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Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland

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ABSTRACT: Grazing experiments were conducted with *Calanus* spp. and *Balanus* cf. *crenatus* nauplii incubated with natural plankton from Disko Bay, West Greenland during the post-spring-bloom period. Both copepod and barnacle nauplii were feeding on different types of protists although at different rates. *Calanus* spp. nauplii preferred large ciliates and dinoflagellates whereas flagellates ~5 µm in diameter and *Myrionecta rubra* were hardly ingested at all. *B.* cf. *crenatus* nauplii preferred diatoms and also consumed the small flagellates at relatively high rates. Compared to *Calanus* spp. nauplii, *B.* cf. *crenatus* nauplii ingested ciliates and dinoflagellates at low rates suggesting a more herbivorous feeding mode than the more predaceous copepod nauplii. The daily grazing impact of the nauplii community in Disko Bay was estimated using the weight-specific mean clearances from the grazing experiments and field biomass values of different categories of prey and nauplii. These calculations showed that the grazing impact by the nauplii community on all prey categories was generally modest (1.3 to 9.2%). However, the dominant part of the total food intake by *Calanus* spp. nauplii in the surface water was composed of ciliates and dinoflagellates, most of which were phagotrophic

KEY WORDS: Nauplii · Copepod · Barnacle · Grazing · Predation · Arctic · Greenland

INTRODUCTION

The nauplius is the initial developmental stage of most crustaceans after the egg, and as such, nauplii are extremely abundant in the marine zooplankton. Copepod nauplii are arguably the most numerous form of metazoans on the planet (Björnberg 1984), with the possible exception of nematodes. When appropriate fine meshes of plankton nets are employed, copepod nauplii usually outnumber later copepodite and adult stages of copepods by several orders of magnitude (Turner 1982, 1994, Webber & Roff 1995, Hansen et al. 1999). Nauplii of other crustaceans, including meroplankton such as barnacle nauplii can also become sporadically abundant (Lang & Ackenhusen-Johns 1981). Copepod and barnacle nauplii are important prey of fish larvae and other planktonic predators, but the feeding ecology of these nauplii is poorly known (Turner 1984, 2000). Since copepod nauplii can ingest pico- and nanophytoplankton (Uye & Kasahara 1983, Berggreen et al. 1988) as well as some forms of bacterioplankton (Turner & Tester 1992, Roff et al. 1995),

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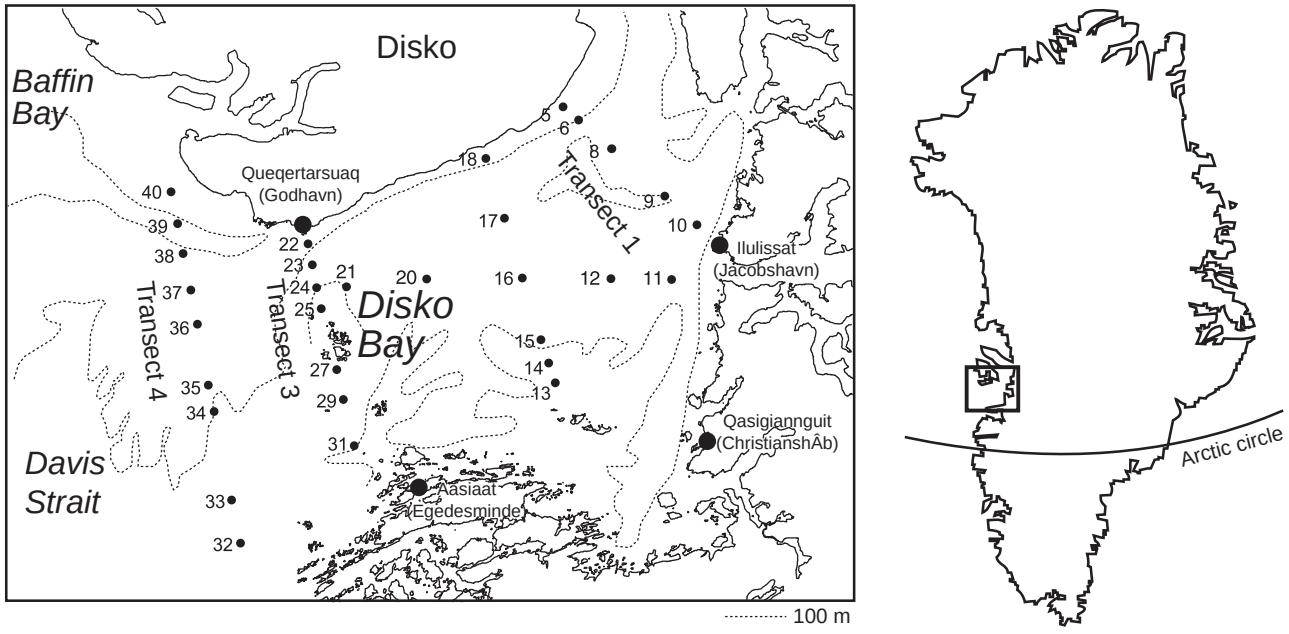

Fig. 1. Map of Disko Bay, West Greenland, showing the sampling stations visited during the cruise. Transect 4 covers Disko Bank (dotted line represents 100 m isobath), Transect 5 consisted of Stns 11, 12, 16, 20, 21, 24, 37

they may serve as important linkages between the microbial and classical food webs (Turner & Roff 1993). This may especially be true in Arctic systems like Disko Bay and other high-latitude regions where large populations of *Calanus* spp. descend as late-stage copepodites into deep water for overwintering during the post spring bloom period well before the productive season ends, leaving nauplii, copepodites and protozoans as primary grazers (Hansen et al. 1999, Madsen et al. 2001).

Most of the limited information on feeding, growth and development by copepod nauplii comes from experimental or rearing studies where laboratory cultured phytoplankton were offered as food (reviewed by Turner 1984, Kiørboe & Sabatini 1995). A few studies have confirmed that copepod nauplii ingest ciliates from monospecific cultures (Stoecker & Egloff 1987) or quasi-natural assemblages of estuarine phytoplankton and microzooplankton in mesocosms (Merrel & Stoecker 1998). There is, however, little information on naupliar predation on ciliates and other protozoans in natural mixed assemblages more typical of offshore waters (we use the term 'protozoans' to distinguish phagotrophic and/or mixotrophic protists such as ciliates and non-pigmented dinoflagellates from eucaryotic autotrophic phytoplankters, which are also 'protists': see Levinsen et al. 1999). Although there have been a few studies of growth rates of copepod nauplii feeding upon natural food suspensions (McKinnon 1996, Hopcroft & Roff 1998), we are unaware of any published studies of the comparative feeding by copepod nauplii on various components of natural mixed assemblages of phytoplankton and protozoans. We know of no information on feeding by planktonic barnacle nauplii beyond the feeding studies on cultured algal diets by Moyse (1963) and Stone (1989), and a handful of studies of barnacle rearing on cultured phytoplankton diets referenced in Lang (1979), Turner (1984) and Anderson (1994). Accordingly, we examined feeding by abundant copepod (*Calanus* spp.) and barnacle (*B.* cf. *crenatus*) nauplii on natural phytoplankton and protozoan suspensions at *in situ* concentrations.

