Vol. 225: 161–167, 2002 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published January 11

Grazing by the heterotrophic dinoflagellate *Protoperidinium steinii* on a *Ceratium* bloom

Christine D. Olseng, Lars-Johan Naustvoll, Eystein Paasche*

Section for Marine Botany, Department of Biology, University of Oslo, PO Box 1069, Blindern, 0316 Oslo, Norway

ABSTRACT: Variations in heterotrophic dinoflagellate populations at a station in the inner Oslofjord, Norway, were studied by sampling at ca 4 d intervals. Cells were concentrated from 1 l samples by filtration before being counted in an inverted microscope. Additional data include autotrophic carbon biomass estimates based on microscopy of the phytoplankton, chlorophyll *a* (chl *a*) concentrations, and hydrography. A modest (2 to 4 µg chl *a* l^{-1}) diatom bloom in September was followed by a large (up to 128 µg chl *a* l^{-1}) dinoflagellate bloom in October, dominated by *Ceratium furca*. Altogether 25 thecate heterotrophic dinoflagellate species were recorded in this study. Their total biomass at all times was <1% of that of the autotrophic phytoplankton. Coinciding with the *Ceratium* bloom, there was a marked growth in *Protoperidinium steinii*, with cell numbers reaching >2000 cells l^{-1}. *P. pyriforme*, *P. brevipes*, *P. curtipes*, and *Oblea rotunda* showed more modest increases, while no significant response was seen in any of the other 20 heterotrophic dinoflagellates. In incubated plankton samples, we recorded 81 instances of *P. steinii* feeding on *C. furca* or on other dinoflagellates. Our study confirms previous laboratory findings suggesting that *P. steinii* belongs to the limited selection of *Protoperidinium* species capable of exploiting dinoflagellate prey in the natural environment.

KEY WORDS: Oslofjord · Heterotrophic dinoflagellates · *Protoperidinium steinii* · Grazing · *Ceratium furca*

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Heterotrophic dinoflagellates are nearly always present in marine plankton, and are sometimes quantitatively important as grazers in the microplankton (20 to 200 µm) fraction (e.g. Hansen 1991, Lessard 1991, Archer et al. 1996). They possess highly specialized feeding mechanisms. Members of *Protoperidinium*, the largest heterotrophic genus within the peridinioid dinoflagellates, acquire their food by means of a pallium; a pseudopod produced by the cell and enabling it to digest plankton algae of its own size, or even considerably larger ones (review by Hansen & Calado 1999). Smaller objects, such as 'naked' nanoplankton flagellates, are generally not captured by *Protoperidinium*. While the majority of *Protoperidinium* species appear to be diatom grazers, some can utilize, and may even require, dinoflagellate prey (review by Jeong 1999). In a pioneering study, Jacobson & Anderson (1986) noted that *P. pyriforme* cells differed from those of 14 other *Protoperidinium* species by preferentially capturing autotrophic dinoflagellates rather than diatoms in their pallium. Subsequent laboratory experiments confirmed that food requirements in this genus may be quite specific. Among the relatively few *Protoperidinium* species that have been brought into culture so far, only *P.* cf. *divergens* and *P. crassipes* (Jeong & Latz 1994), and recently *P. steinii* (Naustvoll 2000), have been shown to grow better on dinoflagellate prey than on diatom prey.

More indirect evidence of specific dinoflagellate prey requirements can be obtained by studying shifts in natural populations associated with biomass fluctuations and species successions in the phytoplankton (e.g. Hansen 1991, Nakamura et al. 1995, 1996, Tise-

*Corresponding author. E-mail: e.paasche@bio.uio.no

© Inter-Research 2002 · www.int-res.com

lius & Kuylenstierna 1996, Matsuyama et al. 1999). This approach was used in a recent investigation of *Protoperidinium* species in the inner Oslofjord, based on approximate monthly sampling through 1 yr (Kjæret et al. 2000). The present study from the same area made use of much more closely repeated sampling, carried out over 2 mo in the autumn during which a modest bloom consisting mainly of the diatom *Pseudo-nitzschia pseudodelicatissima* was succeeded by a large bloom dominated by the dinoflagellate *Ceratium furca*. Our goal was to see if close sampling combined with observations of live samples could provide more conclusive evidence of predator-prey relationships involving *Protoperidinium* spp.

