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Importance of ciliates as prey of the euphausiid *Euphausia pacifica* in the NW North Pacific

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ABSTRACT: We investigated the feeding of *Euphausia pacifica* on ciliates, especially naked ciliates, in laboratory and field experiments in which cultured *Strombidium conicum*, or natural food assemblages, or both were given, and estimated the importance of ciliates as prey. *E. pacifica* ingested cultured *S. conicum* at rates of 0.04 to 0.07 µg C krill^{-1} h^{-1} at low ciliate concentration and 1.01 to 3.24 µg C krill^{-1} h^{-1} at high ciliate concentration, when *S. conicum* was given as the sole prey. The daily ration on naked ciliates ranged from 0.02 to 1.8% of body carbon when natural food assemblages enriched with *S. conicum* were given, and from 0.05 to 2.3% of body carbon when *S. conicum* was given as the sole prey. Our results provide indirect evidence that *E. pacifica* ingests naked ciliates and plays a role in linking microbial food webs to the classical grazing food chains.

KEY WORDS: *Euphausia pacifica* · Feeding · Naked ciliates · *Strombidium conicum* · Food removal

INTRODUCTION

Planktonic protozoans function as important trophic intermediaries in pelagic food webs by repacking small bacterial and algal cells into food items large enough to be consumed by mesozooplankton (Gifford 1993, Båmstedt et al. 2000). The C:N ratio in heterotrophic marine protozoans is lower than the values usually reported for phytoplankton and mixotrophic protozoans, making protozoans a richer source of amino acids and protein than phytoplankton and detritus (Stoecker & Capuzzo 1990). In particular, planktonic ciliates have been recognized as abundant, ubiquitous and therefore important components of marine microbial food webs (Pierce & Turner 1992). The carbon:biomass ratio of ciliates to net-zooplankton could amount to as much as 36% in the sea off NE Japan (Ito 2002). Planktonic ciliates have been considered potentially important prey for mesozooplankton owing to their available size and vertical distribution (Stoecker & Capuzzo 1990). Several studies have documented the consumption of protozoans, including ciliates, by copepods, and have demonstrated the role of copepods in linking the microbial food webs to the classical grazing food chains (reviewed by Stoecker & Capuzzo 1990, Gifford 1993).

Perissinotto et al. (1997) reported that athecate ciliates were very abundant in the gut contents of *Euphausia superba*. However, it is not clear whether *E. superba* ingests planktonic athecate ciliates, since symbiotic ciliates reproduce in the gut (Kawaguchi & Toda 1997). In rearing experiments, calanoid copepods and protozoans proved to be the major prey items of *E. superba* when natural seawater was given as food (Atkinson & Snÿder 1997). Athecate protozoans, including naked ciliates, however, are not identifiable in the stomach contents of euphausiids, because they do not have any hard body parts (Stoecker & Capuzzo 1990, Nakagawa et al. 2001, 2002).

On the basis of gut-content analysis, several studies have suggested that *Euphausia pacifica* is an omnivore (Ponomareva 1963, Mauchline & Fisher 1969, Endo 1981). Nakagawa et al. (2002) suggested that naked ciliates could be a major prey item of *E. pacifica* after copepods, assuming that naked ciliates and tintinnids were ingested equally in proportion to their biomass in

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the ambient water. However, this hypothesis lacks the direct evidence that *E. pacifica* ingests naked ciliates. The present study aimed to investigate the ingestion rates of *E. pacifica* on ciliates, especially naked ciliates, in the field and laboratory to estimate the importance of naked ciliates as prey.

MATERIALS AND METHODS

All the experiments used the food removal method (Båmstedt et al. 2000) under the following 3 food conditions.

***Strombidium conicum* as sole food source.** *S. conicum* was used as the sole food source to examine whether *Euphausia pacifica* ingests this naked ciliate and, if so, what the ingestion rates are. Experiments were carried out from 20 to 23 March 2001 (Table 1) at the Education and Research Center of Marine Bioresources (ERCMB), Tohoku University. Adult *E. pacifica* were collected from a surface swarm in a dip net with a 5 mm mesh at 13:00 h on 20 March 2001 at the port of Tanoshiri (38° 27′ 25″ N, 141° 31′ 12″ E); sea depth was about 2 m and surface water temperature was 5.8°C. Live individuals of *E. pacifica* were transferred to a 20 l polycarbonate bottle filled with the surface seawater after rinsing in filtered seawater. The temperature was maintained at 8.9 to 10.3°C in a water bath, and 50% of the seawater in the bottle was changed daily; the molts and dead individuals were removed from the bottle at the same time.