MATERIALS AND METHODS

The study was conducted in Disko Bay, West Greenland in June 1997 during a cruise with the RV 'Adolf Jensen' (Greenland Institute for Natural Resources). Sampling was done along 4 transects covering stations from near Ilulissat Icefjord and Vaigat (Transect 1) to the Disko Bank area, which separates Disko Bay from Baffin Bay (Transect 4). An additional transect was partly based on stations visited on these 4 transects. This Transect 5 transversed the central bay from Ilulissat Icefjord to Disko Bank at the mouth of the bay (Fig. 1).

Nauplii for the grazing experiments were collected from the upper ~30 m by a WP-2 net with a mesh size of 200 µm, fitted with a large non-filtering cod-end. Copepod nauplii were *Calanus finmarchicus* and/or *C. glacialis*, which are the primary calanoid copepods that

Table 1. *Calanus* spp. (=*C. finmarchicus* + *C. glacialis*) and *Balanus* cf. *crenatus* nauplii grazing experiments conducted in Disko Bay, West Greenland, June 1997. L = mean length (±SD) and W = mean weight of individuals from the 3 replicate grazing bottles in each experiment combined. Length measurements were conducted on Lugol-fixed individuals from all 3 replicates after each experiment (n = 52 ± 5 for *Calanus* nauplii and 14 ± 8 for *B.* cf. *crenatus* nauplii). Only *Calanus* spp. nauplii > NIII were measured, since stages < NIII do not feed. Weight-specific clearances were calculated using the mean weights of separate replicates. *Calanus* spp. nauplii weights were calculated by using length-weight equations for *C. finmarchicus* nauplii (Hygum et al. 2000). *B.* cf *crenatus* nauplii weights were calculated by establishing an equation of the form log C = a log (L) – b from the 2 length-weight values in Uye (1982), where C = carbon weight (µg), L = length (µm), and a, b = constants

Expt	Stn	Date	Nauplii	Nauplii ml^{-1}	L (µm)	W (µg C)	Duration (h)	T (°C)
I	24	14–16	*Calanus*	0.10–0.14	600 ± 95	2.8	47	5 ± 1
IIa	32	15–16	*Calanus*	0.04–0.22	680 ± 95	4.8	23	5 ± 2
IIb	32	15–16	*Balanus*	0.03	735 ± 40	9.8	23	5 ± 2
IIIa	33	15–16	*Calanus*	0.08–0.22	665 ± 110	4.4	23	5 ± 2
IIIb	33	15–16	*Balanus*	0.03	750 ± 35	10.5	23	5 ± 2
IVa	35	15–16	*Calanus*	0.11–0.14	645 ± 285	3.8	24	5 ± 2
IVb	35	15–16	*Balanus*	0.03	760 ± 30	11.1	24	5 ± 2

are reproductive in the upper strata of Disko Bay during this period (Hansen et al. 1999, Madsen et al. 2001). Barnacle nauplii were *Balanus* cf. *crenatus*. After sorting nauplii into petri dishes placed on ice, either 60 *Calanus* spp. or 20 (*B.* cf. *crenatus*) were added to triplicate experimental incubations with 600 ml aliquots of natural food suspensions in acid-washed polycarbonate bottles. Water for incubations was collected from the depth of the fluorescence maximum (20 to 30 m) with a Niskin bottle and screened through a 200 µm plankton net by reverse filtration in order to exclude most extraneous metazoan grazers without removing chain-forming diatoms and larger phytoplankton and protozoan cells. Other triplicate bottles were immediately fixed in acid Lugol solution (2% final concentration) to determine the initial phytoplankton and protozoan concentrations. Triplicate controls (without nauplii) were incubated together with experimental suspensions (with added nauplii) usually for ~1 d (Table 1). Incubations were carried out at *in situ* temperatures in a container with flow-through surface water and bottles were rotated intermittently by hand. The temperature was recorded by a temperature logger every 3 min. At the end of the incubations, controls and experimental suspensions were preserved for subsequent microscopic counting of remaining phytoplankton and protozoans. Subsamples for determination of chlorophyll *a* (chl *a*) were also taken; triplicate 200 ml aliquots were filtered through GF/F filters and dark-extracted in ethanol before measurement on a Turner fluorometer (Jespersen & Christoffersen 1987).

Concentrations of phytoplankton, ciliates, and dinoflagellates were determined using the same procedures as described in Levinsen et al. (2000a). Phytoplankton in preserved aliquots were concentrated by sedimentation and counted at 200× or 400× in Sedgwick-Rafter cells with conventional phase-contrast microscopy. Ciliates and dinoflagellates were concentrated by sedimentation in 50 ml Utermöhl chambers and counted by inverted microscopy with phase-contrast at 100× or 200×. Identified species and morpho-types were pooled into size classes of phytoplankton, ciliates or dinoflagellates. Cell volumes for all these classes, except for diatoms, were estimated from measurements of linear dimensions assuming simple geometric shapes of cells, and converted to organic C content using a relation of 0.13 pg C µm^{-3} (Hansen et al. 1997). Diatom plasma volume was determined and converted to organic C according to Strathmann (1967).

It is difficult to distinguish autotrophic and mixotrophic dinoflagellates from heterotrophic dinoflagellates using light microscopy and Lugol preserved samples. The best procedure for this is epifluorescence microscopy on gluteraldehyde-fixed samples. Absence of fluorescence from chlorophyll indicates that cells are non-pigmented and therefore heterotrophic (see Levinsen et al. 1999 and references therein). Levinsen et al. (2000b) compared abundances of non-pigmented heterotrophic dinoflagellates and pigmented autotrophic or mixotrophic dinoflagellates from Disko Bay over the annual cycle, including the period of the present investigation, using light and epifluorescence microscopy. Using these techniques, it was found that the dominant athecate gymnodinoid dinoflagellates of the genera *Gymnodinium* and *Gyrodinium* were usually non-pigmented. Since many pigmented dinoflagellates are also able to engulf particulate prey, these taxa were all considered to be phagotrophic protists or 'protozoans' in the present study.

