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Gregory J. Teegarden

Robert G. Campbell
University of Rhode Island, rgcampbell@uri.edu

Edward G. Durbin
University of Rhode Island, edurbin@uri.edu

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Zooplankton feeding behavior and particle selection in natural plankton assemblages containing toxic *Alexandrium* spp.

Gregory J. Teegarden[1,*], Robert G. Campbell[2], Edward G. Durbin[2]

[1]Bowdoin College, 6700 College Station, Brunswick, Maine 04011, USA
[2]Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA

ABSTRACT: Laboratory experiments suggest that toxic *Alexandrium* spp. cells are unpalatable to zooplankton grazers, and that toxic cells should be selectively avoided by zooplankton when feeding in mixtures of different prey species. Such avoidance, if practised in the wild, might contribute to harmful bloom formation by reducing losses of *Alexandrium* spp. due to grazing. In the spring of 1998 and 1999, during 'red tide' outbreaks in the southwestern Gulf of Maine, weekly experiments were performed using field collected natural water samples with ambient phytoplankton and dominant mesozooplankton grazers. The feeding response of *Acartia hudsonica*, *Semibalanus balanoides* nauplii, and *Calanus finmarchicus* was tested during various weeks in natural water samples with low concentrations of *Alexandrium* spp. (~1000 cells l^{-1}, typical natural concentrations for this region). *Semibalanus* sp. nauplii consistently avoided toxic *Alexandrium* spp. and other dinoflagellates. *C. finmarchicus* selectively fed on diatoms when they were abundant, and fed non-selectively on all dinoflagellates (except *Ceratium* spp.) when the spring bloom declined and dinoflagellates dominated. *A. hudsonica* non-selectively cleared *Alexandrium* spp. throughout the study periods. During spring *Alexandrium* spp. bloom formation, if non-selective grazers such as *A. hudsonica* dominate the zooplankton, *Alexandrium* spp. losses from grazing depend on grazer abundance (biomass); if selective feeders such as *S. balanoides* nauplii dominate, then *Alexandrium* spp. benefits from reduced grazing losses relative to alternative prey.

KEY WORDS: *Alexandrium* · Paralytic shellfish poisoning · Selective feeding · Zooplankton grazing

INTRODUCTION

Toxic *Alexandrium* spp. (predominantly *Alexandrium fundyense* Balech) in the southwestern Gulf of Maine produce potent neurotoxins known as paralytic shellfish poisoning (PSP) toxins. Harmful *Alexandrium* spp. blooms in this region are seldom monospecific. Blooms initiate from benthic resting cysts during the early spring (Anderson & Morel 1979); at this time, diatoms (*Skeletonema costatum*, *Thalassiosira* spp., and *Chaetoceros* spp.) usually dominate the local flora (authors' unpubl. obs.). As *Alexandrium* spp. proliferation progresses, total abundance of diatoms often declines and dominant species shift, while dinoflagellate and other flagellate populations increase, typical of phytoplankton succession processes (Smayda 1980). Thus *Alexandrium* spp. and other dinoflagellates may form a larger proportion of the total phytoplankton and therefore of prey available to zooplankton. This may present a problem for some zooplankton grazers, as it has been reported that toxic *Alexandrium* spp. are unpalatable food for some zooplankton species (Turriff et al. 1995, Teegarden 1999).

The feeding behavior of zooplankton during *Alexandrium* spp. bloom development is not well understood. Experimental field studies published to date, conducted in salt ponds of Cape Cod, Massachusetts, have used natural seawater treatments enriched with mod-

*E-mail: gteegard@bowdoin.edu

erate to high *Alexandrium* spp. cell concentrations (Turner & Anderson 1983, Watras et al. 1985). These studies concluded that zooplankton abundance was the primary factor affecting rates of *Alexandrium* spp. removal. Turner & Anderson (1983) noted that the copepod *Acartia hudsonica* fed on tintinnid ciliates at higher rates than on co-occurring phytoplankton, but it was not reported in either study whether toxic *Alexandrium* spp. were selectively avoided or consumed relative to ambient non-toxic phytoplankton.

If zooplankton grazers in natural environments avoid *Alexandrium* spp., then selective feeding might contribute to bloom development by reducing grazing pressure. Laboratory experiments have established that many copepod species are capable of selective feeding. Discrimination of food particles may be based on size (Frost 1972, 1977), concentration (Lam & Frost 1976, Price & Paffenhöfer 1986), and quality (Paffenhöfer & Van Sant 1985, Van Alstyne 1986, Cowles et al. 1988). Recently it has been shown that the presence of neurotoxic compounds such as saxitoxin can affect particle selection and discrimination (Turriff et al. 1995, Shaw et al. 1997, Teegarden 1999), but such toxins may not always trigger selective feeding responses (Teegarden & Cembella 1996, Teegarden 1999).

Evidence for selective feeding of copepods in field studies is more equivocal. Selection based on particle size (Cowles 1979, Bautista & Harris 1992) and quality (Morey-Gaines 1980, Gifford & Dagg 1988) has been suggested, but the literature contains numerous examples of non-selective feeding in natural situations, even when discrimination might be expected to be due to differences in food quality (e.g., Huntley 1981, Turner & Tester 1989).

We determined zooplankton feeding rates on natural plankton assemblages during the spring of 1998 and of 1999. We were particularly interested in the grazing response during bloom initiation, when *Alexandrium* spp. abundance is low (≈1000 cells l^{-1}) and the food complex is dominated by alternative prey, principally diatoms from the declining spring bloom. One objective was to test the hypothesis that, if zooplankton feeding is selective, such selective feeding should result in lower rates of *Alexandrium* spp. removal relative to the ambient phytoplankton prey. The study site was the Casco Bay region of the western Gulf of Maine, an area subject to recurring blooms of toxic *Alexandrium* spp. From late April to early June 1998, a moderate bloom of *Alexandrium* spp. developed and then declined in the study region. In 1999, *Alexandrium* spp. cells appeared in low numbers (≈1000 cells l^{-1}) in early May, but fell to background levels by the end of the month. Blooms contained predominantly *Alexandrium* cf. *fundyense*, but possibly also contained *A. ostenfeldii* (see 'Material and methods'); hereafter *Alexandrium* spp. is used. Field sampling of phytoplankton and zooplankton was coupled with grazing experiments using wild zooplankton and natural water samples (occasionally spiked with low concentrations, 500 to 1000 cells l^{-1}, of cultured *A. fundyense* clone GTCA 28).

MATERIALS AND METHODS

Zooplankton and phytoplankton collection. Sampling cruises were conducted weekly from April 20 to June 10, 1998 and April 27 to June 15, 1999, on the RV 'Nucella' of the Darling Marine Center, University of Maine. In 1998, 4 stations were located near the mouth of the Kennebec River: (1) the Damariscotta River estuary, (2) Newagen (Boothbay Harbor), (3) Head Beach, and (4) Cundy's Harbor. These inshore stations had water depths of 10 to 15 m. An additional offshore station (Stn 0) at the mouth of Sheepscot Bay, 60 m water depth, was sampled in Weeks 6, 7, and 8. Cundy's Harbor (Stn 4, 43° 47.45' N, 69° 53.32' W) was selected as the primary location from which experimental materials should be collected, since historically this location has had high PSP toxicity early in the spring bloom season. Offshore Stn 0 (43° 45.81' N, 69° 41.55 W) was incorporated when it became clear that *Alexandrium* spp. was also proliferating offshore (from the work of the ECOHAB-Gulf of Maine group under Dr D. M. Anderson, WHOI, pers. comm.). In 1999, experiments were conducted with materials from Cundy's Stn 4 and an offshore station (Stn 01, 60 m depth, 43° 38.03' N, 69° 51.14' W, 3 nautical miles from Cundy's Harbor).

Vertical temperature and salinity profiles were taken with a (Beckman RS5-3 portable thermometer/salinometer Beckman Coulter Inc., Fullerton, CA, USA), and upper water column chlorophyll was characterized by pumping water from depths of 20 m to the surface with a Teel centrifugal pump (model IP811A, Dayton Electric Mfg. Co., Niles, IL, USA) through a 2 cm inner diameter (ID) hose to a Turner Designs model 10 fluorometer (Turner Designs Inc., Sunnyvale, CA, USA) equipped with a flow-through cell. If a chlorophyll maximum layer was observed, bottle casts were used to collect water from the layer for experimental purposes; if no maximum layer was found, surface water was collected. Water was stored in 20 l carboys in a large cooler. Large zooplankton were collected with a 303 µm net oblique tow from approximately 10 m to the surface at inshore stations and 30 m to the surface at offshore stations. Animals were diluted and stored in 4 l jars in coolers during transportation to the laboratory at the Darling Marine Center, approximately 1 h.

