 when the ecosystem was eutrophic and dominated by larger cells are still able to survive and feed at high rates on smaller cells. Although the reduction in nutrients and primary producers of the bay after the sewage diversion is obvious, the present situation of its waters is still far from strict oligotrophy. When compared to more oceanic waters (Calbet & Landry 1999, Landry et al. in press), the concentrations of nano- and zooplankton of Kaneohe Bay are 2 orders of magnitude greater than those typical of the subtropical North Pacific. Thus, although the planktonic community is dominated by small cells typical of oligotrophic ecosystems (Landry et al. 1984), the relatively high availability of food in the bay explains its high copepod abundances compared to adjacent oceanic waters.

Species differences in feeding rates

Among the more interesting results of the present study were the high copepod grazing rates on small cells, especially for the cyclopoid species (Figs. 1 & 2). Similar rates of ingestion have been previously reported in algal cultures for small calanoids (Paffenhöfer 1984). Cyclopoids, however, have generally been considered to have lower metabolic demands, and consequently lower grazing rates relative to those of similar sized calanoids (Paffenhöfer 1993). Nonetheless, recent studies in tropical waters (Hopcroft & Roff 1998) have shown that the instantaneous growth rates of cyclopoid copepods (i.e. *Oithona nana* and *O. simplex*) can be as high or higher than those of calanoid inhabi-

Fig. 7. Daily rations (% of copepod biomass consumed d^{-1}) for the different components of the nanoplankton community in Kaneohe Bay

tants of the same area (i.e. *Acartia lilljeborgi*, *Calanopia americanus*, *Centropages velificatus* and *Temora turbinata*). Only 1 calanoid species, *Parvocalanus crassirostris*, displayed instantaneous growth rates higher than those of *Oithona* spp. in the Hopcroft & Roff (1998) study, and the same species had the highest biomass-specific ingestion rates in the present study (Fig. 3). On the whole, it appears that cyclopoid copepods in tropical and subtropical ecosystems compare favorably with small co-occurring calanoids in terms of ingestion and growth rates. Thus, their system function and impact should be re-examined in light of their high biomass-specific rates.

According to expectations from studies with temperate species (Peterson et al. 1991), as well as previous results with tropical forms (Hopcroft & Roff 1998), copepods of small size should exhibit higher growth rates than larger species under food-limited conditions. Assuming a gross growth efficiency of 30% (Kjørboe et al. 1985), biomass-specific ingestion rates from the present experiment suggest growth rates up to $0.8 d^{-1}$ for *Parvocalanus crassirostris*, $0.7 d^{-1}$ for *Oithona nana*, $0.6 d^{-1}$ for *O. simplex*, and $0.3 d^{-1}$ for *Acrocalanus inermis*. *A. inermis* is substantially larger than other species and apparently exhibits a comparative disadvantage with regard to the efficient capture and handling of small prey. Thus, it is not surprising that the smallest species, *O. simplex*, dominates the

copepod community of Kaneohe Bay. At the highest conditions of food availability (Expt 4), calculated growth rates of *P. crassirostris*, *O. nana* and *O. simplex* are 6% (*P. crassirostris*) to 50% (*O. simplex*) higher than those found experimentally by Hopcroft & Roff (1998) for the same species. If we assume a chlorophyll to carbon ratio of 50 (Antia et al. 1963, Calbet unpubl.), food resources in the former study were probably somewhere between those found in Expts 2 and 3; thus, the copepods may not have been growing at maximum rates. Alternatively, the gross growth efficiencies may be somewhat less than the 30% assumed. Regardless, the grazing estimates from the present study as well as the growth assessments of Hopcroft & Roff (1998) provide complementary and independent evidence of high physiological rate potential for small calanoid and cyclopoid copepods in tropical and subtropical systems.

According to temperature-dependent predictions of copepod growth from Huntley & Lopez (1992), copepods in Kaneohe Bay should be able to grow at rates of 0.8 to $0.9 d^{-1}$. Values of this order were probably achieved by *Parvocalanus crassirostris*, and approached by *Oithona nana* and *O. simplex*, only at the highest food concentrations in the present study (Expt 4). Given biomass-specific ingestion rates in the other experiments, growth rates near the temperature-dependent predictions would not have been possible. Thus, even very small copepod species may experience rate limiting food conditions during some or much of the year. However, other food sources (nauplii and small metazoans) could also contribute to the diet of the copepods in the bay, in which case growth rates may be higher than those estimated here based solely on the concentration of protozoans.

Size distributions and abundances of the copepod community may also be controlled by factors such as predation. For instance, the chaetognath *Sagitta enflata* is an abundant member of the zooplankton community in Kaneohe Bay (Szyper 1978, Kimmerer 1984b). Previous studies have shown that this species feeds preferentially on the larger copepod inhabitants of the bay (Kimmerer 1984b). Thus, predation on larger mesozooplankton in combination with a dominance of small size-fractions in the food resources might explain the relative scarcity of larger suspension-feeding copepods in Kaneohe Bay.

Efficient feeding on small particles

Even though the adult female copepods examined in the present study did not feed on picoplankton-sized cells, there is evidence that at least some nauplii can consume bacterial-sized prey, either directly (Roff et al. 1995) or as an indirect consequence of feeding on larger organisms (Souza-Santos et al. 1999), or by osmoregulatory 'drinking' (Turner & Tester 1992). These possible nutritional links between microbes and classical zooplankton consumers should perhaps be examined in more detail given the present findings. Most previous studies have suggested that neither adult calanoids nor cyclopoids can efficiently feed on particles smaller than 5 μm (Conover 1982, Lampitt & Gamble 1982, Berggreen et al. 1988, Hansen et al. 1994, Nakamura & Turner 1997). In contrast, Turner (1986) found mainly diatoms <5 μm diameter in the fecal pellets of *Oithona simplex*. Our results indicate that *Parvocalanus crassirostris*, *O. nana* and *O. simplex* do feed at high rates on particles smaller than 5 μm (actually most of cells in the 2–5 μm fraction were smaller than 3 μm). That comparable, or even the same, species show very different responses to the spectrum of available food in these different studies may have its explanation in 2, not mutually exclusive, hypotheses.