Grazing experiments were conducted at 4 stations with *Calanus* spp. and at 3 stations with (*Balanus* cf. *crenatus*) nauplii (Table 1). Clearance and ingestion were calculated according to Frost (1972) for feeding upon chl *a*, nanoflagellates, diatoms and the photosynthetic ciliate *Myrionecta rubra* (=*Mesodinium rubrum*), as well as for feeding upon oligotrichous ciliates and

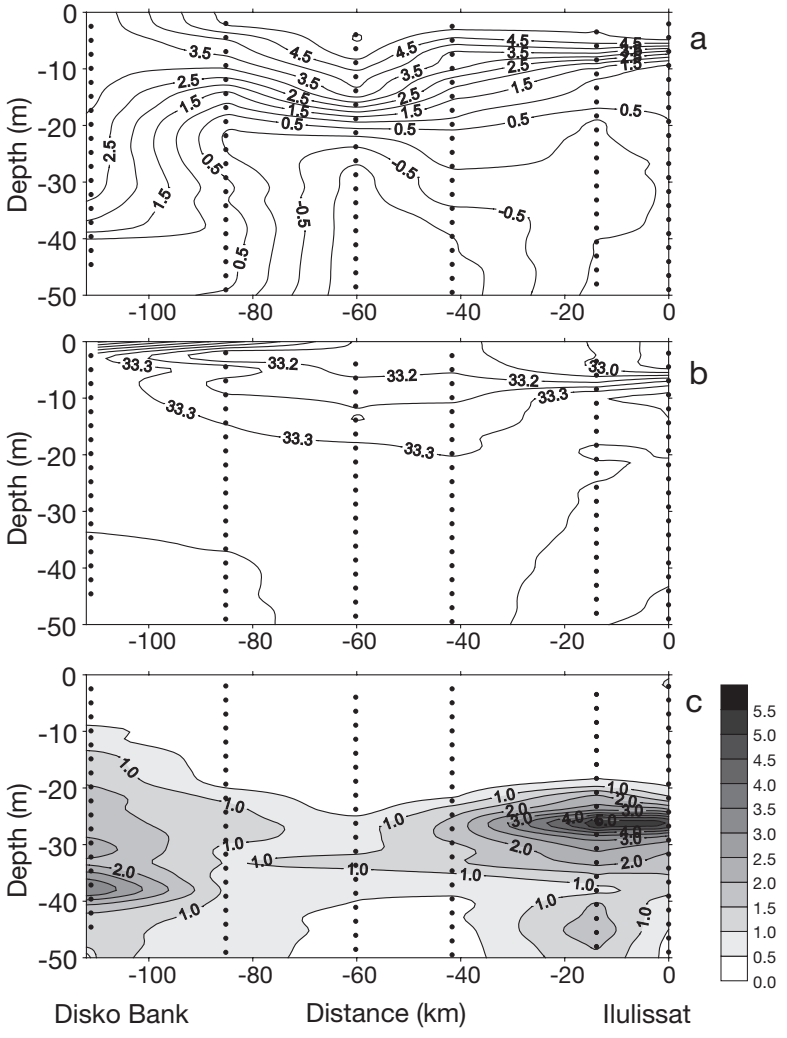

Fig. 2. (a) Temperature, °C, (b) salinity and (c) chlorophyll *a* relative fluorescence (arbitrary units), along Transect 5 (0 to 50 m)

athecate dinoflagellates smaller or larger than 20 µm. Cell concentrations from triplicate initial and control bottles in each experiment were averaged before calculation of the clearance. The standard error of the clearance for the different food components therefore represents the variation among the 3 replicate grazing bottles. Carbon ingestion was obtained from the product of the number of cells of a particular cell category ingested and the weighted mean C content for that cell category in the initial bottles. Total ingestion was the sum of the different prey categories ingested.

During addition of nauplii to the grazing bottles there was the possibility that individuals might remain stuck in the pipette, thus biasing nauplii concentrations from the intended values of 60 grazing nauplii per bottle. Therefore, the actual concentrations of nauplii counted in Lugol fixed sub-samples from the experimental suspensions after incubation were used in the grazing calculations. For *Calanus* spp. nauplii, each counted individual was staged (NI and NII, NIII and NIV or NV and NVI) and the weight estimated using the length-weight relations for *C. finmarchicus* provided by Hygum et al. (2000). The most dominant copepod nauplii in the grazing experiments were Stages NV and NVI. Stages of *Calanus* spp. nauplii younger than NIII were rare and were neglected from clearance calculations, as these do not feed (Marshall & Orr 1955, Williams et al. 1987). All *Balanus* cf. *crenatus* added to experimental bottles were nauplii at the time of addition, but a few (<5%) developed into cyprid larvae during incubation. Visual inspection of bottles prior to preservation revealed actively swimming copepod and barnacle nauplii, so nauplii mortality was considered insignificant and was calculated as zero. The weight-specific clearance (ml µg C^{-1} d^{-1}) of *Calanus* spp. and *B.* cf. *crenatus* nauplii was estimated using the mean nauplii carbon-weight in each grazing replicate.

Field estimates of chl *a* concentrations and the biomass of ciliates and dinoflagellates from the surface water in Disko Bay were determined using the same procedures as described above except that fractionated chl *a* was also determined by filtration through 10 and 45 µm mesh-size plankton nets. *Calanus* spp. and *Balanus* cf. *crenatus* nauplii field abundance and biomass in the upper 50 m was estimated from depth-integrated samples collected by a submersible pump equipped with a flow meter (Digital Model 438 100, Hydro-Bios Kiel). Collected samples were concentrated from a large non-filtering cod-end and preserved in buffered formalin (2% final concentration). Lengths of at least 50 nauplii per sample were measured and converted to biomass based on length-weight regressions (Hygum et al. 2000).

RESULTS

The entire area of Disko Bay was stratified, with warmer temperatures and reduced salinity in the upper strata due to melt water (Fig. 2a,b). A distinct fluorescence maximum at a depth of 20 to 40 m also characterized the bay (Fig. 2c). This structure of the water column is typical for Disko Bay during the post spring bloom stratified summer period (Nielsen & Hansen 1999).

Chl *a* at the surface (2.5 m) from stations along the transects ranged from a total of 0.1 to 4.7 µg l^{-1}, with most in the >45 and <10 µm size fractions (Fig. 3).