Experimental procedure. Upon return to laboratory facilities, zooplankton samples were examined and the

dominant taxa identified. At the inshore stations, *Acartia hudsonica* Pinhey was the dominant zooplankton species (10^2 to 10^5 copepodites m^{-3}) in the spring of 1998 and of 1999, while nauplii of the barnacle *Semibalanus balanoides* L. were abundant (10^3 to 10^4 m^{-3}) or co-dominant at most stations from April to mid-May. At offshore Stn 0, *Calanus finmarchicus* Gunnerus was common (>10^2 m^{-3}).

Water samples for grazing experiments were prepared by reverse filtering 20 l of water through a 250 µm mesh to remove large grazers. Some protozoa, notably ciliates, were included in the samples and may have grazed some of the available food, but their abundance was low (″100 l^{-1}), and attempts to remove such protozoa would have inevitably caused unacceptable changes in the ambient prey field (e.g., removal of *Chaetoceros socialis* colonies). Furthermore, protozoa are a natural food source for larger grazers such as copepods, so their presence was desirable.

Alexandrium fundyense was previously reported as the dominant or sole species of *Alexandrium* in the Casco Bay region of the Gulf of Maine (Anderson 1997). More recent evidence (Dietz & Townsend 2000) has shown that *A. ostenfeldii* may also be present, although measured abundance is <10% of total *Alexandrium* spp. abundance from our study. *Alexandrium* spp. from water samples were not separated by species in this study, and are hereafter referred to as *Alexandrium* spp. A 50· concentrated preserved water sample was counted for *Alexandrium* spp. cell abundance. If natural *Alexandrium* spp. abundance was less than 1000 cells l^{-1}, then experimental water was spiked with *A. fundyense* clone GTCA 28 (isolated from the southwest Gulf of Maine) to provide a final concentration of approximately 1000 cells l^{-1} (simulating low bloom abundance). This was considered the minimum concentration necessary for acceptable counting statistics. Natural water *Alexandrium* spp. concentrations were augmented with GTCA 28 in 1998 on April 28 and on May 5 and 12, and in 1999 throughout the very moderate bloom season. When samples were augmented, cultured *A. fundyense* cells constituted between 25 and 100% of total available *Alexandrium* spp. cells. Clone GTCA 28 was cultured in an incubator at 14°C in f/2 –Si with a 14:10 h light:dark cycle. Toxicity of the *A. fundyense* culture, measured by high performance liquid chromatography with fluorescence detection (HPLC-FD, at the Institute for Marine Biosciences, National Research Council Canada, Halifax, Nova Scotia), was 20 to 25 pgSTXeq $cell^{-1}$. Only exponentially growing cultures were used in experiments. Toxicity of natural *Alexandrium* spp., measured by HPLC-FD from field samples of phytoplankton, was estimated at slightly lower levels of 10 to 15 pgSTXeq $cell^{-1}$ (R. G. Campbell et al. unpubl. data). Toxin profiles (% molar composition) revealed relatively more saxitoxin and less C-toxin in natural samples than in cultures, while other toxin profile differences were negligible.

Water samples were maintained at the temperature of the Damariscotta River estuary (9 to 11°C during the study period) until experimental set-up. Replicate initial containers were preserved at the start of an experiment. One liter, 500 ml, or 280 ml experimental containers were used, depending on prey concentrations and the number of grazers present. Triplicate experimental and control containers were prepared, and sufficient grazers were added to experimental containers to remove approximately 30% of the available prey, based on estimates of potential grazing rates and phytoplankton density (e.g., 30 to 40 *Acartia hudsonica* adult females l^{-1}, 5 to 8 *Calanus finmarchicus* C4 l^{-1}). Zooplankton were sorted directly from storage in natural seawater into experimental containers. Containers were placed on a grazing wheel rotating at 1 rpm, immersed in flowing seawater to maintain temperature (9 to 11°C). The duration of experiments was between 14 and 18 h.

At the end of an experiment, animals were removed from experimental jars. Zooplankton condition was excellent, with no evidence of impairment, and mortality was very rare. Initial, control, and experimental suspensions were preserved by the following method: 30 or 50 ml subsamples were preserved with 1% buffered formaldehyde, and larger subsamples of either 250 ml (from 500 ml and 280 ml bottles) or 500 ml (from 1 l bottles) were concentrated 5-fold by reverse filtration through a 10 µm mesh and preserved with 1% buffered formaldehyde.

Sample processing. Since *Alexandrium* spp. cell density was typically low, concentration techniques were used to allow counting of sufficient cells for feeding rate determinations. For *Alexandrium* spp. and other less abundant dinoflagellates and protozoa, 25 to 50 ml of 5· concentrated samples were placed in settling chambers and allowed to settle for 24 h. Samples prepared this way were then examined with epifluorescence and phase contrast microscopy. Depending on cell abundance and size, dominant diatoms were counted using either ambient or concentrated preserved solutions in a Sedgwick-Rafter chamber or a Palmer-Maloney chamber. Microflagellates (<10 µm) did not contribute significantly to the available food complex and therefore were not considered. All counts were converted to cells ml^{-1}, and algal growth and zooplankton clearance and ingestion rates were calculated with the equations of Frost (1972). Carbon content of microplankton food items in the samples was estimated from cell measurements with modified Strathmann equations for diatoms and dinoflagellates (Smayda 1978) and the carbon:volume ratios of Putt & Stoecker (1989) for ciliates.

Data analyses. Ambient diatom cells were usually 1 or more orders of magnitude more abundant than *Alexandrium* spp. cells. Therefore, for each experiment, comparisons of zooplankton clearance rates are more appropriate than ingestion rates. For each zooplankton species in each experiment, clearance rates for the major identifiable prey cell types were compared using 2-way ANOVA, and significant differences were clarified with Tukey post-hoc tests, using the SAS program (SAS Institute Inc, Cary, NC, USA). In addition, for each species of grazer, clearance rates among experiments were compared with unbalanced factorial ANOVA (global general linear model) using SAS.

Another measure of selective grazing is comparison of electivity indices (e.g., Ivlev 1961). In a review of electivity indices, Lechowicz (1982) recommended the selection coefficient W_i and electivity index E_i* of Vanderploeg & Scavia (1979a,b) as the most useful, especially in cases where food types are not equally abundant in the food complex. Since *Alexandrium* spp. usually constituted < 5% of the available food in terms of carbon (Tables 1 & 2), W_i and E_i* of Vanderploeg & Scavia (1979a,b) were the most appropriate selectivity measures for the present study. The selection coefficients W_i for each major food type i in experiments were calculated from clearance (filtration) rates by

$$W_i = F_i/\bullet F_i$$

where F_i is the clearance rate of food type i, and $\bullet F_i$ is the sum of clearance rates on all food types. The electivity index E_i* for each food type was then calculated by

$$E_i^* = [W_i - (1/n)]/[W_i + (1/n)]$$

where n is the total number of food types in the food complex. This value can theoretically vary between –1 and 1, where 0 signifies no electivity (no selective grazing), negative numbers correspond to negative selection (avoidance), and positive numbers correspond to selection for species in the food complex.

RESULTS

Selective feeding in the presence of *Alexandrium* spp. cells was not consistent among experiments, and depended on the species of zooplankton grazer and co-occurring microplankton prey. Complete results of feeding experiments with *Acartia hudsonica* are shown in Table 3; as a visual aid, representative results from early, mid- and late bloom periods of 1998 and 1999 are depicted in Fig. 1. No clear pattern of either preference for or rejection of *Alexandrium* spp. is evident. Ciliates were often cleared at higher rates than other prey, and certain dinoflagellates (*Ceratium* spp., *Dinophysis* spp.) were frequently avoided, but *Alexandrium* spp. cells were in almost every case cleared at rates equivalent to those of ambient non-toxic phytoplankton (Fig. 1, Table 3). The significance of any differences in clearance rates on algal food species within each experiment (as determined by ANOVA/Tukey post-hoc tests) is listed in Table 3. Global unbalanced ANOVA of clearance rates did not reveal any significant differences among microplankton species in the *A. hudsonica* diet. E_i* (Table 3) were used for comparisons, and the results agreed with clearance rate comparisons, showing no consistent trend of positive or negative selective feeding on *Alexandrium* spp. cells. W_i is amenable to parametric inter-experiment comparisons, while E_i* is not (Lechowicz 1982). ANOVA/Tukey tests of W_i) suggested that ciliates (*Laboea* sp. and aloricate species) were selectively ingested ($p = 0.028$).