Strombidium conicum had been cultured, with the haptophyte *Isochrysis* sp. as food, at 20°C for 12 h in the dark, and were in active growth phase. Their average carbon content was 12.2 ± 2.3 ng C cell^{-1}. They measured 83.6 ± 4.2 µm long × 47.5 ± 3.6 µm wide (mean ± SD). Cultured *S. conicum* was given at either high (5000 cells l^{-1}) or low (300 cells l^{-1}) concentration at night on 22 March and during the day on 23 March. We prepared two 1 l bottles containing 1 euphausiid each for both concentrations of *S. conicum*, and another 2 bottles without a euphausiid for both concentrations as controls. Incubation water with a high concentration of *S. conicum* was prepared by mixing 280 ml of *S. conicum* culture with 820 ml of seawater filtered through a Whatman GF/F filter, to give a final concentration of 5000 cells l^{-1}. Water with a low concentration was prepared by mixing 20 ml of *S. conicum* culture with 1230 ml of GF/F-filtered seawater, to give a final concentration of 300 cells l^{-1}. These concentrations of ciliates were within the reported range of the abundance of total naked ciliates in the northwestern North Pacific (Ito & Taniguchi 2001, Ito 2002). Diatoms contaminated the incubation water (probably brought in with *Euphausia pacifica*) at concentrations ranging from 0 to 1630 cells l^{-1} at the start of the experiment.

Table 1. Experimental conditions and initial biomass of phytoplankton, naked ciliates and tintinnids in each experiment. Surface seawater was filtered through 200 µm mesh, except where otherwise indicated

Food source	Mean body carbon (mg)	Experimental temperature (°C)	Initial biomass		
			Phytoplankton (µg C l^{-1})	Naked ciliates (µg C l^{-1})	Tintinnids (µg C l^{-1})
Strombidium conicum					
22 Mar 01	3.4	10.2–10.3	20.87		
22 Mar 01	1.6	10.2–10.3	1.37		
23 Mar 01	2.6	9.8–10.2	24.34		
23 Mar 01	1.8	9.8–10.2	2.71		
Natural seawater					
14 Sep 00	1.6	11.9–12.1	40.62	0.56	0.04
3 Oct 00	1.8	5.2–7.1	31.31	1.26	0.20
5 Oct 00	2.9	12.2–12.9	41.58	1.04	0.04
6 Oct 00	3.0	12.6–12.7	5.64	0.67	0.07
7 Oct 00	3.2	11.8–12.1	10.34	1.02	0
22 Mar 01	2.6	10.2–10.3	28.50	16.22	0.31
23 Mar 01	2.5	9.8–10.0	53.62	23.45	0.12
11 Apr 01	4.2	8.7–9.6	151.05	8.43	1.85
14 Apr 01	3.6	8.9–10.2	42.07	2.91	0.66
14 Apr 01[a]	3.8	8.9–10.2	74.85	2.36	0.06
15 Apr 01[a]	4.9	11.1–11.3	35.23	6.93	0
Natural seawater + *S. conicum*					
20 Mar 01	3.4	9.4–9.8	79.56	6.01	0.30
21 Mar 01	1.6	9.4–9.8	61.98	13.60	0.11
21 Mar 01	2.6	9.4–9.7	122.72	20.32	0.36
22 Mar 01	2.8	8.9–9.4	91.10	5.52	0

[a]Surface seawater filtered through 40 µm mesh

The incubation water was left for 2.8 to 3.5 h after introduction of the *S. conicum* cultures into the bottles to acclimatize the *S. conicum* (Gifford 1993, Båmstedt et al. 2000). All experiments and acclimatization were carried out in the dark at 9.8 to 10.9°C by covering the experimental container with a sheet of black rubber. Experiments lasted only 6 h in order to conform to 2 other experiments in which natural food assemblages were given.