MATERIALS AND METHODS

The material was collected in the inner Oslofjord at or near the station Nakkholmen (59° 53′ N, 10° 41′ E) at time intervals of 2 to 7 d, from September 7 to November 1, 2000. Data on water temperature and salinity were obtained by means of a mini-STD probe. Sampling for chlorophyll *a* (chl *a*) was carried out by Niskin bottle casts from the surface to 20 m depth. The samples were filtered onto Whatman GF/C glass fiber filters (pore size ca 1 µm) and extracted with 90% acetone according to Strickland & Parsons (1972) for subsequent analysis in a Turner Designs TD-700 fluorometer. Samples for quantitative microscopy and for observations on live plankton were taken from 2 m depth, supplemented by horizontal net-hauls. Diatoms in formaldehyde-preserved samples were counted in 2 ml sedimentation chambers on an inverted microscope. Thecate autotrophic and heterotrophic dinoflagellates larger than 20 µm were counted in samples concentrated by filtration as described by Kjæret et al. (2000). Essentially, this involved draining a 1000 ml water sample through a small piece of 20 µm mesh plankton net, and resuspending the collected material in a small volume of seawater containing formaldehyde, with Calcofluor White M2R added for visualization of the dinoflagellate thecae by epifluorescence (Fritz & Triemer 1985). The suspension was then distributed into 2 ml sedimentation chambers for counting on an inverted epifluorescence microscope. Dinoflagellates smaller than 30 µm, mainly the heterotroph *Oblea rotunda* and the autotroph *Prorocentrum micans*, were probably not quantitatively retained by the 20 µm mesh. Specific carbon biomasses were computed assuming the same cell volumes as in previous investigations in the Oslofjord (see Kjæret et al. 2000), using the equation of Strathmann (1967) for diatoms and those of Menden-Deuer & Lessard (2000) for autotrophic and heterotrophic dinoflagellates. The standing stock of each species was then calculated as the product of cell density (cells l^{-1}) and cell carbon (pg C $cell^{-1}$), and the products were summed to give total carbon biomass (µg C l^{-1}) for each species or group. The biomass values do not express total autotrophic standing stock, as the microscopic counts did not include non-diatom cells smaller than 20 µm such as 'naked' flagellates and cyanobacteria.

On all sampling dates, live material was collected for monitoring of heterotrophic dinoflagellate grazing. Unconcentrated samples from 2 m depth were transferred to cell culture flasks (Costar, 73 ml capacity) which were incubated on a plankton wheel rotating at ca 2 rpm, in a temperature-controlled room at 11°C, under continuous illumination of 3 µmol photons m^{-2} s^{-1}. The samples were examined daily for up to 2 wk in a Nikon Eclipse TE300 inverted microscope. Grazing events were documented on Kodak EliteChrome 400 film by means of a Nikon Fe 10 camera, for subsequent electronic scanning.

RESULTS

Salinity at 2 m depth dropped from 23.5 early in September to ca 22 on October 13, and then quite abruptly to ca 18 during the following few days (Fig. 1). This latter event was in all likelihood caused by outflow from land following heavy rainfall on October 10, 11, and 12. Precipitation during this 3 d period corresponded to the amount normally received in the whole month of October (data from The Norwegian Meteorological Institute). Temperature at 2 m depth showed a gradual decline from ca 16.5°C at the beginning of the sampling period to ca 10°C at the end (data not shown). The chlorophyll data (Fig. 2) indicate a small bloom of 2 to 4 µg chl *a* l^{-1} in the uppermost 4 m layer from September 21 to 28. A much heavier bloom was observed in the same layer from October 16, with maximum values of 128 µg chl *a* l^{-1} at 0 m depth on October 20 and 81 µg chl *a* l^{-1} at 2 m depth on October 23. The average chlorophyll concentration in the 0 to 4 m layer increased by a factor of 26 from October 13 to October 16. This increase is much too large to be explained by local algal growth. We conclude that it was due to advection of a different water mass. Freshwater outflow occasioned by the rainfall a few days earlier was the likely reason for this, as already suggested by the salinity data.