During the spring of 1998 and of 1999, the species dominating the microplankton flora changed (Table 1, Table 2). In the early spring, small diatoms such as *Skeletonema costatum* chains (in 1998) and *Chaetoceros socialis* colonies (in 1999) dominated both cell abundance and carbon concentration in the available food complex at all stations, while *Alexandrium* spp. and other dinoflagellates were minor constituents. As the spring bloom of diatoms declined, dinoflagellates (including *Alexandrium* spp.) and ciliates contributed substantially to the total available carbon as determined by cell counts, particularly offshore (Table 2). This was primarily a result of the decline of diatoms, rather than a large increase in dinoflagellate concentrations. Regardless of changes in the food environment, *Acartia hudsonica* cleared *Alexandrium* spp. cells at rates similar to those on other phytoplankton species throughout the study period.

Nauplii of the barnacle *Semibalanus balanoides* consistently preferred abundant diatoms to dinoflagellates. Complete experimental results are shown in Table 4 and representative results in Fig. 2. ANOVA for individual experiments and global ANOVA of clearance rates and selectivity coefficients all indicated significant selective feeding on diatoms such as *Chaetoceros* spp. and *Eucampia* sp. ($p < 0.001$). Electivity indices suggested that *Alexandrium* spp., other dinoflagellates, and ciliates were avoided as a group, since selection among dinoflagellates and ciliates was not common (Table 4). The abundance of barnacle nauplii declined rapidly in mid-May of both years, preceding the sharp decline in diatom abundance, so no information is available on naupliar feeding rates and selectivity in plankton assemblages dominated by dinoflagellates.

Calanus finmarchicus copepodites preferred diatoms when they were abundant in the food complex

Table 1. Composition of the natural microplankton prey field at the Cundy's Harbor (inshore) station for 1998 and 1999. First column shows plankton species, and subsequent columns show experimental dates, with cells ml^{-1} above and µg carbon l^{-1} below for each species. Abundance of dinoflagellates was generally low, but became relatively more important as diatoms declined in June of each year

	April 28, 1998	May 5, 1998	May 12, 1998	May 19, 1998	May 25, 1998	June 9, 1998	April 27, 1999	May 4, 1999	May 11, 1999	May 18, 1999	May 25, 1999	June 1, 1999	June 8, 1999	June 14, 1999
Skeletonema costatum														
Cells ml^{-1}	5191.0	9409.0	8923.0	5391.0	20.0	61.0	151.0	20.0	37.0	25.0	14.0	6.0	4.0	5.0
µgC l^{-1}	259.6	470.5	446.2	269.6	1.0	3.1	7.6	1.0	1.9	1.3	0.7	0.3	0.2	0.3
Thalassiosira spp.														
Cells ml^{-1}	86.0	3.0	3.0	4.0	9.0	9.0	173.0	4.0	6.0	2.0	1.0	–	–	–
µgC l^{-1}	30.1	1.1	1.1	1.4	3.2	3.2	60.6	1.4	2.1	0.7	0.4	–	–	–
Chaetoceros socialis														
Cells ml^{-1}	72.0	–	–	5.0	48.0	667.0	367.0	468.0	2886.0	5521.0	1248.0	4400.0	2211.0	182.0
µgC l^{-1}	1.4	–	–	0.1	1.0	13.3	7.3	9.4	57.7	110.4	25.0	88.0	44.2	3.6
Chaetoceros spp.														
Cells ml^{-1}	31.0	–	–	17.0	11.0	139.0	76.0	40.0	54.0	63.0	17.0	16.0	3.0	2.0
µgC l^{-1}	9.6	–	–	5.3	3.4	43.1	23.6	12.4	16.7	19.5	5.3	5.0	0.9	0.6
Eucampia zodiacus														
Cells ml^{-1}	–	–	–	–	–	–	17.0	102.0	19.0	4.0	–	–	–	–
µgC l^{-1}	–	–	–	–	–	–	21.3	127.5	23.8	5.0	–	–	–	–
Detonula confervacea														
Cells ml^{-1}	–	–	–	–	–	–	–	–	–	–	13.0	39.0	43.0	61.0
µgC l^{-1}	–	–	–	–	–	–	–	–	–	–	3.5	10.5	11.6	16.5
Alexandrium spp.														
Cells ml^{-1}	0.9	1.6	0.8	2.5	1.7	1.0	0.8	1.1	1.0	1.3	1.3	1.0	0.9	0.8
µgC l^{-1}	1.8	3.4	1.7	5.2	3.5	2.1	1.7	2.3	2.1	2.7	2.7	2.1	1.9	1.8
Scrippsiella trochoidea														
Cells ml^{-1}	–	–	0.8	1.6	0.3	0.1	–	0.5	0.4	0.5	2.8	–	–	–
µgC l^{-1}	–	–	1.0	2.0	0.4	0.1	–	0.6	0.5	0.6	3.5	–	–	–
Heterocapsa triquetra														
Cells ml^{-1}	–	–	1.1	0.9	–	–	–	0.2	–	–	1.2	–	–	–
µgC l^{-1}	–	–	0.4	0.4	–	–	–	0.1	–	–	0.5	–	–	–
Prorocentrum micans														
Cells ml^{-1}	–	–	–	–	–	–	–	–	–	–	–	–	0.1	0.1
µgC l^{-1}	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.2
Ceratium spp.														
Cells ml^{-1}	–	–	–	–	–	–	–	0.1	–	0.1	0.1	–	–	0.1
µgC l^{-1}	–	–	–	–	–	–	–	0.4	–	0.4	0.4	–	–	0.4
Dinophysis spp.														
Cells ml^{-1}													0.1	0.1
µgC l^{-1}													0.2	0.2
Helicostomella spp.														
Cells ml^{-1}	–	–	0.1	3.3	–	0.1	–	–	0.1	0.2	0.4	0.6	–	–
µgC l^{-1}	–	–	0.8	26.4	–	1.0	–	–	0.8	1.6	3.2	4.8	–	–
Laboea sp.														
Cells ml^{-1}	–	–	0.1	0.1	–	–	–	0.1	0.1	0.2	–	–	–	–
µgC l^{-1}	–	–	0.8	0.4	–	–	–	0.8	0.8	1.6	–	–	–	–
Aloricate ciliates														
Cells ml^{-1}	–	–	0.1	0.3	–	0.2	–	0.1	0.1	0.6	0.3	–	0.1	0.1
µgC l^{-1}	–	–	0.5	3.0	–	2.0	–	1.0	1.0	6.0	3.0	–	1.4	0.7

Table 2. Composition of the natural microplankton prey field at the offshore station for 1998 and 1999. See Table 1 for abbreviations. In 1999, diatoms virtually disappeared from the upper water column, resulting in low food levels dominated by dinoflagellates