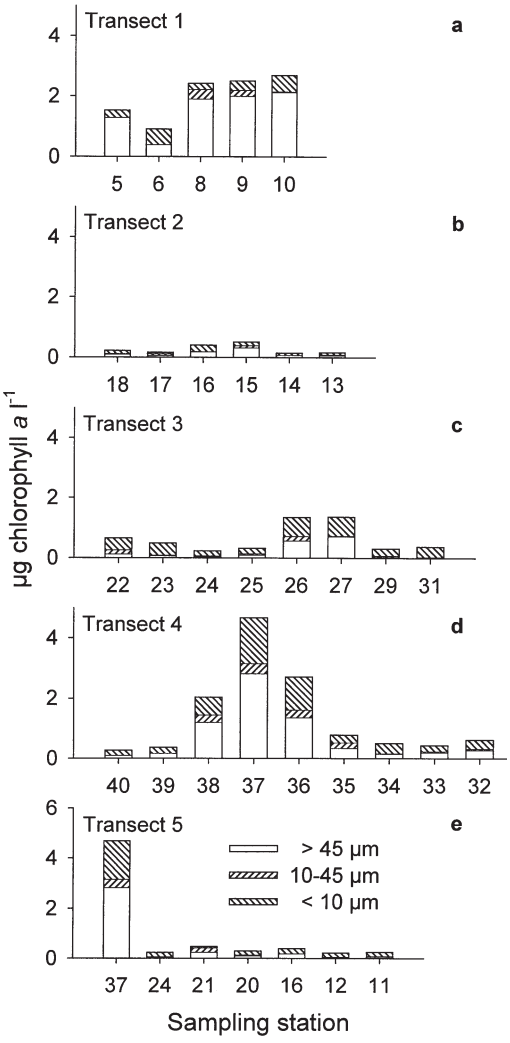

Fig. 3. Phytoplankton concentrations at 2.5 m depth measured as size-fractionated chlorophyll *a* along Transects 1 to 5

Ciliate and dinoflagellate biomass from selected stations ranged from 0.7 to 5.6 and 3.4 to 24.0 µg C l^{-1}, respectively (Fig. 4). Biomass of dinoflagellates was generally higher than that of ciliates, with >20 µm-sized cells dominating.

Nauplii biomass of *Calanus* spp. and *Balanus* cf. *crenatus* ranged from 0.9 to 19.3 and 0 to 7.5 µg C l^{-1}, respectively (Fig. 5). Most *Calanus* spp. nauplii were Stages NIII or NIV and NV or NVI of *C. finmarchicus*, with lesser contributions by the same stages of *C. glacialis*.

Over an experimental range of natural mean chl *a* concentrations of 1.5 to 6.2 µg l^{-1} (Fig. 6a), rates of chl *a* clearance averaged 1.3 to 4.9 ml ind.$^{-1}$ d^{-1} for *Calanus* spp. nauplii (Fig. 6b), and 0.8 to 6.7 ml ind.$^{-1}$ d^{-1} for *Balanus* cf. *crenatus* nauplii (Fig. 6c).

While feeding on natural phytoplankton assemblages with a concentration range of 55.7 to 136.0 cells ml^{-1} (Fig. 7a), most of which were ~5 µm chlorophyll-bearing nanoflagellates (Levinsen et al. 2000a), rates of clearance of *Thalassiosira* spp.-dominated diatoms ~20 µm in size by *Calanus* spp. nauplii were 4.8 to 11.6 ml ind.$^{-1}$ d^{-1} (Fig. 7c), and 8.4 to 32.6 ml ind.$^{-1}$ d^{-1} by *Balanus* cf. *crenatus* nauplii (Fig. 7d). Clearance of nanoflagellates by *Calanus* spp. nauplii was low (1.6 to 1.8 ml ind.$^{-1}$ d^{-1}), and half the experiments gave negative values, since nanoflagellate growth during incubations exceeded removal by grazing (Fig. 7c). Clearance of nanoflagellates by *B.* cf. *crenatus* nauplii averaged 4.8 to 36.0 ml ind.$^{-1}$ d^{-1} (Fig. 7d).

At mean initial concentrations of 0.8 to 6.1 *Myrionecta rubra* ml^{-1}, 1.3 to 2.6 oligotrichous ciliates <20 µm ml^{-1}, and 1.3 to 4.1 oligotrichous ciliates >20 µm ml^{-1} (Fig. 8a), in which the biomass was dominated by the latter (Fig. 8b), clearance of oligotrichous ciliates by *Calanus* spp. nauplii was much greater than clearance of *M. rubra* (Fig. 8c). Similarly, *Balanus* cf. *crenatus* nauplii generally exhibited higher clearance of oligotrichous ciliates than of *M. rubra*, although some calculated clearances were negative (Fig. 8d).

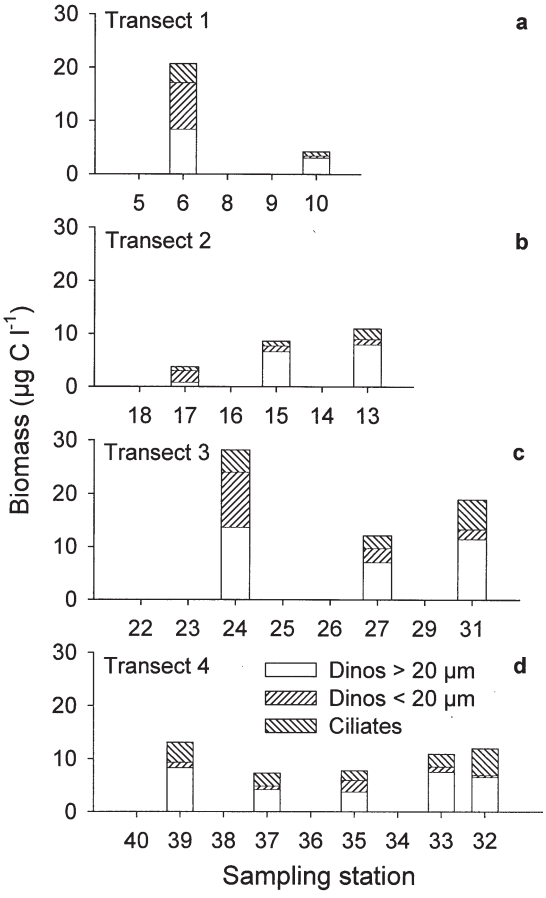

Fig. 4. Protozoan biomass at 2.5 m depth at selected stations along Transects 1 to 4. Protozoans include dinoflagellates and ciliates. Stations with no data shown are those at which protozoans were not counted, *not* stations for which protozoan biomass was zero