(1) Most experiments aimed at understanding the physical limits of food ingestion by copepods have been conducted under laboratory conditions using unialgal cultures. Single species, particularly those absent or rare in the natural diet, might not be the best food resource for copepods conditioned to feed on natural prey mixtures (Huntley 1981). It is known, for example, that copepods display different grazing rates on mixed prey than on unialgal cultures (Schnack 1979). In particular, the genus *Oithona* has been shown to increase its egg production rates when fed a combination of autotrophic and heterotrophic cells (Sabatini & Kiørboe 1994), while some small species may prey heavily on calanoid nauplii (McKinnon & Klumpp 1998).

(2) Another possible explanation for the ability of the copepods in Kaneohe Bay to feed on small cells would be community-level environmental adaptations. In other words, comparable, or even the same, species inhabiting distinct ecosystems might have developed small anatomical (space between setae, body size) or behavioral (changes in the filtration pattern) modifications that would allow them to exploit different food resources. In the laboratory studies of Lampitt & Gamble (1982), for instance, *Oithona nana*, nominally the same species as in the present study, did not feed efficiently on particles smaller than 8 μm . However, these copepods were inhabitants of relatively cold waters (10°C) and certainly experienced a different size spectrum of food resources than the *O. nana* in Kaneohe

Bay. The subtropical version of *O. nana* can, in fact, efficiently exploit small nanoplankton down to 2 μm in size. Further microscopical analysis of the specimens from both environments should be done to clarify the existence of habitat-specific anatomical differences and/or perhaps to highlight deficiencies in the current taxonomy of this genus.

Patterns of food selection

No clear selection upon larger cells was detected in the present grazing experiments (Fig. 4). At first glance, all of the species behaved as opportunistic feeders, consuming more cells of the size-class available in the environment at higher concentrations. Nonetheless, electivity indices indicated that autotrophs were generally chosen over heterotrophs (Fig. 5). Since most of the community of both auto- and heterotrophs consisted of motile flagellated cells, the stimulus driving the observed selective behavior likely has its origin in a chemosensorial rather than a mechanical mechanism (Poulet & Marsot 1978, Cowles et al. 1988). Nevertheless, we cannot discount the possibility that differences in the swimming patterns of auto- and heterotrophic organisms could generate different signals detected by copepods.

The absence of selection for cell size has been suggested as the most energy-efficient behavior during bloom conditions (Huntley 1981). The indiscriminate feeding by copepods on the nanoplankton community during Expt 4 led to daily rations higher than 200% body C d^{-1} for the 3 most abundant species (Fig. 7). Actually, grazing rates on >5 μm cells, even if numerically lower than those for 2–5 μm cells, accounted for most of the daily rations of copepods in Expts 3 and 4. Nevertheless, the absence of selective behavior during periods of lower food is surprising. It is possible that the extremely low abundances of large cells in Expts 1 and 2 (Table 1) may have made highly selective search or capture behaviors disadvantageous.

Saturation of feeding

Although ingestion rates of total nanoplankton cells remained relatively constant at concentrations higher than 10 000 cells ml^{-1} , the copepods were clearly able to consume more carbon when the mean cell size was larger (Fig. 6). This observation, coupled with the lack of any clear size-dependent pattern in the feeding rates, suggests that ingestion might be held below potential by the physical handling of food items rather than the physiological constraints of food ingestion and digestive processing.

There must be a limit to the number of items that a copepod can detect, catch and handle per unit time. In the present experiments, the maximum number of cells consumed per second varied from 0.5 for *Oithona simplex* to 1.5 for *Parvocalanus crassirostris* and *O. nana*, assuming continuous grazing. The existence of feeding rhythms (Fuller 1937, Petipa 1958, Dagg & Grill 1980, Haney 1988, Saito & Taguchi 1996), discontinuities in the grazing (Cowles & Strickler 1983, Price & Paffenhöfer 1986, Jonsson & Tiselius 1990, Saiz 1994) and active rejection of cells (Paffenhöfer et al. 1995) implies that the number of cells handled per animal per second of active feeding was even higher. In addition, ingestion rates may appear to slow down, when quantified as cells copepod⁻¹ d⁻¹, because copepods may take longer to handle the larger cells that became more prevalent as the concentration of nanoplankton increased.

As stated previously, the conditions in Kaneohe Bay are far from severely oligotrophic. When compared with data from the open-ocean at Station Aloha (100 km North of Oahu), for example, the nanoplankton concentrations in the bay are 1 order of magnitude higher in Expts 1 and 2 orders of magnitude higher in Expt 4 (Calbet & Landry 1999). If ingestion rates decrease proportionally with food concentration, under rigorous conditions of food scarcity in the open ocean, the daily rations of copepods in the present study would be on the order of 3 % of body C d⁻¹, and specific growth rates would be less than 0.01 d⁻¹. These values are probably unrealistically low for the diverse community of copepods that inhabit and apparently thrive in oligotrophic waters of the central North Pacific (e.g. McGowan & Walter 1979, 1985), implying that such copepods possess behavioral and/or energetic adaptations to locate and exploit low prey concentrations even more efficiently than those investigated here. Further studies emphasizing the feeding interactions, adaptations and capabilities of copepods inhabiting oligotrophic open-ocean areas are needed to understand the global functioning of these vast and poorly known ecosystems.

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