The carbon biomass standing stocks of the most important species or groups of primary producers are shown in Table 1. Even though these data may not describe a succession in the strict sense, they indicate a development from a modest diatom bloom, from September 21 to 28, to a massive dinoflagellate bloom from

October 16 onwards. The diatom bloom was composed mainly of *Pseudo-nitzschia pseudodelicatissima*, while the dinoflagellate bloom was dominated by *Ceratium* species, *C. furca* forming 80 to 95% of *Ceratium* biomass as well as of *Ceratium* cell number at any time. The ratio of calculated autotrophic carbon biomass to chlorophyll concentration at 2 m depth during both blooms was mostly of the order of 20 to 30 g C g chl a^{-1}. This is somewhat low, particularly for dinoflagellates, as was to be expected from the non-inclusion of small autotrophic algae in our cell counts (see 'Materials and methods').

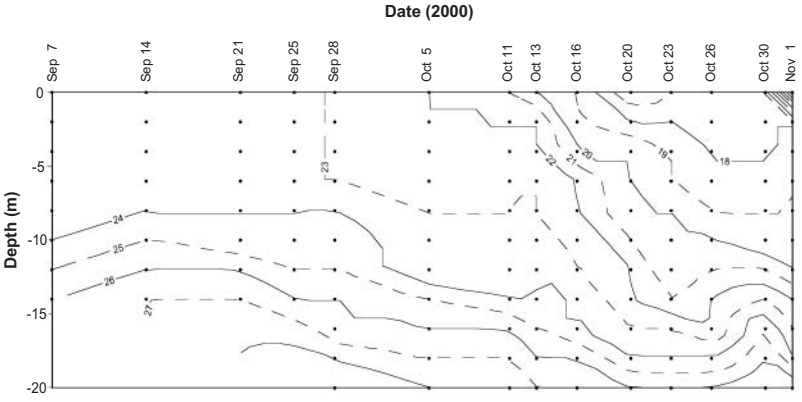

Fig. 1. Variations in salinity in the upper 20 m at the sampling station

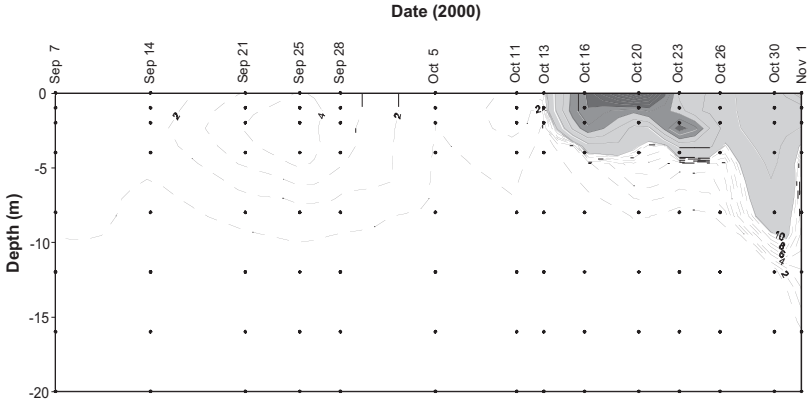

Fig. 2. Variations in chlorophyll concentration (µg chl *a* l^{-1}) in the upper 20 m at the sampling station

The total carbon biomass of thecate heterotrophic dinoflagellates (Table 2) was insignificant compared to the calculated autotrophic biomass (Table 1), amounting to, at most, 1% of the latter during either bloom period. The maximum cell counts of thecate heterotrophic dinoflagellate species during the *Pseudo-nitzschia* and *Ceratium* blooms are listed in Table 3. Throughout the study, the majority of heterotrophic dinoflagellates were present in small and randomly fluctuating numbers, typically < 50 cells l^{-1}. An exception was formed by *Protoperidinium steinii*, the cell numbers of which declined during September and then increased markedly during the *Ceratium* bloom to a maximum of > 2000 cells l^{-1} at the end of October (Fig. 3A). Increases were also seen in *P. pyriforme* (Fig. 3A), and to a lesser extent in *P. brevipes* and *P. curtipes* (Table 3); these 3 species were not recorded in September. During the *Ceratium* bloom, *P. steinii* made up 55 to 73% of thecate heterotrophic dinoflagellate cell numbers and 20 to 51% of the corresponding biomass (Table 2). Regression analysis (using square-root-transformed cell numbers for the whole sampling period) demonstrated a significant correlation between *P. steinii* and *C. furca* abundances ($r^2 = 0.60$; $p = 0.001$). The only other heterotrophic dinoflagellate responding markedly to the dinoflagellate bloom situation was *Oblea rotunda* (Table 3).