At the start and end of the experiment, a 100 to 250 ml sample was collected with a siphon from each bottle after mixing, and preserved in 1% Lugol's solution for enumeration of ciliates. Each *Euphausia pacifica* was then rinsed with distilled water to remove attached materials, and preserved in 5% Bouin's solution.

Natural food assemblages. Experiments in which natural food assemblages were given as food source were carried out during 3 cruises of the RV 'Wakataka-Maru', RV 'Tankai-Maru' and RV 'Tansei-Maru', and at ERCMB from 14 September 2000 to 15 April 2001 (Table 1) in the coastal waters off northeastern Japan. Adult *Euphausia pacifica* were collected at night by vertical tow from 100 m depth, in a conical net with a mouth diameter of 56 cm, a mesh aperture of 200 µm and a 1 l cod end. At ERCMB, after rinsing in filtered seawater, live animals were transferred to 20 l polycarbonate bottles filled with surface seawater and were maintained at 8.7 to 12.9°C in a water bath (except for the experiment on 3 October: 5.2 to 7.1°C), for 1.4 to 3.0 h to acclimatize them before experiments. The incubation water, with food, was collected from the sea surface in a plastic bucket on board the research vessels, while the water at ERCMB was collected from the innermost part of Onagawa Bay (38° 25' N, 141° 30' E), and was transferred gently to 20 l polycarbonate bottles through a silicon tube with a 40 or 200 µm mesh attached to eliminate copepods and larger zooplankton, which can ingest ciliates (Båmstedt et al. 2000). These bottles were left for 1.4 to 3.0 h to acclimatize the natural food assemblage. Experiments were done in 20 l bottles with 3 to 5 live euphausiids or without euphausiids as a control. Experiments lasted only 6 h in order to reduce grazing by zooplankton other than euphausiids in the control bottles (Gifford 1993).

At the start and end of the experiment, after mixing, two 250 to 500 ml samples were collected with a siphon from each bottle for chlorophyll *a* analysis and for enumeration of ciliates. The sample for enumeration of ciliates was preserved in 1% Lugol's solution. Subsamples of 100 ml for chlorophyll *a* analysis were size-fractionated through 10 µm nylon mesh and a GF/F filter. No size-fractionation was done in the experiments in September and October 2000: 100 ml subsamples were just filtered though GF/F filters. After 6 h incubation, *Euphausia pacifica* was checked for activity. Individuals were rinsed with distilled water to remove attached materials, transferred to a pre-combusted (450°C, 6 h) and pre-weighed GF/C filter, and frozen at −80°C until dry weight measurement, with 2 exceptions: at night on 22 March and during the day on 23 March, they were rinsed with distilled water and preserved in 5% Bouin's solution.

Natural food assemblages enriched with *Strombidium conicum*. Natural seawater containing cultured *S. conicum* was given as food from the night of 20 March to the day of 22 March at ERCMB (Table 1). *S. conicum* was added to obtain various biomasses of naked ciliates. Natural surface seawater was collected in a plastic bucket from the innermost part of Onagawa Bay and was filtered through a 200 µm mesh. Incubation water was prepared by mixing 20 l of filtered natural seawater with 250 ml of *S. conicum* culture, to give a final *S. conicum* density of 2500 cells l^{-1}. However, no enrichment effect was apparent, and the *S. conicum* in the culture bottles may have been dead. Incubation water was left for 1.8 to 3.0 h, and then for a further 1 h after addition of the *S. conicum* cultures in order to acclimatize the food assemblage. Experiments were done in two 20 l bottles — 1 with 5 live euphausiids, 1 without euphausiids as a control — which were incubated for 6 h at 9.4 to 10.9°C in the dark. The preparation of water samples for chlorophyll *a* analysis and ciliate enumeration was the same as the above experiments using natural food assemblages. Incubated *Euphausia pacifica* was rinsed with distilled water to remove attached materials, and preserved in 5% Bouin's solution.