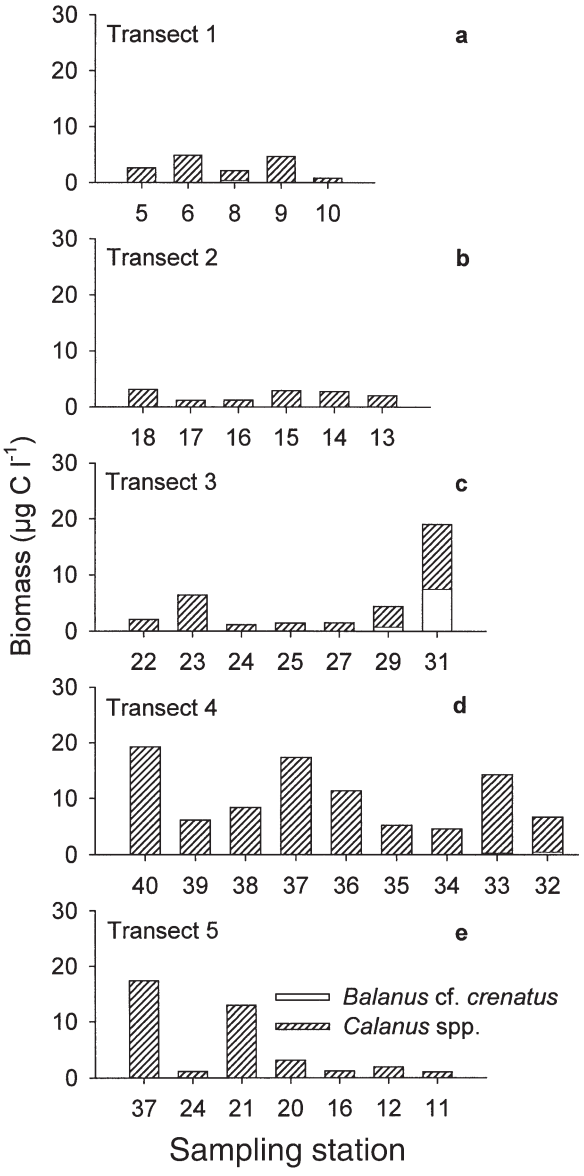

Fig. 5. *Calanus* spp. and *Balanus* cf. *crenatus* nauplii biomass values (means for 0 to 50 m) along Transects 1 to 5

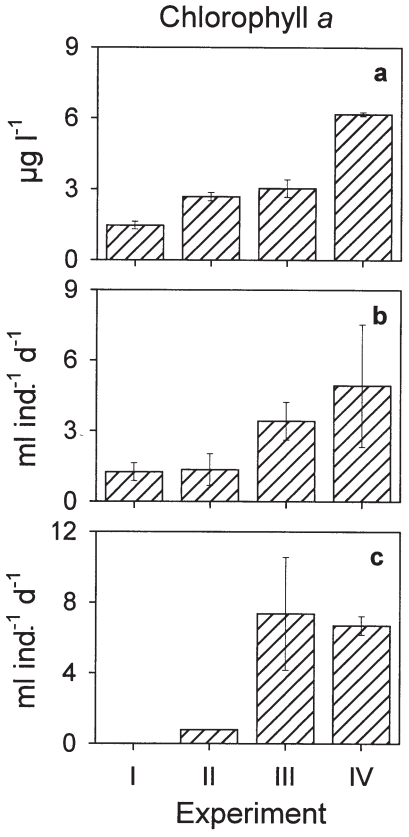

Fig. 6. (a) Initial concentrations of chlorophyll *a*, (b) clearances on chlorophyll *a* by nauplii of *Calanus* spp. and (c) *Balanus* cf. *crenatus*. Error bars represent standard errors of the mean. Note different scales on *y*-axis for (b) and (c)

Over a natural mean abundance range of 6.5 to 15.1 dinoflagellates ml^{-1} (Fig. 9a), in which abundance was dominated by athecate cells <20 µm (Fig. 9a), but biomass was dominated by athecate cells >20 µm (Fig. 9b), the mean clearance rate by *Calanus* spp. nauplii was highest on the larger cell sizes (Fig. 9c). Clearance of dinoflagellates by *Balanus* cf. *crenatus* nauplii was more variable (Fig. 9d).

Weight-specific mean clearance rates for *Calanus* spp. nauplii reveal different amounts of feeding upon different components of natural food suspensions (Table 2). While chl *a* and diatoms were clearly grazed, nanoflagellates generally were not. Among the larger protists, *Myrionecta rubra* was only slightly consumed, whereas athecate dinoflagellates, particularly those >20 µm, were eaten at higher rates. By far the highest clearances by *Calanus* spp. nauplii were when feeding on oligotrichous ciliates.

Weight-specific clearance rates for barnacle nauplii were different from those of copepod nauplii (Table 2). *Balanus* cf. *crenatus* nauplii displayed higher clearance of diatoms and nanoflagellates than *Calanus* spp. nauplii, but clearance of oligotrichous ciliates was lower. Clearance of dinoflagellates by *B.* cf. *crenatus* nauplii was also lower than by *Calanus* spp. nauplii. Considering that *B.* cf. *crenatus* nauplii have a higher biomass (10.4 ± SD 1.9 µg C $ind.^{-1}$) than *Calanus* spp. nauplii (2.8 to 4.8 µg C $ind.^{-1}$: Table 1), these disparities become even more marked, emphasizing the generally herbivorous feeding mode of barnacle nauplii and the substantial predation of copepod nauplii upon oligotrichous ciliates, and dinoflagellates, most of which were phagotrophic (Levinsen et al. 2000b).

Ingestion by *Calanus* spp. nauplii based on clearance measurements and mean concentrations of the different prey categories was 1.9 to 22.2 ng chl *a* $ind.^{-1}$ d^{-1}, 4.2 to 48.7 ng phytoplankton C $ind.^{-1}$ d^{-1}, 0 to 0.9 ng *Myrionecta*