In terms of cumulate numbers throughout the sampling period, *Protoperidinium divergens* and *P. pallidum* were next in importance after *P. steinii*, *P. pyri-*

Table 1. Carbon biomass (µg C l^{-1}) of the most important categories of autotrophic microplankton algae at 2 m depth

Species or group	Sep 7	Sep 14	Sep 21	Sep 25	Sep 28	Oct 5	Oct 11	Oct 13	Oct 16	Oct 20	Oct 23	Oct 26	Oct 30	Nov 1
Ceratium furca	7.2	3.5	1.3	0.3	0.3	1.1	40.8	10.5	791.2	294.4	331.0	300.3	697.2	431.8
Ceratium spp.	1.2	0.3	0.1	0.0	0.0	0.1	3.1	0.7	105.2	76.9	12.9	21.2	65.4	74.9
Dinophysis spp.	1.3	0.5	1.1	0.6	0.7	0.1	3.9	2.7	102.8	37.6	26.1	79.2	62.0	46.8
Prorocentrum micans	6.8	1.5	3.4	0.9	0.8	0.2	0.7	0.1	14.4	7.1	2.8	6.4	12.5	4.2
Other dinoflagellates	0.6	0.1	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.1	0.0	0.3	0.2	0.1
Pseudo-nitzschia pseudodelicatissima	29.3	1.6	61.7	63.0	49.2	0.1	0.0	0.1	0.8	0.6	0.1	0.0	0.0	0.0
Other diatoms	9.6	1.1	20.8	19.6	8.1	0.7	0.0	0.1	1.7	0.5	2.8	0.9	0.0	0.0

Table 2. Cell numbers (cells l^{-1}) and carbon biomass (µg C l^{-1}) of all thecate heterotrophic dinoflagellates (THD) and of *Protoperidinium steinii* at 2 m depth

Group or species	Sep 7	Sep 14	Sep 21	Sep 25	Sep 28	Oct 5	Oct 11	Oct 13	Oct 16	Oct 20	Oct 23	Oct 26	Oct 30	Nov 1
(a) THD, cells l^{-1}	1590	258	299	152	187	24	23	78	916	2062	769	1426	3278	3158
(b) *P. steinii*, cells l^{-1}	750	127	123	41	35	1	2	6	529	1500	420	861	2091	2125
b as % of a	47	49	41	27	19	4	9	8	58	73	55	60	64	67
(c) THD, µg C l^{-1}	2.13	0.43	0.72	0.50	0.65	0.11	0.11	0.48	1.81	3.16	1.99	2.51	3.98	4.11
(d) *P. steinii*, µg C l^{-1}	0.73	0.12	0.12	0.04	0.03	0.00	0.00	0.01	0.51	1.45	0.41	0.83	2.02	2.05
d as % of c	34	29	16	8	5	1	2	1	28	46	20	33	51	50

forme, and *Oblea rotunda* among the thecate heterotrophic dinoflagellates. In Fig. 3B, the dynamics of the *P. divergens* and *P. pallidum* populations (note the 10× expansion of the ordinate scale) are shown for comparison with those of *P. steinii* and *P. pyriforme* (Fig. 3A). There was no suggestion that either *P. divergens* or *P. pallidum* reacted positively to the *Ceratium* bloom.

Pallium feeding by *Protoperidinium steinii* on dinoflagellate prey, particularly on *Ceratium furca*, was observed on a number of occasions throughout the sampling period (Fig. 4, Table 4). Besides this, *P. steinii* was seen to capture a ciliate and to practice cannibalism (Table 4). Feeding by 2 or 3 cells on one and the same food item (Fig. 4C), as well as cannibalism, became more frequent as autotrophic food became depleted during prolonged incubation. More than one cell feeding on a common prey object has previously been noted in *P.* cf. *divergens* (Jeong 1994) and in the mixotrophic *Fragilidium subglobosum* (Skovgaard 1996). Although *P. steinii* was present in substantial numbers during the diatom bloom in September, it was never seen to feed on diatoms.