	May 25, 1998	June 2, 1998	April 27, 1999	May 4, 1999	May 11, 1999	May 18, 1999	June 1, 1999	June 8, 1999	June 14, 1999
Skeletonema costatum									
Cells ml^{-1}	168.0	–	3.6	19.0	42.0	52.0	–	–	–
µgC l^{-1}	8.4	–	0.2	1.0	2.1	2.6	–	–	–
Thalassiosira spp.									
Cells ml^{-1}	35.0	104.0	15.0	13.0	11.0	5.3	–	–	–
µgC l^{-1}	12.3	36.4	5.3	4.6	3.9	1.9	–	–	–
Chaetoceros socialis									
Cells ml^{-1}	509.0	548.0	1652.0	1134.0	2335.0	2059.0	801.0	–	–
µgC l^{-1}	10.2	11.0	33.0	22.7	46.7	41.2	16.0	–	–
Chaetoceros spp.									
Cells ml^{-1}	86.0	–	115.0	123.0	104.0	50.0	2.0	–	–
µgC l^{-1}	26.7	–	35.7	38.1	32.2	15.5	0.6	–	–
Eucampia zodiacus									
Cells ml^{-1}	–	–	114.0	212.0	49.0	3.0	–	–	–
µgC l^{-1}	–	–	142.5	265.0	61.3	3.8	–	–	–
Alexandrium spp.									
Cells ml^{-1}	1.2	0.5	0.8	0.5	1.2	1.5	0.9	0.9	0.9
µgC l^{-1}	2.4	1.1	1.7	1.1	2.5	3.2	1.8	1.8	1.9
Scrippsiella trochoidea									
Cells ml^{-1}	0.3	0.6	–	0.1	0.6	1.0	0.1	–	–
µgC l^{-1}	0.4	0.7	–	0.1	0.8	1.3	0.2	–	–
Prorocentrum micans									
Cells ml^{-1}	–	–	–	–	–	–	0.3	0.1	0.1
µgC l^{-1}	–	–	–	–	–	–	0.5	0.1	0.1
Ceratium spp.									
Cells ml^{-1}	–	–	–	–	0.1	0.2	0.3	1.5	0.7
µgC l^{-1}	–	–	–	–	0.4	0.8	1.1	5.9	2.6
Dinophysis spp.									
Cells ml^{-1}					0.6	–	–	0.0	0.0
µgC l^{-1}					0.8	–	–	0.0	0.1
Laboea sp.									
Cells ml^{-1}	–	–	2.0	0.1	0.1	0.2	–	–	–
µgC l^{-1}	–	–	28.0	1.4	1.4	2.8	–	–	–
Aloricate ciliates									
Cells ml^{-1}	–	–	3.5	0.1	0.1	1.0	0.4	0.1	0.0
µgC l^{-1}	–	–	35.0	1.0	1.0	10.0	4.2	0.8	0.4

(complete results in Table 4, representative results in Fig. 3). In particular, small chain-forming and colonial diatoms (e.g., *Chaetoceros socialis*) were selectively ingested when present (Table 4). Electivity indices for *Alexandrium* spp. and most dinoflagellates and ciliates were generally negative or non-selective until June of both years, after diatoms had declined. At that point, with the absence of other prey, microplankton that had been generally avoided (dinoflagellates and ciliates) constituted the bulk of available food resources. The much lower abundance of available prey (Table 2) suggests probable food limitation at this time. *Alexandrium* spp. cells were not selectively avoided compared with other microplankton after the decline of the diatoms (Table 4). *Ceratium* spp. dinoflagellates were always avoided, probably owing to their large size and intractable shape. Global ANOVA of clearance rates from all experiments with *C. finmarchicus* indicated significant overall selective feeding on *Chaetoceros* spp. diatoms ($p < 0.001$). Global ANOVA of selectivity coefficients did not reveal significant differences ($p = 0.08$). *Alexandrium* spp. was not generally avoided relative to other dinoflagellates, which were either avoided or ingested as a group.

DISCUSSION

Selective feeding on various microplankton prey was apparent in most experiments (Tables 3 & 4). The zooplankton species examined in this study displayed varying degrees of avoidance of *Alexandrium* spp. and other dinoflagellates. *Acartia hudsonica* did not generally avoid *Alexandrium* spp., and *Calanus finmarchicus*

Table 3. Clearance rates, electivity indices, and ANOVA results for adult female *Acartia hudsonica* experiments of 1998 and 1999. Microplankton food items are listed in the first column, and subsequent columns are individual experiments, with dates at the head of columns, showing the mean clearance rate ± SD (upper) and electivity index E_i (lower) for each prey item. Clearance rates on a prey item that are significantly different ($p < 0.05$) from rates on other prey are indicated in **bold**, and small arrows indicate whether the prey item was cleared at rates significantly higher (↑) or lower (↓) than those of other prey types (e.g., May 11, 1999, *Eucampia zodiacus* was cleared at a significantly lower rate than most species, while *Laboea* sp. and aloricate ciliates were cleared at significantly higher rates). Species within each of the genera *Thalassiosira*, *Chaetoceros*, *Ceratium*, and *Dinophysis* were combined for simplification, as they were similar in size and shape (excepting *C. socialis*)

Acartia hudsonica	April 28, 1998	May 12, 1998	May 19, 1998	May 25, 1998	June 9, 1998	April 27, 1999	May 4, 1999	May 11, 1999	May 18, 1999	May 25, 1999	June 1, 1999	June 8, 1999	June 14, 1999
Skeletonema costatum	0.60 ± 0.17 E_i = 0.014	0.67 ± 0.12 E_i = –0.429	0.85 ± 0.13 E_i = –0.107	0.74 ± 0.94 E_i = –0.468	2.44 ± 0.06 E_i = 0.081	0.62 ± 0.01 E_i = 0.118	0.77 ± 0.15 E_i = 0.189	0.87 ± 0.27 E_i = –0.107	0.73 ± 0.09 E_i = –0.160	1.83 ± 0.27 E_i = 0.132	**1.76 ± 0.47↑** **E_i = 0.419**	0.75 ± 0.66 E_i = 0.156	0.38 ± 0.65 E_i = –0.507
Thalassiosira spp.	0.77 ± 0.24 E_i = 0.140	0.27 ± 0.02 E_i = –0.852	1.12 ± 0.35 E_i = 0.033	**2.81 ± 0.93↑** **E_i = 0.158**	1.98 ± 0.60 E_i = –0.024	0.47 ± 0.06 E_i = –0.024	0.69 ± 0.88 E_i = 0.134	1.18 ± 0.19 E_i = 0.046	0.80 ± 0.69 E_i = –0.115	2.31 ± 1.10 E_i = 0.244	–	–	–
Chaetoceros socialis	0.78 ± 0.67 E_i = 0.147	–	**2.22 ± 1.13↑** **E_i = 0.359**	2.29 ± 1.23 E_i = 0.057	1.52 ± 0.44 E_i = –0.154	0.50 ± 0.27 E_i = 0.008	0.01 ± 0.01 E_i = –0.996	0.56 ± 0.34 E_i = –0.317	1.00 ± 0.29 E_i = –0.001	2.23 ± 1.12 E_i = 0.227	0.34 ± 0.59 E_i = –0.359	0.80 ± 0.35 E_i = 0.184	**2.49 ± 0.48↑** **E_i = 0.366**
Chaetoceros spp.	0.53 ± 0.66 E_i = –0.040	–	1.05 ± 0.29 E_i = –0.001	**3.64 ± 0.04↑** **E_i = 0.281**	1.46 ± 1.48 E_i = –0.176	0.93 ± 0.43 E_i = 0.311	0.16 ± 0.05 E_i = –0.525	0.78 ± 0.24 E_i = –0.157	0.67 ± 0.07 E_i = –0.202	**2.69 ± 0.88↑** **E_i = 0.314**	0.28 ± 0.35 E_i = –0.439	–	0.98 ± 0.99 E_i = –0.079
Eucampia zodiacus	–	–	–	–	–	**0.05 ± 0.08↓** **E_i = –0.819**	0.20 ± 0.19 E_i = –0.454	**0.01 ± 0.01↓** **E_i = –0.994**	0.32 ± 0.28 E_i = –0.521	–	–	–	–
Detonula confervacea	–	–	–	–	–	–	–	–	–	0.85 ± 0.33 E_i = –0.248	0.36 ± 0.21 E_i = –0.339	0.28 ± 0.26 E_i = –0.361	0.51 ± 0.07 E_i = –0.390
Alexandrium spp.	0.23 ± 0.07 E_i = –0.432	0.81 ± 0.14 E_i = –0.239	**1.41 ± 0.07↑** **E_i = 0.146**	1.15 ± 0.33 E_i = –0.282	2.72 ± 0.32 E_i = 0.134	0.37 ± 0.21 E_i = –0.136	0.04 ± 0.01 E_i = –0.870	0.87 ± 0.27 E_i = –0.106	0.71 ± 0.12 E_i = –0.169	1.49 ± 0.16 E_i = 0.029	0.93 ± 0.33 E_i = 0.129	0.81 ± 0.23 E_i = 0.192	1.46 ± 0.16 E_i = 0.116
Scrippsiella trochoidea	–	0.57 ± 0.18 E_i = –0.231	0.97 ± 0.02 E_i = –0.041	1.64 ± 0.18 E_i = –0.111	1.97 ± 0.42 E_i = –0.027	–	0.12 ± 0.21 E_i = –0.631	0.91 ± 0.48 E_i = –0.082	0.38 ± 0.20 E_i = –0.454	1.15 ± 0.12 E_i = –0.099	–	–	–
Heterocapsa triquetra	–	**2.21 ± 0.23↑** **E_i = –0.112**	**0.50 ± 0.23↓** **E_i = –0.351**	–	–	–	0.76 ± 0.87 E_i = 0.187	–	–	**0.22 ± 0.13↓** **E_i = –0.724**	–	–	–
Prorocentrum micans	–	–	–	–	–	–	–	–	–	–	–	0.45 ± 0.51 E_i = –0.100	0.20 ± 0.27 E_i = –0.701
Ceratium spp.	–	–	–	–	–	–	0.42 ± 0.36 E_i = –0.114	–	0.01 ± 0.01 E_i = –0.996	**0.19 ± 0.25↓** **E_i = –0.932**	–	–	0.15 ± 0.22 E_i = –0.768
Dinophysis spp.	–	–	–	–	–	–	0.03 ± 0.05 E_i = –0.892	–	–	–	–	0.01 ± 0.01 E_i = –0.986	0.22 ± 0.38 E_i = –0.680
Helicostomella spp.	–	–	**0.50 ± 0.07↓** **E_i = –0.355**	–	2.45 ± 0.40 E_i = 0.082	–	–	1.50 ± 0.57 E_i = 0.165	0.66 ± 0.24 E_i = –0.203	1.34 ± 0.33 E_i = 0.024	0.79 ± 0.83 E_i = 0.049	–	–
Laboea sp.	–	**2.61 ± 1.04↑** **E_i = 0.566**	0.83 ± 0.33 E_i = –0.117	–	–	–	**2.18 ± 1.29↑** **E_i = 0.612**	**2.56 ± 0.62↑** **E_i = 0.410**	**3.52 ± 0.49↑** **E_i = 0.557**	2.28 ± 0.14 E_i = 0.238	–	–	–
Aloricate ciliates	–	–	–	–	–	–	–	**2.47 ± 0.24↑** **E_i = 0.394**	**1.72 ± 0.29↑** **E_i = 0.263**	1.39 ± 0.82 E_i = –0.005	–	0.95 ± 0.38 E_i = 0.269	0.97 ± 0.57 E_i = –0.086