Analysis of samples. A 50 to 100 ml subsample, depending on ciliate abundance, was collected from the Lugol-preserved water samples in replicate at the start and end of each experiment (a single subsample was collected in the experiments in September and October 2000) and allowed to settle for 24 h. The numbers of the different groups of microplankton were then counted using a modification of the Utermöhl method (Taniguchi 1977) under 100× or 200× magnification. The dimensions of the cells of naked ciliates and live tintinnids were measured, and their carbon content was estimated from cell volume with a conversion factor of 0.19 pg μm^{-3} (Putt & Stoecker 1989).

Chlorophyll *a* on the filters was extracted in 10 ml 90% acetone for 24 h at −25°C, and fluorescence was determined before and after acidification on a Turner Designs fluorometer (Holm-Hansen et al. 1965). Phytoplankton carbon was estimated assuming a carbon: chlorophyll *a* ratio of 30 (Strickland 1960, Geider 1987).

Total length, from the anterior tip of the rostrum to the distal end of the telson, of *Euphausia pacifica* was measured immediately after the experiment. Individual dry mass was obtained by drying at 60°C for 24 h in a drying oven (Lovegrove 1962), desiccation for 24 h

while cooling to room temperature, and weighing on a Mettler microbalance with a reading accuracy of 0.01 mg. Except for March, the carbon weight of *E. pacifica* was calculated from the dry mass by assuming that the carbon weight of an adult is 43% of its dry mass (Iguchi & Ikeda 1998). For the experiments in which *Strombidium conicum* was used as the sole prey, the carbon weight of *E. pacifica* was estimated from its total length using the equation of Ross (1982). The ingestion rates of *E. pacifica* on ciliates and chlorophyll *a* were calculated with a modification of Frost's (1972) equation (Båmstedt et al. 2000).

RESULTS AND DISCUSSION

Euphausia pacifica did not consume copepods of any developmental stages, although nauplii were present at <60 individuals l^{-1} in the experimental bottles. Chlorophyll *a* and the number of ciliates (tintinnids and naked ciliates) and copepods in the control bottles did not change significantly during the experiments (*t*-test, $p > 0.15$). Therefore, the effect of feeding of copepods on phytoplankton or ciliates seemed small.

When cultured *Strombidium conicum* was given as the sole prey at high concentration (HSC), ingestion rates of *Euphausia pacifica* were 3.24 µg C krill^{-1} h^{-1} at night, and 1.01 µg C krill^{-1} h^{-1} during the day (Table 2). The ingestion rates at low *S. conicum* concentration (LSC) were lower, being 0.04 µg C krill^{-1} h^{-1} at night and 0.07 µg C krill^{-1} h^{-1} during the day (Table 2). In the experiments in which natural seawater with or without cultured *S. conicum* was given, ingestion rates of *E. pacifica* on naked ciliates ranged from 0.03 to 1.98 µg C krill^{-1} h^{-1} (Table 2). Our results suggest that *E. pacifica* ingests naked ciliates.

Based on incubation experiments, Atkinson & Snÿder (1997) reported that protozoans were a significant food item for *Euphausia superba*. In the present study, the daily ration at HSC ranged from 0.94 to 2.28% of body carbon, while that at LSC ranged from 0.05 to 0.06% of body carbon (Table 2). When natural seawater with or without cultured *Strombidium conicum* was given, the daily ration on naked ciliates ranged from 0.02 to 1.76% of body carbon (Table 2). In an experimental study at 8 and 12°C, 2 to 4% of body carbon was needed per day for *E. pacifica* to maintain their growth, respiration, and reproduction (Ross 1982). Our incubation temperature ranged from

Table 2. *Euphausia pacifica*. Ingestion (µg C krill^{-1} h^{-1}) and clearance rates (l krill^{-1} h^{-1}), and daily ration (% body C) of naked ciliates, tintinnids and phytoplankton in each experiment. Surface seawater filtered through 200 µm mesh. N: night; D: day; HSC: high *Strombidium conicum* concentration (5000 cells l^{-1}); LSC: low *S. conicum* concentration (300 cells l^{-1}); –: not determined