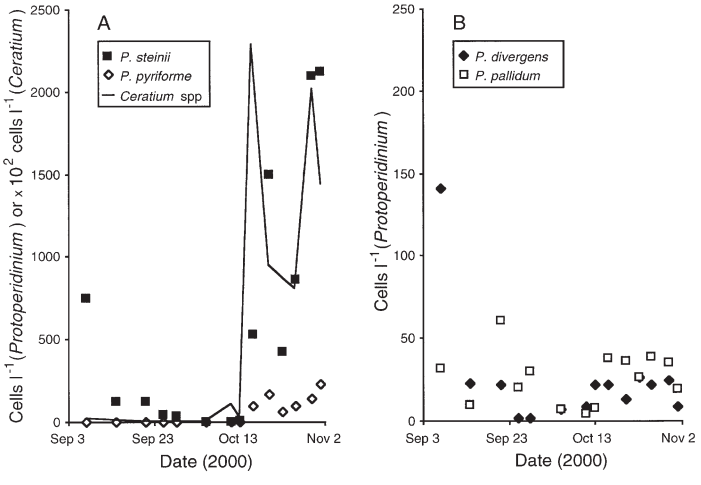

Fig. 3. Variations at 2 m depth in cell numbers of selected dinoflagellates. (A) *Protoperidinium steinii* (■), *P. pyriforme* (◇), and *Ceratium* spp. (——); note factor ×100 for *Ceratium* spp. (B) *P. divergens* (◆) and *P. pallidum* (□); note 10× expansion of ordinate scale in B relative to A

DISCUSSION

Protoperidinium species and other heterotrophic dinoflagellates occurring in Scandinavian waters are generally eurythermal, except for a few cold-water forms restricted to winter and spring (Kjæret et al. 2000). Within the narrow temperature and salinity ranges of the present study, *Protoperidinium* population dynamics were in all likelihood governed by food availability.

A *Pseudo-nitzschia pseudodelicatissima* bloom in the Oslofjord in September and October 1994 encouraged population growth of *Protoperidinium granii* and

Table 3. Maximum cell numbers of heterotrophic dinoflagellates during the diatom bloom (September 21 to 28; 3 dates) and the dinoflagellate bloom (October 16 to November 1; 6 dates)

Species	Maximum cell number (cells l^{-1}) Sep 21–28	Oct 16 to Nov 1
Protoperidinium spp.		
P. bipes	3	1
P. brevipes	0	90
P. conicum	65	8
P. crassipes	0	1
P. curtipes	0	74
P. depressum	0	10
P. divergens	22	26
P. cf. *excentricum*	0	13
P. granii	2	4
P. oblongum	2	6
P. cf. *ovatum*	0	1
P. pallidum	61	39
P. pellucidum	1	6
P. pentagonum	1	0
P. punctulatum	29	8
P. pyriforme	0	226
P. steinii	123	2125
P. thorianum	0	3
P. sp.	4	4
Others		
Dinophysis hastata	1	2
D. rotundata	13	36
Diplopelta bomba	4	24
Diplopsalis lenticula	11	8
Oblea rotunda	50	711
Zygabikodinium lenticulatum	0	2

Table 4. Observed grazing incidents with *Protoperidinium steinii* as the grazer. The numbers are cumulate for the period September 7 to November 1

Prey type	Number of observed incidents
Ceratium furca	40
C. tripos	4
C. fusus	1
C. lineatum	1
C. sp.	5
Dinophysis acuta	1
Prorocentrum micans	1
Protoperidinium steinii (cannibalism)	2
Unidentified dinoflagellate	26
Unidentified ciliate	1
Diatom	None