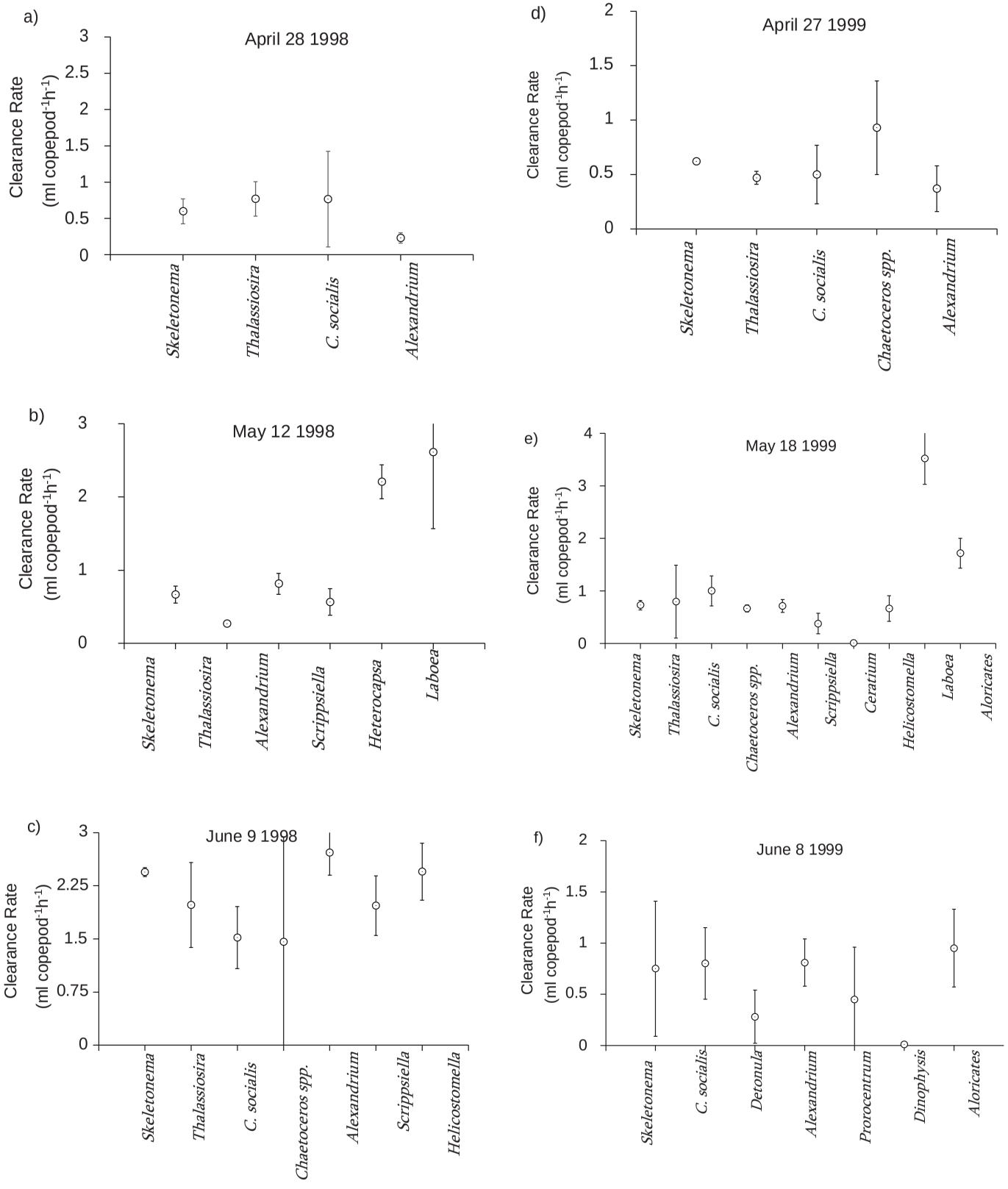

Fig. 1. Clearance rates (means ± SD) of *Acartia hudsonica* feeding on various microplankton, from early, mid-, and late spring experiments of (a,b,c) 1998, and (d,e,f) 1999. *Alexandrium* spp. cells were cleared at rates similar to those of other prey types. See Table 3 for details of clearance rates and significant differences as determined by ANOVA

Table 4. Clearance rates, electivity indices, and ANOVA results for experiments of 1998 and 1999 with *Semibalanus balanoides* nauplii and *Calanus finmarchicus* copepodites (stage listed in first row). See Table 3 for abbreviations