Food source	Naked ciliates			Tintinnids			Phytoplankton				
	Ingestion rate	Clearance rate	Daily ration	Ingestion rate	Clearance rate	Daily ration	Ingestion rate <10µm	Ingestion rate >10µm	Clearance rate <10µm	Clearance rate >10µm	Daily ration
Strombidium conicum											
22 Mar 01 (N) HSC	3.24	0.21	2.28								
22 Mar 01 (N) LSC	0.04	0.03	0.05								
23 Mar 01 (D) HSC	1.01	0.03	0.94								
23 Mar 01 (D) LSC	0.07	0.05	0.06								
Natural seawater											
14 Sep 00 (N)	0.06	0.14	0.09	–	–	–	–	–	–	–	–
3 Oct 00 (D)	–	–	–	–	–	–	–	–	–	–	–
5 Oct 00 (N)	–	–	–	–	–	–	–	0.40[b]	–	0.01[b]	0.33
6 Oct 00 (N)	–	–	–	–	–	–	–	0.14[b]	–	0.03[b]	0.11
7 Oct 00 (N)	0.80	0.84	0.61	–	–	–	–	–	–	–	–
22 Mar 01 (N)	1.30	0.09	1.22	–	–	–	–	–	–	–	–
23 Mar 01 (D)	–	–	–	0.13	1.46	0.13	10.45	–	0.25	–	10.24
11 Apr 01 (N)	1.95	0.29	1.12	0.47	0.32	0.27	–	34.25	–	0.27	19.73
14 Apr 01 (N)	0.34	0.14	0.23	–	–	–	–	–	–	–	–
14 Apr 01[a] (N)	–	–	–	–	–	–	0.56	–	0.14	–	0.35
15 Apr 01[a] (N)	–	–	–	–	–	–	0.07	–	0.11	–	0.04
Natural seawter + *S. conicum*											
20 Mar 01 (N)	–	–	–	0.04	0.13	0.03	–	–	–	–	–
21 Mar 01 (D)	0.03	0.01	0.02	0.09	0.92	0.07	–	0.69	–	0.24	0.56
21 Mar 01 (N)	1.98	0.12	1.76	0.16	0.49	0.14	–	4.41	–	0.37	3.94
22 Mar 01 (D)	1.53	0.33	1.26	–	–	–	–	0.84	–	0.03	0.70

[a]Surface seawater filtered through 40 µm mesh
[b]Clearance and ingestion rates for total chlorophyll *a*

8.7 to 12.9°C except on 3 October, and was similar to that in the study of Ross (1982). In stomach-content analyses, daily rations calculated by converting prey volumes to carbon weight were less than 3.6% of the body carbon throughout the year (Nakagawa et al. 2001, Taki et al. 2002). In the present study, however, diatoms were present in the incubation water in the experiments in which *S. conicum* was given as the sole prey. Ingestion rates of *E. pacifica* on diatoms by number ranged from 0 to 2.8 cells krill^{-1} h^{-1} at LSC, and from 0 to 95.9 cells krill^{-1} h^{-1} at HSC. Ingestion rates on naked ciliates were higher, ranging from 0 to 14.1 cells krill^{-1} h^{-1} at LSC and from 7.6 to 216.6 cells krill^{-1} h^{-1} at HSC, than those on diatoms. Moreover, *Isochrysis* sp. was not eliminated from *S. conicum* cultures in order not to hurt *S. conicum* in washing it, although *E. pacifica* could not consume *Isochrysis* sp. effectively because of its small size (Parsons et al. 1967). Therefore, when diatoms and *Isochrysis* sp. are not present in the incubation water, ingestion rates and daily rations of *E. pacifica* on *S. conicum* might be higher than the values we obtained. These results suggest that naked ciliates alone could fulfill much of the energy requirements of *E. pacifica*.