other *Protoperidinium* species likely to be diatom grazers (Kjæret et al. 2000). The diatom bloom in September 2000 may have been too weak or too short-lived to permit a similar situation to develop. By contrast, the massive *Ceratium* bloom in October was the probable reason for the increase in the *Protoperidinium steinii* population. Naustvoll (2000) previously showed that *P. steinii* requires dinoflagellate prey, in the form of *Heterocapsa triquetra* or *Prorocentrum micans*, for rapid growth in the laboratory. A similar convergence of field and laboratory observations exists for *Protoperidinium* cf. *divergens* and *P. crassipes* (Jeong & Latz 1994), but not so far for any other *Protoperidinium* species specialized in dinoflagellate prey. There is no absolute requirement for dinoflagellate food in *P. steinii*, since it shows positive but slow growth on diatoms (Naustvoll 2000). It is noteworthy however that the initial fairly high *P. steinii* population in our study seemed to decline during the *Pseudo-nitzschia* bloom. Our observations on *Protoperidinium pyriforme*, together with the finding by Jacobson & Anderson (1986) that it preferentially captures dinoflagellate prey, suggests that also the growth of this species is

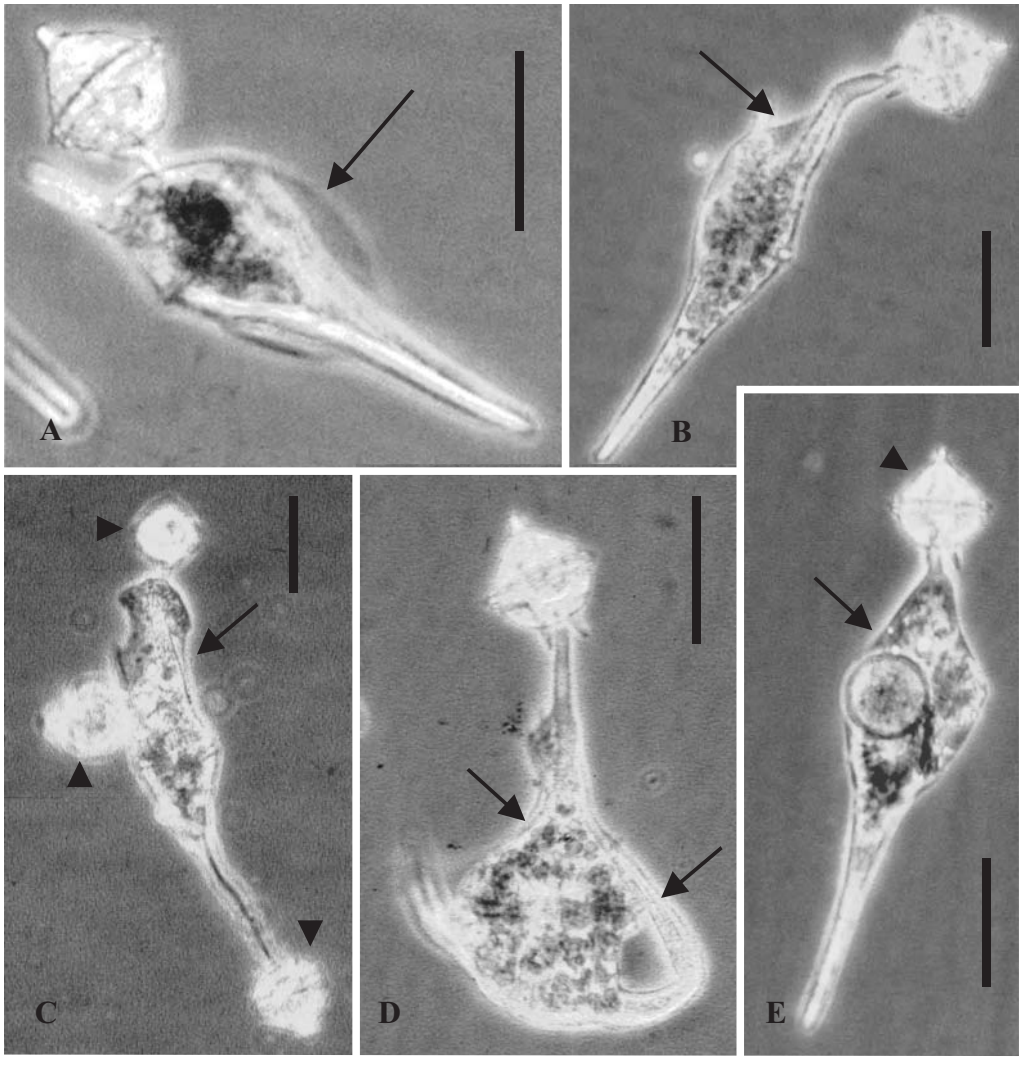

Fig. 4. Grazing by *Protoperidinium steinii* (sampling date/observation date in parentheses) on: (A) on *Ceratium furca* cell (Oct 23/24); (B) on *C. furca* cell (Oct 16/18); (C) 3 cells on 1 *C. furca* cell (Nov 1/5); (D) on *C. tripos* cell (Oct 20/22); (E) on *C. furca* cell (Oct 30/Nov 1). Arrows indicate pallium stretched around the prey. Arrowheads in C and E indicate *P. steinii*. In E, an unidentified round object, unmarked, is inside the *C. furca* cell. Scale bars: 50 µm

selectively promoted by dinoflagellate blooms. It may be significant that *P. pyriforme* is taxonomically close to *P. steinii*. The ability of these small predators to attack the much larger *Ceratium* spp. is remarkable in view of the failure of several common copepod species to feed on *Ceratium* cells, apparently because they are too large for them (Nielsen 1991).

Heterotrophic dinoflagellate population development has been shown to trail phytoplankton blooms by a few days (Nakamura et al. 1995, 1996, Tiselius & Kuylenstierna 1996), suggesting an opportunistic strategy that restricts population growth to periods of prey abundance. Unfortunately, existing quantitative data on predator-prey relationships are equivocal. In published laboratory studies on *Protoperidinium* spp., maximum growth rates were achieved only at food concentrations of 250 to 400 µg C l^{-1} (Buskey et al. 1994, Buskey 1997) or higher (estimated from data in Jeong & Latz 1994). In *P. steinii* feeding on the dinoflagellate *Heterocapsa triquetra*, food saturation of growth required at least 1000 µg C l^{-1} (L.