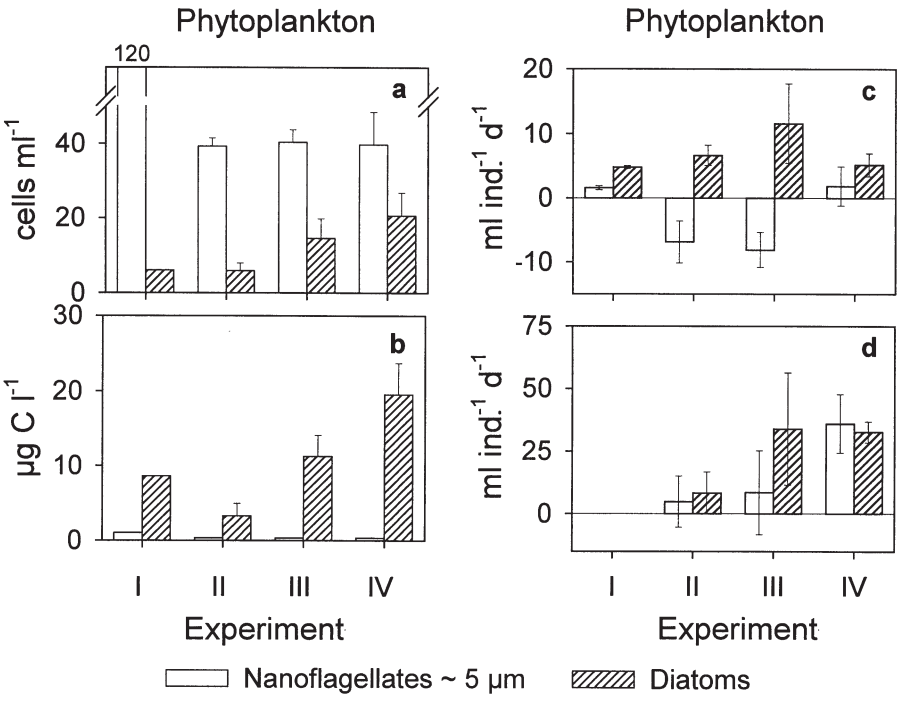

Fig. 7. (a) Initial concentrations and (b) biomass of the dominant phytoplankton groups and clearance of diatoms and nanoflagellates by nauplii of (c) *Calanus* spp. and (d) *Balanus* cf. *crenatus*. Diatoms consisted of *Thalassiosira* spp. and *Chaetoceros* spp.; nanoflagellates were dominated by cells with a diameter of ~5 µm. Error bars represent standard errors of the mean. Note different scales on *y*-axis for (c) and (d)

rubra C ind.$^{-1}$ d^{-1}, 4.8 to 10.3 ng ciliate C ind.$^{-1}$ d^{-1} and 5.1 to 11.8 ng dinoflagellate C ind.$^{-1}$ d^{-1} (Fig. 10a–d). *Balanus* cf. *crenatus* nauplii ingested these prey categories at rates of 2.4–39.8, 7.5–260, 0–2.7, 0–23.2 and 0–47 ng ind.$^{-1}$ d^{-1} (Fig. 10e–h). Total daily ingestion of *Calanus* spp. nauplii ranged from 20.2 to 67.8 ng C ind.$^{-1}$ d^{-1} and *B.* cf. *crenatus* nauplii consumed between 54.9 and 294.6 ng C ind.$^{-1}$ d^{-1}.

What was the daily grazing impact of field populations of copepod and barnacle nauplii upon various components of prey assemblages in Disko Bay? Using weight-specific mean clearances of prey categories obtained in the grazing experiments (Table 2), and field biomass in Disko Bay of these prey categories (phytoplankton biomass converted from chl *a* in Fig. 3, ciliate and dinoflagellate biomass as in Fig. 4) as well as for copepod and barnacle nauplii (Fig. 5), it is possible to obtain a rough estimate of: (1) percent clearance of the surface water on specific prey categories, (2) values for ingestion (Table 3), and (3) relative ingestion of protozoans versus phytoplankton by copepod and barnacle nauplii (Table 4). In general, grazing on phytoplankton and predation on protozoans accounted for only a few percent of the standing stock of a particular prey category (Table 3). In grazing experiments, where the water for food suspensions was collected from the fluorescence maximum depth, calculated ingestion of protozoans accounted for a minor fraction of the total ingestion (Table 5). However, when weight-specific mean clearances calculated from grazing experiments were applied to assemblages in surface waters, which had lower chl *a* concentrations, the calculated proportion of ingestion of protozoans was much greater (Table 4).

DISCUSSION

The comparatively higher predation of copepod nauplii on protozoans than on co-occurring phytoplankton in natural mixed assemblages appears to be previously undocumented. However, it should not be surprising, considering the increasing evidence that many adult copepods also feed

Table 2. *Calanus* spp. and *Balanus* cf. *crenatus.* Weight-specific clearances (F_{spec}, ml µg C^{-1} d^{-1}) at 5°C for nauplii preying on chlorophyll *a* and different groups of protists. n = total number of replicates of all experiments

Prey	*Calanus* spp. nauplii F_{spec}	(SE)	n	*Balanus* nauplii F_{spec}	(SE)	n
Chlorophyll *a*	0.68	(0.20)	23	0.43	(0.14)	11
Phytoplankton						
Autotrophic flagellates ~5 µm	−0.47	(0.46)	12	1.52	(0.76)	9
Diatoms[a]	1.94	(0.41)	12	2.34	(0.77)	9
Total	−0.23	(0.48)	12	1.49	(0.67)	9
Ciliates						
Myrionecta rubra	0.04	(0.19)	12	−0.21	(0.33)	9
Oligotrichous ciliates <20 µm	3.09	(0.47)	12	0.65	(0.71)	9
Oligotrichous ciliates >20 µm	5.28	(0.89)	12	1.56	(0.71)	9
Total	1.25	(0.35)	12	0.06	(0.32)	9
Dinoflagellates						
Athecate dinoflagellates <20 µm	1.05	(0.17)	12	0.55	(0.28)	9
Athecate dinoflagellates >20 µm	1.94	(0.27)	12	0.71	(0.31)	9
Total	1.19	(0.15)	12	0.61	(0.25)	9

[a]Primarily cells of the genera *Thalassiosira* and *Chaetoceros*

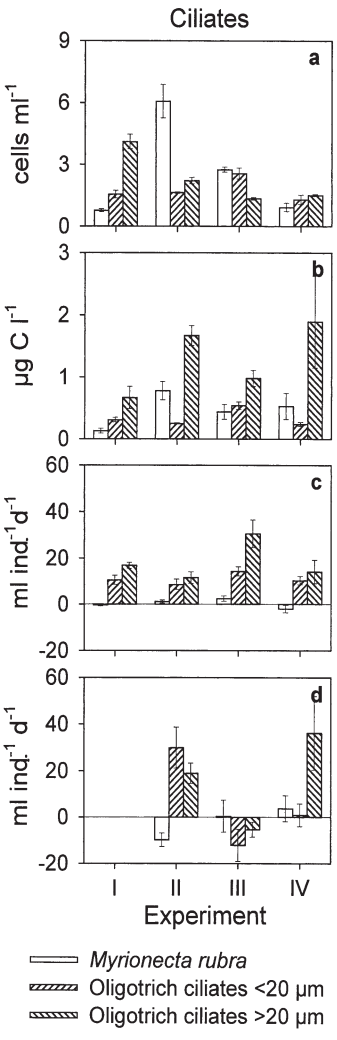

Fig. 8. (a) Initial concentrations and (b) biomass of *Myrionecta rubra*, nano- (<20 µm) and micro- (>20 µm) sized oligotrich ciliates and clearance of these ciliate groups by nauplii of (c) *Calanus* spp. and (d) *Balanus* cf. *crenatus*. Error bars represent standard errors of the mean