In several laboratory and field experiments, copepods ingested protozoans, mainly ciliates, at higher rates than they ingested phytoplankton (Wiadnyana & Rassoulzadegan 1989, Gifford & Dagg 1991, Fessenden & Cowles 1994). In the present study, although the initial biomass was dominated by phytoplankton in all the experiments, ranging from 63.3 to 98.6%, and the initial biomass of ciliates (tintinnids and naked ciliates) was less than 36.0%, ciliates dominated in the diet in some instances: on 14 September and 7 October 2000, and on 22 March and 14 April 2001, when natural food assemblages were given, and 20 and 22 March when natural seawater enriched with *Strombidium conicum* was given (Fig. 1). *Euphausia pacifica* ingested tintinnids at higher clearance rates (0.13 to 1.46 l krill^{-1} h^{-1}) than phytoplankton (0.01 to 0.37 l krill^{-1} h^{-1}) (Table 2). The clearance rates on naked ciliates ranged from 0.01 to 0.84 l krill^{-1} h^{-1}, which lies between the values for tintinnids and phytoplankton (Table 2). *E. pacifica* ingested ciliates (tintinnids and naked ciliates) at higher clearance rates than phytoplankton. Moreover, Broglio et al. (2001) reported that the copepod *Acartia clausi* ingested the tintinnid *Metacylis* sp. at a higher rate than *S. spiralis*, *S. spiralis* escaping the attacking *A. clausi* with rapid jumps. *Metacylis* sp. lacked any effective behavioral response to the predator, showing a swimming pattern typical of many tintinnids, with steep helical trajectories without jumps. Therefore, it may be easier for *E. pacifica* to capture tintinnids than to capture naked ciliates. However, naked ciliates may be more important as prey of *E. pacifica* because they are more numerous than tintinnids.

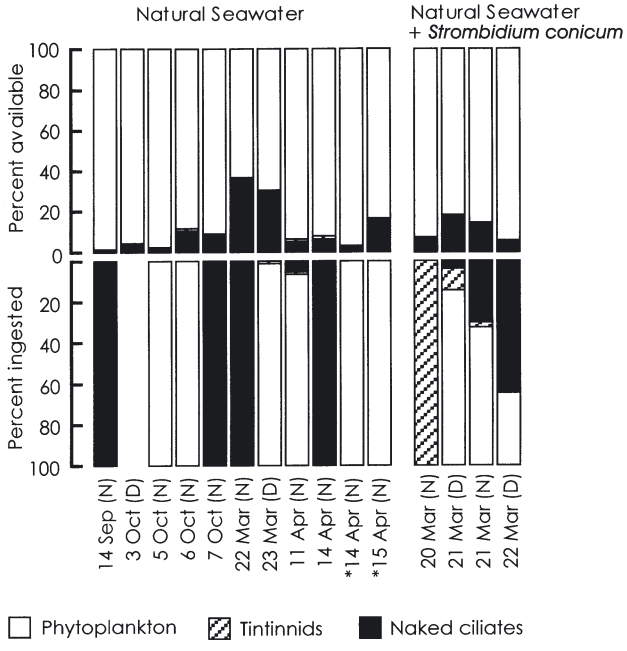

Fig. 1. *Euphausia pacifica*. Initial contribution (carbon biomass) of each prey item to total prey biomass (Percent available) and contribution to total stomach content-carbon (Percent ingested) in each experiment from September 2000 to April 2001. N: night; D: day; surface seawater filtered through 200 µm mesh; *through 40 µm mesh

Based on stomach fullness, feeding activity of *Euphausia pacifica* at night is reported to be higher than during the day (Ponomareva 1963, Endo 1981, Nakagawa et al. 2003). When *Strombidium conicum* was given as the sole prey at HSC, feeding rates on *S. conicum* at night were higher than that during the day. When natural food assemblages were given, however, there was an instance (22 March) when feeding rates on naked ciliates during the day were higher than those at night. Moreover, ingestion rates and initial concentrations did not show a significant correlation (*t*-test, $p > 0.2$) even when excluding the daytime experiments (*t*-test, $p > 0.06$). For a better understanding of the feeding behavior of *E. pacifica* on ciliates, more work is needed, taking into account the availability and size composition of other food items.

Naked ciliates have been recognized as ubiquitous and important components of marine microbial food webs (Beers 1986). *Euphausia pacifica* does not ingest smaller components of microbial food webs such as bacteria either directly and efficiently. However, the present study indirectly demonstrates that *E. pacifica* ingests naked ciliates and plays a role in linking microbial food webs to the classical grazing food chains.

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