	Semibalanus balanoides					*Calanus finmarchicus*							
	May 5, 1998	May 19, 1998	April 27, 1999	May 4, 1999	May 11, 1999	May 25, 1998 C5	June 2, 1998 C5	May 11, 1999 C3	May 18, 1999 C3	May 18, 1999 C4	June 1, 1999 C4	June 8, 1999 C4	June 14, 1999 C4
Skeletonema costatum	**0.31 ± 0.04** E_i **= 0.085**	0.23 ± 0.02 E_i = –0.047	0.18 ± 0.07 E_i = –0.632	0.39 ± 0.01 E_i = –0.185	0.34 ± 0.04 E_i = –0.400	**11.62 ± 4.97** E_i **= 0.217**	–	5.41 ± 0.33 E_i = 0.192	2.01 ± 0.20 E_i = –0.275	**4.82 ± 0.46** E_i **= –0.009**	–	–	–
Thalassiosira spp.	0.13 ± 0.01 E_i = –0.333	0.18 ± 0.06 E_i = –0.159	0.61 ± 0.18 E_i = –0.132	0.57 ± 0.14 E_i = 0.003	0.70 ± 0.55 E_i = –0.064	4.34 ± 0.53 E_i = –0.320	1.59 ± 1.49 E_i = –0.154	3.76 ± 0.93 E_i = 0.099	3.31 ± 1.73 E_i = –0.032	**10.24 ± 9.52** E_i **= 0.352**	–	–	–
Chaetoceros socialis	–	**0.84 ± 0.30** E_i **= 0.539**	**1.27 ± 0.33** E_i **= 0.234**	1.33 ± 0.36 E_i = 0.406	**2.90 ± 0.50** E_i **= 0.568**	**9.27 ± 1.71** E_i **= 0.107**	–	4.95 ± 0.24 E_i = 0.233	**8.85 ± 2.79** E_i **= 0.430**	**15.59 ± 4.33** E_i **= 0.521**	**16.37 ± 5.00** E_i ***i* = 0.268**	–	–
Chaetoceros spp.	–	**0.36 ± 0.07** E_i **= 0.179**	**1.45 ± 0.11** E_i **= 0.293**	**2.17 ± 0.85** E_i **= 0.589**	**3.28 ± 0.21** E_i **= 0.608**	**8.98 ± 1.97** E_i **= 0.091**	–	**8.44 ± 1.33** E_i **= 0.466**	4.47 ± 1.24 E_i = 0.117	**9.99 ± 1.53** E_i **= 0.341**	**17.55 ± 7.19** E_i **= 0.300**	–	–
Eucampia zodiacus	–	–	**1.54 ± 0.22** E_i **= 0.321**	**2.82 ± 0.41** E_i **= 0.668**	**2.36 ± 0.17** E_i **= 0.493**	–	–	3.67 ± 0.86 E_i = 0.088	5.66 ± 5.08 E_i = 0.232	0.927 ± 1.61 E_i = –0.682	–	–	–
Dinobryon sp.	–	–	–	0.09 ± 0.07 E_i = –0.717	0.43 ± 0.72 E_i = –0.302	–	–	–	–	–	**11.01 ± 3.73** E_i **= 0.076**	–	–
Alexandrium spp.	0.18 ± 0.05 E_i = –0.206	0.21 ± 0.06 E_i = –0.091	0.35 ± 0.10 E_i = –0.386	0.09 ± 0.03 E_i = –0.734	0.31 ± 0.05 E_i = –0.445	4.42 ± 0.79 E_i = –0.257	2.57 ± 0.01 E_i = 0.085	**1.28 ± 0.34** E_i **= –0.413**	3.53 ± 0.18 E_i = 0.000	2.95 ± 0.74 E_i = –0.250	5.78 ± 1.03 E_i = –0.241	5.43 ± 0.53 E_i = 0.333	7.05 ± 1.44 E_i = 0.149
Scrippsiella trochoidea	–	0.05 ± 0.03 E_i = –0.678	–	0.07 ± 0.07 4 E_i = –0.78	0.25 ± 0.08 E_i = –0.529	6.72 ± 1.70 E_i = –0.053	2.35 ± 0.69 E_i = 0.040	**1.16 ± 0.39** E_i **= –0.451**	2.84 ± 0.36 E_i = –0.108	1.68 ± 0.68 E_i = –0.489	2.34 ± 2.85 E_i = –0.603	–	–
Heterocapsa triquetra	**0.44 ± 0.37** E_i **= 0.247**	0.12 ± 0.02 E_i = –0.340	0.51 ± 0.28 E_i = –0.217	0.03 ± 0.04 E_i = –0.901	0.27 ± 0.26 E_i = –0.493	–	–	4.95 ± 1.20 E_i = 0.233	2.61 ± 0.29 E_i = –0.149	3.17 ± 1.82 E_i = –0.216	–	–	–
Prorocentrum micans	–	–	–	–	–	–	–	–	–	–	6.62 ± 2.44 E_i = –0.176	3.12 ± 3.45 E_i = 0.069	8.42 ± 7.29 E_i = 0.235
Ceratium spp.	–	–	–	0.88 ± 0.14 E_i = –0.054	0.21 ± 0.25 E_i = –0.579	–	–	**1.05 ± 0.96** E_i **= –0.491**	1.79 ± 0.74 E_i = –0.327	0.71 ± 1.23 E_i = –0.747	0.75 ± 0.66 E_i = –0.854	0.25 ± 0.42 E_i = –0.835	1.10 ± 0.70 E_i = –0.651
Dinophysis spp.	–	–	–	0.08 ± 0.11 E_i = –0.845	0.33 ± 0.17 E_i = –0.422	–	–	**1.56 ± 0.58** E_i **= –0.328**	–	–	–	3.56 ± 3.04 E_i = 0.134	4.05 ± 1.56 E_i = –0.127
Laboea sp.	–	0.02 ± 0.03 E_i = –0.860	–	0.05 ± 0.09 E_i = –0.824	0.19 ± 0.21 E_i = –0.619	–	–	**0.47 ± 0.81** E_i **= –0.737**	4.91 ± 1.67 E_i = 0.164	3.16 ± 3.86 E_i = –0.218	–	–	–
Aloricate ciliates	–	–	–	0.05 ± 0.09 E_i = –0.826	0.15 ± 0.14 E_i = –0.678	–	–	2.84 ± 1.02 E_i = –0.040	1.55 ± 0.11 E_i = –0.390	0.11 ± 0.19 E_i = –0.957	3.90 ± 4.56 E_i = –0.416	1.24 ± 1.72 E_i = –0.375	5.48 ± 0.12 E_i = 0.024

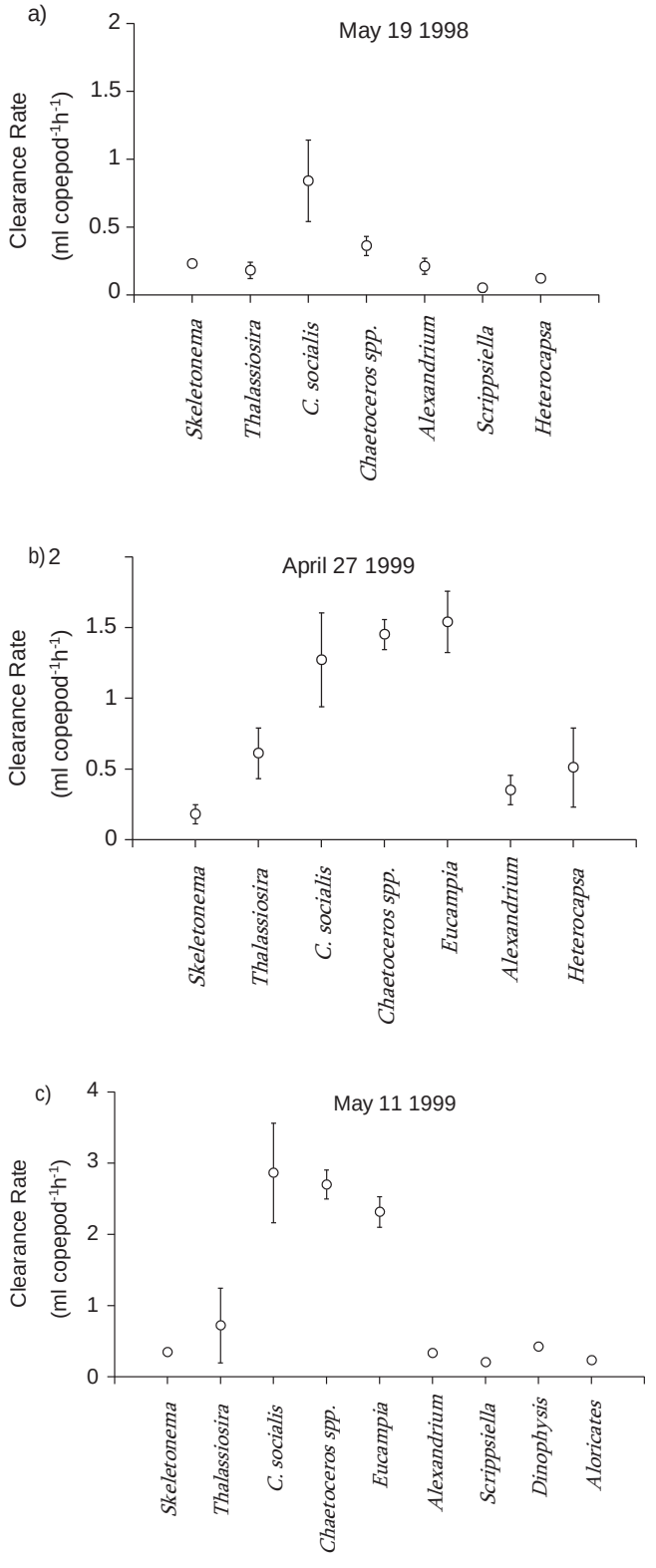

Fig. 2. Clearance rates (means ± SD) of nauplii of the barnacle *Semibalanus balanoides*, from (a) 1998 and (b,c) 1999. Diatoms were selectively ingested, but *Alexandrium* spp. cells were not discriminated from the remaining prey field. See Table 4 for significant differences