-J. Naustvoll unpubl. data). Estimated phytoplankton biomasses during the *Ceratium* bloom, though exceptionally high for the Oslofjord, were well below this level. It seems unlikely that *Protoperidinium* populations should be permanently barred from realizing their inherent growth potential. This seeming discrepancy between field and laboratory data can only be resolved by further research. It should be noted that the increase in abundance of *P. steinii* from October 13 to October 20 (Fig. 3A) is likely to reflect advection and patchiness as much as it reflects net growth: the increase corresponds to a growth rate of >1 division d^{-1}, much higher than the highest growth rates measured by Naustvoll (2000) in laboratory experiments on this species.

The failure of *Protoperidinium pallidum* to respond to the *Ceratium* bloom is in agreement with experimental results indicating that this species cannot utilize dinoflagellate food for growth (Naustvoll 2000). In the case of *P. divergens*, it is less easy to account for the lack of a positive response. In the Oslofjord (Kjæret et al. 2000), and in Danish waters (Hansen 1991), this species is usually associated with late-summer biomass maxima of autotrophic dinoflagellates, including *Ceratium* spp. Growth of *Oblea rotunda* appeared to be stimulated during the *Ceratium* bloom, but no grazing incidents involving this species were observed. It may have fed on *Prorocentrum micans* which was present during the bloom and which has been shown to serve as excellent food for it (Strom & Buskey 1993).

Interactions between grazers and their prey are among the main factors responsible for the structuring of the planktonic food web. Although the standing stocks of heterotrophic dinoflagellates in our study were too small to have an impact on the autotrophic biomass, our data underline the high degree of grazing selectivity in *Protoperidinium* species. Effects such as those reported here may contribute to the remarkable species diversity in the marine microplankton. The extreme complexity of the microplanktonic food web is also shown by the fact that the main prey in the present investigation, *Ceratium furca*, can act as a predator on ciliates (Bockstahler & Coats 1993, Smalley et al. 1999).

Acknowledgements. We thank 4 anonymous referees for their constructive criticism of the manuscript.