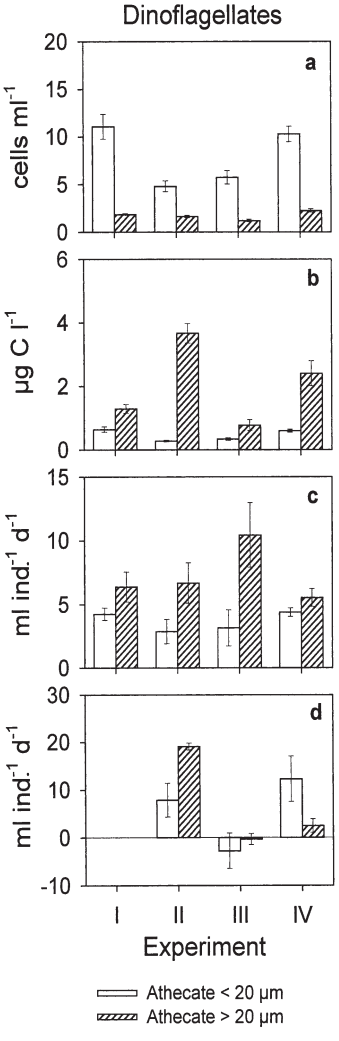

Fig. 9. (a) Initial concentrations and (b) biomass of nano- (<20 µm) and micro- (>20 µm) sized athecate dinoflagellates and clearance of these dinoflagellate size-groups by nauplii of (c) *Calanus* spp. and (d) *Balanus* cf. *crenatus*. Error bars represent standard errors of mean. Note different scales on *y*-axis

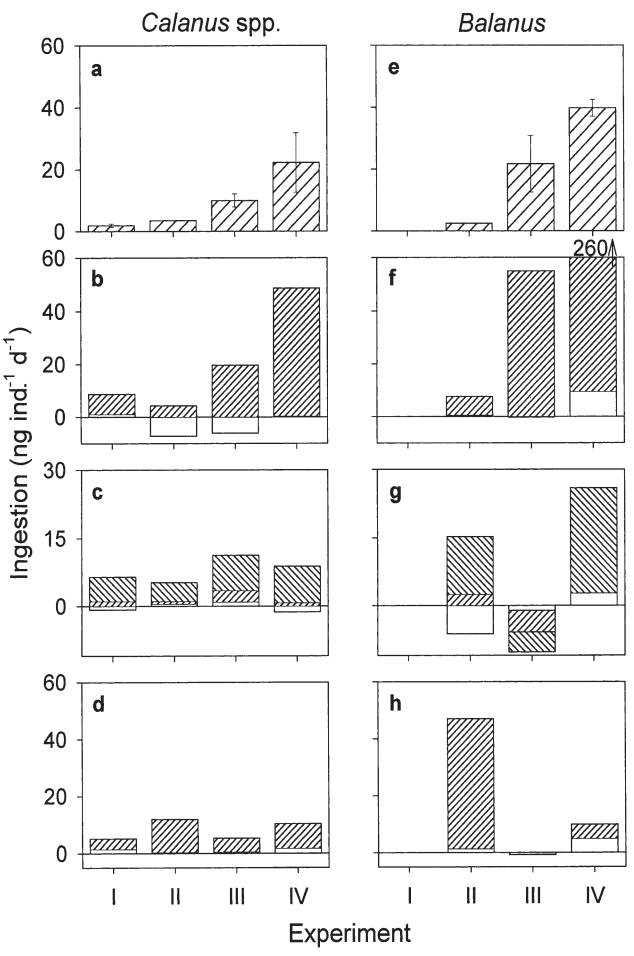

Fig. 10. *Calanus* spp. nauplii (a–d) and *Balanus* cf. *crenatus* nauplii (e–h). Ingestion of chlorophyll *a* (a, e), phytoplankton (b, f), ciliates (c, g) and dinoflagellates (d, h). Hatching patterns in (a,e), (b,f), (c,g) and (d,h) correspond to those in keys to Figs 6, 7, 8 and 9, respectively. Note different scaleson *y*-axis

extensively upon phagotrophic ciliates and dinoflagellates (Tiselius 1989, Wiadnyana & Rassoulzadegan 1989, Gifford & Dagg 1991, Jonsson & Tiselius 1990, Stoecker & Capuzzo 1990, Pierce & Turner 1992, Turner & Granéli 1992, Fessenden & Cowles 1994, Nakamura & Turner 1997, Levinsen et al. 2000a, Turner 2000). Together with information that nauplii of certain copepod species can be both bacterivorous (Turner & Tester 1992, Roff et al. 1995), and detritivorous (Green et al. 1992), it is clear that copepod nauplii can also be quite omnivorous, as is now generally agreed for most adult copepods. Thus, previous characterizations of copepod nauplii as primarily grazers upon small phytoplankton (see references in Turner 1984) are oversimplifications. Conversely, our results as well as successful laboratory culture of barnacle nauplii, suggest that they are primarily herbivorous, consuming mainly small phytoflagellates and diatoms (Anderson 1994 and references therein). Release of barnacle nauplii in nature also appears to be linked to phytoplankton blooms (Starr et al. 1991).

Following increased appreciation of the 'microbial loop' in pelagic food webs (Pomeroy 1974, Williams 1981, Azam et al. 1983), there has been mounting evidence for considerable intertwining of the 'microbial' and 'classical' food webs (reviewed by Turner & Roff 1993). Although the importance of the pelagic microbial food web has been well-established for several

Table 3. *Calanus* spp. Estimates (mean ± SD) of clearance, *F*, of specific prey categories (% of surface water d^{-1}) and ingestion, *I* (ng d^{-1}) by the *Calanus* nauplii community, calculated using mean weight-specific clearances from grazing experiments and field biomass values in Disko Bay of the different prey categories (chlorophyll *a*, oligotrich ciliates, athecate dinoflagellates) and the copepod nauplii. n = number of stations where calculations were conducted. Range of values in parentheses