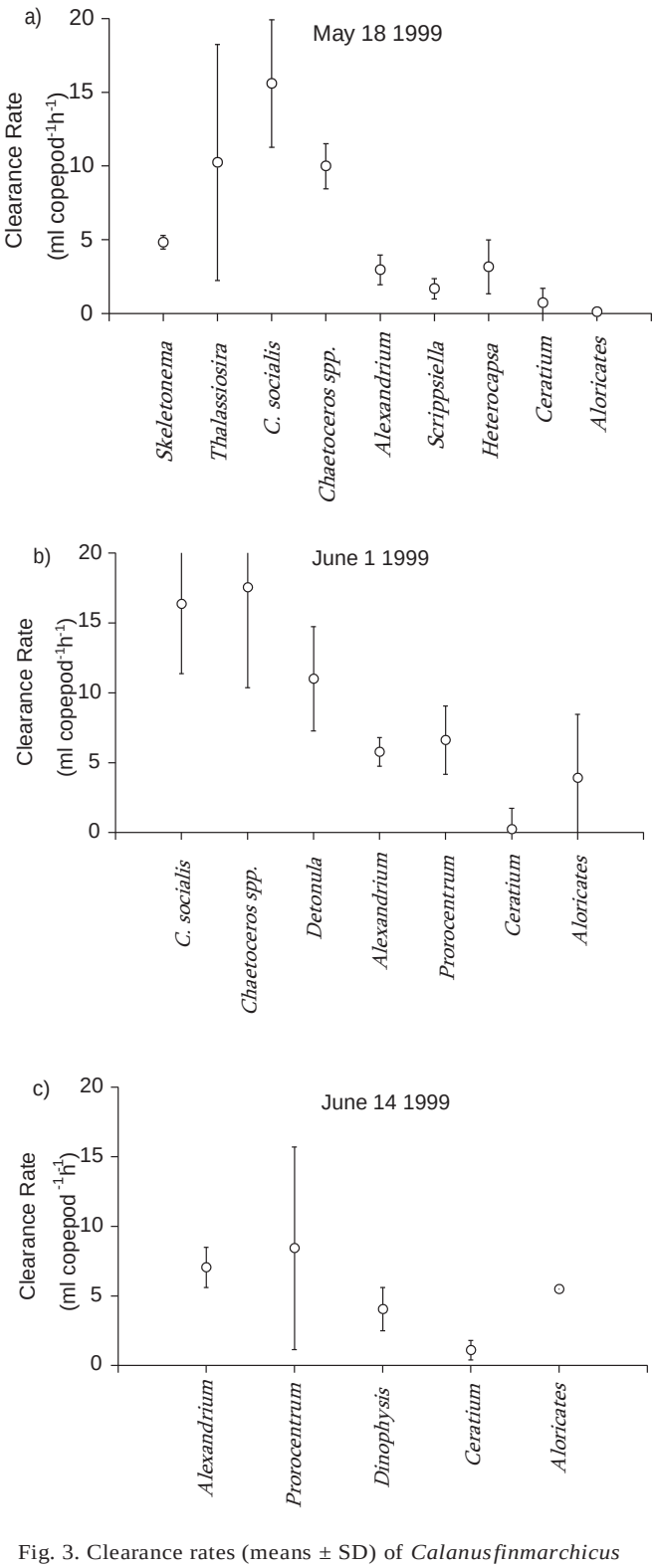

Fig. 3. Clearance rates (means ± SD) of *Calanus finmarchicus* from 1999. (a,b) Early to mid-spring; *Chaetoceros* spp. were cleared at higher rates than other microplankton. (c) After diatoms declined, *Alexandrium* spp. cells were cleared at rates similar to those of most other microplankton, while *Ceratium* spp. dinoflagellates were avoided

and *Semibalanus balanoides* nauplii often avoided dinoflagellates but did not clearly discriminate between *Alexandrium* spp. and other dinoflagellates. These results contrast with laboratory studies that clearly demonstrate selective feeding by copepods, based on PSP toxin content (Teegarden 1999).

Acartia hudsonica did not display consistent patterns of selective feeding but frequently cleared ciliates at higher rates than other microplankton. On only 1 occasion (June 14, 1999) did *A. hudsonica* selectively feed on the most abundant particle or biomass dominant particle. In general no size-selective feeding behavior was identified for *A. hudsonica*. Preference for ciliate prey by the Acartidae has been noted in the past (Tiselius 1989, Wiadnyana & Rassoulzadegan 1989), and may be due to mechanoreception of relatively large swimming prey (Jonsson & Tiselius 1990). Maximum ingestion of ciliate prey corresponded to <10% of total carbon intake (May 18, 1999) and was usually <3%. The low abundance of ciliates present in the natural water used in these experiments argues against consideration of ciliates as a quantitatively important food source during the spring bloom (this conclusion was also reached by Tiselius 1989 and Irigoien et al. 1998). Given the omnivorous nature of Acartidae, non-selective feeding on most prey is not surprising, but the ready inclusion of toxic *Alexandrium* spp. cells in the diet is less easily explained. The congener *Acartia tonsa* has displayed strong avoidance of toxic *Alexandrium* spp. in the laboratory and impairment when forced (by hunger) to ingest toxic *Alexandrium* spp. (Teegarden 1999).

Toxin content cell^{-1} may affect selective feeding by zooplankton on *Alexandrium* spp. (Turriff et al. 1995, Teegarden 1999). Although there were slight differences in estimated toxin content between laboratory cultures and field populations of *Alexandrium* spp. in this study, these differences were not substantial. Toxin content cell^{-1} was in all cases in the normal range for the southwestern Gulf of Maine. Furthermore, all zooplankton species tested displayed consistent responses, whether the *Alexandrium* spp. present was from natural populations, laboratory cultures, or both sources. Observed patterns of selective (or non-selective) feeding are therefore probably not attributable to any fluctuation in *Alexandrium* spp. cellular toxin content.

It has been suggested that optimal diet theory may be a useful predictor of selective feeding behavior of suspension feeding zooplankton (Lehman 1976, DeMott 1989). In theory, toxic cells should be rejected because they are inimical (DeMott 1989), especially when alternative food is abundant and lower quality food items may be discarded without restricting intake. This was not the result obtained in this study, nor in other recent studies. Laboratory experiments with various species of calanoid copepods fed 2 food types (including toxic *Alexandrium* spp.) have shown that rejection of toxic *Alexandrium* spp. cells is maximal when they are abundant and alternative food is also abundant (Turriff et al. 1995, Teegarden 1999). In a previous study (Teegarden 1999), laboratory experiments with mixtures of several dinoflagellate species suggested that toxic *Alexandrium* spp. cells were never positively selected but could be consumed at rates equal to alternative non-toxic prey. The conclusions of the latter study suggested that the degree of selection displayed in mixtures is a function of the grazer's ability to tolerate PSP toxin ingestion. Grazers such as *Acartia tonsa* displayed severe impairment when feeding on monocultures of toxic *Alexandrium* spp. and displayed strong avoidance of toxic *Alexandrium* spp. in mixtures. The copepod *Eurytemora herdmani*, however, never displayed strong impairment when feeding on toxic *Alexandrium* spp. and further removed toxic *Alexandrium* spp. cells at rates equivalent to consumption of some alternative non-toxic food types. If *Acartia hudsonica* is not impaired by moderate PSP toxin ingestion, then that species may not be constrained to selectively avoid toxic cells.