LITERATURE CITED

Archer SD, Leakey RJG, Burkill PH, Sleigh MA (1996) Microbial dynamics in coastal waters of East Antarctica: herbivory by heterotrophic dinoflagellates. Mar Ecol Prog Ser 139:239–255

Bockstahler KR, Coats DW (1993) Spatial and temporal aspects of mixotrophy in Chesapeake Bay dinoflagellates. J Eukaryot Microbiol 40:49–60

Buskey EJ (1997) Behavioral components of feeding selectivity of the heterotrophic dinoflagellate *Protoperidinium pellucidum*. Mar Ecol Prog Ser 153:77–89

Buskey EJ, Coulter CJ, Brown SL (1994) Feeding, growth and bioluminescence of the heterotrophic dinoflagellate *Protoperidinium huberi*. Mar Biol 121:373–380

Fritz L, Triemer RE (1985) A rapid simple technique utilizing Calcofluor White M2R for the visualization of dinoflagellate thecal plates. J Phycol 21:662–664

Hansen PJ (1991) Quantitative importance and trophic role of heterotrophic dinoflagellates in a coastal pelagial food web. Mar Ecol Prog Ser 73:253–261

Hansen PJ, Calado AJ (1999) Phagotrophic mechanisms and prey selection in free-living dinoflagellates. J Eukaryot Microbiol 46:382–389

Jacobson DM, Anderson DM (1986) Thecate heterotrophic dinoflagellates: feeding behavior and mechanism. J Phycol 22:249–258

Jeong HJ (1994) Predation by the heterotrophic dinoflagellate *Protoperidinium* cf. *divergens* on copepod eggs and early naupliar stages. Mar Ecol Prog Ser 114:203–208

Jeong HJ (1999) The ecological roles of heterotrophic dinoflagellates in marine planktonic community. J Eukaryot Microbiol 46:390–396

Jeong HJ, Latz MI (1994) Growth and grazing rates of the heterotrophic dinoflagellates *Protoperidinium* spp on red tide dinoflagellates. Mar Ecol Prog Ser 106:173–185

Kjæret AH, Naustvoll LJ, Paasche E (2000) Ecology of the heterotrophic dinoflagellate genus *Protoperidinium* in the inner Oslofjord (Norway). Sarsia 85:453–460

Lessard EJ (1991) The trophic role of heterotrophic dinoflagellates in diverse marine environments. Mar Microb Food Webs 5:49–58

Matsuyama Y, Miyamoto M, Kotani Y (1999) Grazing impact of the heterotrophic dinoflagellate *Polykrikos kofoidii* on a bloom of *Gymnodinium catenatum*. Aquat Microb Ecol 17:91–98

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol Oceanogr 45:569–579

Nakamura Y, Suzuki S, Hiromi J (1995) Population dynamics of heterotrophic dinoflagellates during a *Gymnodinium*

mikimotoi red tide in the Seto Inland Sea. Mar Ecol Prog Ser 125:269–277

Nakamura Y, Suzuki S, Hiromi J (1996) Development and collapse of a *Gymnodinium mikimotoi* red tide in the Seto Inland Sea. Aquat Microb Ecol 10:131–137

Naustvoll LJ (2000) Prey size spectra and food preferences in thecate heterotrophic dinoflagellates. Phycologia 39: 187–198

Nielsen TG (1991) Contribution of zooplankton grazing to the decline of a *Ceratium* bloom. Limnol Oceanogr 36:1091–1106

Skovgaard A (1996) Engulfment of *Ceratium* spp (Dinophyceae) by the thecate photosynthetic dinoflagellate *Fragilidium subglobosum*. Phycologia 35:490–499

Smalley GW, Coats DW, Adam EJ (1999) A new method using fluorescent microspheres to determine grazing on ciliates by the mixotrophic dinoflagellate *Ceratium furca*. Aquat Microb Ecol 17:167–179

Strathmann RR (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol Oceanogr 12:411–418

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, 2nd edn. Bull Fish Res Board Can 167:1–310

Strom SL, Buskey EJ (1993) Feeding, growth, and behavior of the thecate heterotrophic dinoflagellate *Oblea rotunda*. Limnol Oceanogr 38:965–977

Tiselius P, Kuylenstierna M (1996) Growth and decline of a diatom spring bloom: phytoplankton species composition, formation of marine snow and the role of heterotrophic dinoflagellates. J Plankton Res 18:133–155

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: March 12, 2001; Accepted: June 12, 2001
Proofs received from author(s): December 18, 2001