	F (% d^{-1})	*I* (ng d^{-1})	n
Chlorophyll *a*	0.4 ± 0.3 (0.1–1.3)	4.5 ± 10.3 (0.1–55.3)	31
Oligotrichs <20 µm	1.8 ± 1.7 (0.2–5.4)	4.8 ± 7.5 (0.3–26.1)	13
Oligotrichs >20 µm	3.0 ± 2.8 (0.4–9.2)	73.6 ± 76.8 (2.5–248.5)	13
Athecate <20 µm	0.6 ± 0.6 (0.1–1.8)	10.9 ± 12.0 (0.3–44.6)	13
Athecate >20 µm	1.1 ± 1.0 (0.2–3.4)	78.6 ± 78.8 (1.8–257.4)	13

decades for temperate and tropical waters, particularly in oligotrophic offshore habitats, evidence for a similar importance in Arctic ecosystems is much more recent (Andersen 1988, Nielsen & Hansen 1995, Levinsen et al. 1999, and references therein). Partly for historical reasons, and supported by the 'cold ocean paradigm' (referenced in Rivkin et al. 1996), which infers that low temperature suppresses bacterial growth, thus reducing microbial loop activity, by far the most attention has been given to the classical food web and adult copepods of the genus *Calanus* in high northern latitude waters. Copepod nauplii are known to bridge the microbial and classical food webs by feeding upon picoplankton such as bacteria and small phytoplankton, which are generally considered to be inefficiently exploited by later-stage copepods. Subsequent transfer of portions of the microbial production to higher trophic levels occurs when nauplii are consumed by carnivorous zooplankton and planktivorous fishes. It is generally thought, however, that protozoans are more important than copepods (of any stage) in utilizing microbial production and conveying it to larger consumers in Arctic waters (Nielsen & Hansen 1995, Hansen et al. 1996, 1999). Knowledge that copepod nauplii can facilitate trophic transfer through their predation on protozoans extends our understanding of potential pathways for mobility of nutrients and energy through pelagic food webs. It may also help explain why copepod nauplii often remain abundant, and as prey facilitate recruitment of upper-level consumers under conditions when availability of phytoplankton food appears to be insufficient (Ohman & Runge 1994, Runge & de Lafontaine 1996). Finally, it adds further to the recently-realized key role of ciliates and heterotrophic dinoflagellates in Disko Bay and other cold-water areas (Bjørnsen & Kuparinen 1991, Burkill et al. 1995, Archer et al. 1996, Sherr et al. 1997, Levinsen & Nielsen unpubl.).

In summary, when feeding in natural mixed plankton assemblages in Disko Bay during the post spring bloom stratified period, nauplii of *Calanus* spp. were feeding omnivorously to various degrees upon abundant nanoflagellates, as well as less-abundant diatoms, *Myrionecta rubra*, dinoflagellates and oligotrichous ciliates. However, the highest feeding rates by *Calanus* spp. nauplii were on oligotrichous ciliates. Conversely,

Table 4. *Calanus* spp. Ingestion (ng chlorophyll *a* or C l^{-1} d^{-1}) by nauplii community of various components of prey assemblages in Disko Bay, June 1997, calculated using field biomass values of the different types of prey and nauplii and the respective mean weight-specific clearances from grazing experiments. Relative contribution of protozoans (oligotrich ciliates + athecate dinoflagellates) to total ingestion (phytoplankton + protozoans) is shown in **bold**. Phytoplankton carbon calculated from chlorophyll *a* applying a C/chl *a* conversion factor of 44 (Nielsen et al. unpubl.)

Stn	Chl *a*	Phytoplankton carbon	Oligotrichs		Athecate dinoflagellates		Protozoans (sum)	Ingestion (% protozoans)
			<20 µm	>20 µm	<20 µm	>20 µm		
6	2.9	127	6	58	45	79	188	**60**
10	1.5	65	0	3	0	5	8	**11**
13	0.2	10	1	19	2	32	54	**85**
15	1.0	44	2	11	3	37	53	**55**
17	0.1	5	1	3	3	2	8	**60**
24	0.2	8	1	19	12	30	62	**89**
27	1.4	60	0	16	4	20	40	**40**
31	2.9	126	26	249	23	257	555	**81**
32	2.6	116	2	148	3	78	231	**67**
33	4.1	181	3	134	15	204	355	**66**
35	2.8	122	3	43	12	38	96	**44**
37	55.3	2434	15	145	13	141	314	**11**
39	1.5	67	3	109	6	99	217	**76**

Table 5. *Calanus* spp. and *Balanus* cf. *crenatus* nauplii. Ingestion (ng C ind.$^{-1}$ d^{-1}) of various components of the prey assemblage in grazing experiments conducted in Disko Bay, June 1997, calculated as explained in the 'Methods'. Mean relative contribution of protozoans (*Myrionecta rubra* + oligotrich ciliates + athecate dinoflagellates) to total ingestion of protists (phytoplankton + protozoans) shown in **bold**. Standard errors of triplicates in parentheses. Phytoplankton carbon calculated from chlorophyll *a* applying a C/chl *a* conversion factor of 44 (Nielsen et al. unpubl.). Ia to IVb: expt numbers; (–) only 1 replicate counted

Prey	*Calanus* spp. nauplii				*Balanus* cf. *crenatus* nauplii		
	Ia	IIa	IIIa	IVa	IIb	IIIb	IVb
Myrionecta rubra	–0.8 (0.1)	0.5 (0.3)	0.9 (0.3)	–1.3 (1.4)	–6.2 (1.9)	–1.1 (2.2)	2.7 (2.1)
Oligotrichs <20 µm	1.1 (0.2)	0.6 (0.1)	2.5 (0.2)	0.7 (0.1)	2.5 (0.6)	–4.7 (2.7)	0.1 (0.5)
Oligotrichs >20 µm	5.4 (0.8)	4.2 (0.5)	7.8 (1.5)	8.1 (4.3)	12.7 (3.7)	–4.4 (2.8)	23.1 (9.7)
Athecate <20 µm	1.5 (0.1)	0.4 (0.1)	0.6 (0.2)	1.7 (0.1)	1.3 (0.5)	–0.7 (0.9)	4.7 (1.5)
Athecate >20 µm	3.6 (0.6)	11.4 (0.9)	4.7 (2.1)	8.6 (0.6)	45.7 (3.9)	–0.1 (0.7)	5.1 (3.2)
Protozoans (sum)	10.8 (1.7)	17.1 (1.8)	16.5 (4.4)	17.8 (6.5)	56.0 (10.6)	–11.1 (9.3)	35.7 (17.0)
Phytoplankton	84.0 (23.3)	151.4 (–)	438.7 (92.4)	979.0 (424.6)	105.6 (–)	956.1 (403.9)	1750.8 (120.1)
% protozoans	**11.4**	**10.1**	**3.6**	**1.8**	**34.6**	**–1.2**	**2.0**

barnacle nauplii *Balanus* cf. *crenatus* fed primarily upon phytoplankton, with lower rates of feeding on ciliates and dinoflagellates. The observation of comparatively higher feeding upon oligotrichous ciliates by copepod nauplii is similar to results for later-staged copepods in many studies. Also, primarily herbivorous feeding by barnacle nauplii is in agreement with numerous observations in studies using laboratory diets, but there is apparently such limited information on feeding by barnacle nauplii on natural plankton assemblages that further comparisons are precluded.

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