Selection may also be impractical when *Alexandrium* spp. concentrations are very low. Even at the highest natural concentration of *Alexandrium* spp. encountered by *Acartia hudsonica* (2500 cells l^{-1}, May 19, 1998), with reasonably high clearance rates (Table 3), ingestion was only ~3 cells h^{-1}. It is probable that such low rates of encounter and ingestion would not prompt selective feeding, particularly when scarce *Alexandrium* spp. cells co-occur with abundant alternative food. Natural field conditions usually contain diverse prey cell types, and relative abundance of species (both cell numbers and carbon concentrations) span orders of magnitude. Even though larger cells such as *Thalassiosira* spp. and dinoflagellates were probably recognized and 'handled', it is probable that smaller diatoms were processed simultaneously (e.g., as noted by Price & Paffenhöfer 1986). This may have contributed to a masking effect whereby several chemical cues were experienced while handling multiple particles. The difficulty of recognizing and rejecting large particles in a complex mixture of smaller diatoms may have had an effect on the ability or willingness to feed selectively. Other examples of this potential phenomenon are the works of Frost (1977) and Sykes & Huntley (1987), who have noted that indigestible plastic beads were consumed by copepods at higher rates when palatable phytoplankton were included in the food complex. The low frequency of encounter with *Alexandrium* spp. cells by zooplankton in this study may have been insufficient to trigger a selective feeding re-

sponse, i.e., to develop a chemo- or mechano-receptive 'search image' for toxic cells. It is interesting to note that, on the 1 occasion when the carbon contribution of *Alexandrium* spp. cells to the total food complex was on the same order as other prey (May 25, 1998, Table 1), clearance of other prey (*Thalassiosira* spp., *Chaetoceros* spp., Table 3) was significantly higher.

Selection of food types was more apparent in experiments with *Semibalanus balanoides* nauplii and *Calanus finmarchicus* copepodites. The number of experiments conducted with *S. balanoides* nauplii was limited because of the brief duration of their dominance in the plankton during our study period. Their peak abundance coincided with maximal abundance of small diatoms (*Skeletonema costatum* in 1998 and *Chaetoceros socialis* in 1999), and their feeding behavior showed preference for small and medium size diatoms, and avoidance of most dinoflagellates and ciliates (Table 4). Very little has been published on the feeding processes of *S. balanoides* nauplii. This is somewhat surprising, since they are regularly abundant and even dominant in the net zooplankton of northeastern USA nearshore waters during the spring diatom bloom. White (1981) showed that *S. balanoides* nauplii could feed on toxic *Alexandrium excavatum* at very high concentrations (3 to $5 \cdot 10^6$ l^{-1}), but this cultured alga was the only food offered in his experiments.

Our results agree with earlier literature that has noted a preference for diatoms over flagellates in the diet of *Semibalanus balanoides* nauplii (Moyse 1963, Moyse & Knight-Jones 1967). It has been suggested that *S. balanoides* nauplii cannot successfully develop without diatom food resources (Moyse 1963). This may be related to morphology; ultrastructural studies of feeding appendages suggest that *S. balanoides* nauplii are more efficient at feeding on colonial and chain-forming diatoms than solitary flagellates (Rainbow & Walker 1976). Regardless of mechanism, *S. balanoides* nauplii did not effectively graze on flagellates and ciliates in the present study, and displayed little or no selection among species in this group of motile prey, avoiding all more or less equally.

Much more work has been done on the diet and feeding processes of *Calanus finmarchicus*. Omnivory has been shown in numerous studies (see Harris 1996), and ciliates and dinoflagellates may be especially important in the diet of *Calanus* spp. after the decline of the spring diatom bloom (Ohman & Runge 1994). The results of our study clearly suggest that *C. finmarchicus* preferentially cleared diatoms while they were dominant, and did not clear dinoflagellates and ciliates in proportion to their abundance. Selective feeding on diatoms during the spring bloom has been shown in other recent field studies (Meyer-Harms et al. 1999) and, as in our study, ciliates have been found to be quantitatively unimportant during the bloom because of their low concentrations (Tiselius 1989, Irigoien et al. 1998). After diatoms declined, the food resources in our experiments consisted almost entirely of dinoflagellates and ciliates, on which *C. finmarchicus* fed. Clearance rates on these food items were not significantly different before and after the disappearance of the diatoms. Thus this is not a case of 'prey switching' to dinoflagellates, but merely a greatly reduced food intake by *C. finmarchicus* after the demise of the spring bloom, under probable food-limiting conditions.

It is interesting that *Alexandrium* spp. was not selectively avoided relative to other available dinoflagellates. The dinoflagellate species most likely to co-occur with *Alexandrium* spp. at this time are *Scrippsiella trochoidea* (which is frequently found with *Alexandrium* spp. in the Gulf of Maine and generally follows the same population dynamics), *Prorocentrum micans*, *Dinophysis* spp., and *Ceratium* spp. There is reason to believe that this group is a grazer-resistant assemblage. *S. trochoidea* has been reported to be poor food for *Calanus* spp. and is frequently avoided (Huntley et al. 1986, Gill & Harris 1987, Hassett & Landry 1990). *P. micans* is often considered to be a beneficial food item in copepod diets, but experiments with mixtures of dinoflagellates have suggested that *P. micans* is not preferred over other dinoflagellates (Teegarden 1999). *Dinophysis* spp. have also been reported to be poor food or largely avoided by copepod grazers (Carlsson et al. 1995). *Ceratium* spp. are large (>100 µm) and intractable dinoflagellates, and it has been suggested that the difficulty of handling and ingesting such prey affords a measure of protection from grazers (Harvey 1937, Granéli et al. 1993, Nejstgaard et al. 1994). Certainly, *Ceratium* spp. were avoided by all the grazers tested in our study.

Ecological significance

We specifically studied *Alexandrium* spp. blooms in the Casco Bay area, a region that suffers considerable economic hardship from seemingly moderate blooms (Shumway et al. 1988). *Acartia hudsonica* is usually the spring dominant zooplankton grazer in the nearshore waters of the southwestern Gulf of Maine. Natural *Alexandrium* spp. concentrations in this region are low, even at the peak of a bloom (on the order of 10^3 cells l^{-1}). If *A. hudsonica* dominates the zooplankton, because of its apparent non-selective feeding at these low *Alexandrium* spp. concentrations, removal of *Alexandrium* spp. from the water column would depend principally on grazer abundance (biomass). This general-

ization apparently would not hold true if nauplii of *Semibalanus balanoides* were dominant nearshore, as is sometimes the case; their preference for diatoms may afford *Alexandrium* spp. and other dinoflagellates some protection. Offshore waters are dominated by other zooplankton species, such as *Calanus finmarchicus* and *Pseudocalanus* spp. *Alexandrium* spp. cells were often avoided by *C. finmarchicus* relative to abundant diatoms. Despite this, while *C. finmarchicus* clearance of *Alexandrium* spp. cells was lower than that of *A. hudsonica* on a weight-specific basis, it was not negligible, and removal of *Alexandrium* spp. again would depend principally on grazer biomass.

Questions remain regarding the possibility of toxin-based grazer deterrence by *Alexandrium* spp. While this has been shown in the laboratory (Teegarden 1999), the present field study did not always show evidence of such an effect. One possible explanation for this discrepancy is that chemical deterrence is concentration dependent. This type of defense has been hypothesized by Sykes (1991), who noted that toxic dinoflagellates (*Protoceratium reticulatum*) induced grazer avoidance only when they attained sufficient density (relative to co-occurring prey), and thus the chemical defense served principally to protect a bloom that had already formed, rather than allowing a sparse 'seed' population to grow free from grazing pressure. Concentration-dependent grazer inhibition has also been shown with the tintinnid ciliate *Favella ehrenbergii* feeding on toxic *Alexandrium tamarense* (Hansen 1989). Preliminary studies indicate that varying the concentrations of *Alexandrium* spp. in food mixtures affects the strength of copepod selective feeding behavior (Teegarden unpubl. data).

The southwestern Gulf of Maine harbors low *Alexandrium* spp. cell concentrations, but populations of *Alexandrium* spp. in other regions of the northwest Atlantic frequently attain much higher densities (e.g., Bay of Fundy, Martin & White 1988, and St. Lawrence estuary, Therriault et al. 1985, Cembella et al. 1988). If selective grazing is concentration dependent, the significance of PSP toxin production for *Alexandrium* spp. grazer deterrence and thus bloom proliferation may differ in the various regions that experience blooms. In any environment during bloom initiation, when *Alexandrium* spp. concentrations are low and alternative prey are abundant, it is likely that zooplankton grazers can inhibit bloom formation if they are abundant and non-selective (e.g., *Acartia hudsonica*). Harmful blooms are more likely to form when grazers (such as *Semibalanus balanoides* nauplii) that avoid *Alexandrium* spp. are present, or when higher concentrations of *Alexandrium* spp. are attained before grazer biomass becomes sufficient to have a significant impact.

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