

Quantitative importance and trophic role of heterotrophic dinoflagellates in a coastal pelagial food web

Per Juel Hansen

Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, DK-3000 Helsingør, Denmark

ABSTRACT: The quantitative importance and trophic role of heterotrophic dinoflagellates was studied at a permanent station in the Kattegat, Denmark. Heterotrophic dinoflagellates were most abundant during periods characterized by large phytoplankton forms (e.g. diatoms and dinoflagellates). During these periods the heterotrophic dinoflagellate biomass corresponded to between 13 and 77 % of the phytoplankton biomass. Large forms (> 20 µm) dominated the heterotrophic dinoflagellate biomass, but smaller forms were important during periods dominated by nanoplankton. Observations on the feeding mechanisms of the most abundant heterotrophic dinoflagellates revealed species which engulf prey directly as well as species which feed with a peduncle and a pallium – mechanisms which all allow the ingestion of large prey. The succession of heterotrophic dinoflagellates is also discussed in relation to the distribution of potential competitors and predators.

INTRODUCTION

Dinoflagellates which lack chloroplasts have been known by taxonomists for about a century (Gaines & Elbrächter 1987). The naked forms were early recognized as phagotrophs since they contain food bodies (Gaines & Elbrächter 1987). The feeding mechanisms and the prey of colourless thecate dinoflagellates have been studied only recently and it has been revealed that they also are phagotrophs (Gaines & Taylor 1984, Jacobson & Anderson 1986, Hansen 1991). Although rarely quantified, the heterotrophic dinoflagellates can make up a substantial biomass which at times even exceeds that of other zooplankton groups (Le Fèvre & Grall 1970, Kimor 1981, Smetacek 1981, Uhlig & Sahling 1982, Carreto et al. 1986, Dale & Dahl 1987, Lessard 1991). Until now zooplankton ecologists and protozoologists have not paid much attention to these organisms because they have been regarded as representatives of the phytoplankton. The reason for this is insufficient knowledge on their ecological role as grazers in the marine pelagial.

Three different types of feeding mechanisms occur among heterotrophic dinoflagellates (see Gaines & Elbrächter 1987). One group of species engulf intact prey organisms. The prey is usually ingested through the sulcus at the posterior end of the cell. When large

prey organisms are ingested these dinoflagellates alter their shape to resemble that of the prey. A second group of species feed with a pallium: a pseudopodium that extends through the flagellar pore and envelopes the prey. Finally, a third group of species suck the cell contents of the prey through a feeding tube, a peduncle. This feeding mechanism has been called myzocytosis (Schnepf & Deichgräber 1984).

Heterotrophic dinoflagellates have been reported to feed on prey such as bacteria, flagellates, diatoms, other dinoflagellates, ciliates and metazoans (e.g. Jacobson & Anderson 1986, Gaines & Elbrächter 1987, Hansen 1991). Prey size spectra have not been studied and only few attempts have been made to measure growth and clearance rates of these dinoflagellates (Lessard & Swift 1985, Jacobson 1987, Goldman et al. 1989). This makes it difficult to interpret their trophic role. The aim of the present work is to describe the quantitative importance and the trophic role of heterotrophic dinoflagellates in a marine pelagial.

MATERIALS AND METHODS

Sampling. Sampling was conducted at a permanent station located in the southern part of Kattegat (56°15.42' N, 12°00.12' E); water depth: 30 m. The sta-

tion was visited every second week during 1989. During 2 intensive periods (28 Mar to 14 Apr; 21 Aug to 8 Sep) sampling was conducted daily, weather permitting. Sampling was always carried out between 09:30 and 12:00 h.

Vertical profiles of temperature, salinity and in situ fluorescence were obtained to describe the water column structure. Water samples for determination of chlorophyll *a* and enumeration of heterotrophic dinoflagellates were taken with a 30 l Niskin water sampler from 2.5 m and at the pycnocline/depth of maximum fluorescence. Chlorophyll *a* was measured according to the method described in Kiørboe & Nielsen (1990). The conversion factor used to estimate carbon from chlorophyll *a* was 50 (Richardson et al. 1986). In the study on the vertical distribution of phytoplankton and heterotrophic dinoflagellates during a dinoflagellate bloom the phytoplankton > 20 µm were counted and treated like the heterotrophic dinoflagellates.

For the enumeration of heterotrophic dinoflagellates > 20 µm, water samples (300 ml) were fixed in Lugol's iodine (final conc. 0.33 to 1%). The cells in at least 50 ml were allowed to sediment and the flagellates identified and counted with an inverted microscope. The dinoflagellates were identified from Kofoid & Swezy (1921), Lebour (1925), Schiller (1933, 1937), Hulburt (1957) and Dodge (1985). Identification of thecate forms was checked by microscopical examination of cells from net samples (mesh size 20 µm) fixed in glutaraldehyde or Lugol's (final conc. 1%). This procedure was not possible with naked (athecate) dinoflagellates which are not retained in net samples and the characters used to identify these organisms disappear or change during fixation. These forms were therefore examined live. Heterotrophs were distinguished from autotrophs by microscopical (including epifluorescence microscopy) examination of live cells and cells fixed in glutaraldehyde.

Enumeration of heterotrophic dinoflagellates < 20 µm was carried out using epifluorescence microscopy. Water samples of 15 ml were fixed in glutaraldehyde (final conc. 1%) and stained with proflavine hemisulfate (Haas 1982). After filtration on black nuclepore filters (1 µm), these were dried, mounted in paraffin oil and stored in a refrigerator. Dinoflagellates are easily distinguished from other flagellates due to the morphology of the nucleus. Discrimination between autotrophic and heterotrophic dinoflagellates was facilitated by using a green excitation filter to reveal pure chlorophyll autofluorescence. Cells were counted using 600× magnification and divided into 3 size groups (6–10, 11–15, 16–20 µm).

Cell volumes were calculated separately for each species/size group on the basis of linear dimensions, assuming simple geometrical shapes. Cell carbon was

estimated by multiplying volumes by 0.11 for naked species and 0.13 for thecate species (Edler 1979, Les-sard 1991).

Observations on feeding mechanisms and food preferences. Live plankton was filtered through a 200 µm net to remove large zooplankters and subsequently concentrated using a 20 µm net. The concentrated plankton was incubated in 60 ml tissue culture flasks (Nunclon, Denmark) and placed on a plankton wheel (2 rpm) in continuous light ($5 \mu\text{E m}^{-2} \text{s}^{-1}$) at 18°C. Crude cultures of heterotrophic dinoflagellates were maintained by adding fresh f/2 medium (Guillard 1972) weekly. The feeding mechanism as well as preference of food items were observed for the most abundant heterotrophic dinoflagellates by microscopy while the organisms were still in the flat tissue culture flasks. A combination of binocular and inverted microscopes were used at magnifications of 50 to 200 times. This method allowed repeated observations of the most abundant species. Throughout the study period suspensions of the cryptophyte *Rhodomonas baltica* (size $4 \times 10 \mu\text{m}$) were added to crude cultures in order to study the ability of differently sized heterotrophic dinoflagellates to feed and grow on a nanoflagellate.

RESULTS

Dinoflagellate feeding mechanisms

The most common thecate heterotrophic dinoflagellates found in the Kattegat belonged to the genus *Protoperidinium* and the '*Diplopsalis* group'. Without exception these species feed with a pallium. A number of species not previously reported to use this feeding mechanism were found: *Protoperidinium brevipes*, *P. divergens*, *Diplopsalis lenticula*, *Diplopelta bomba*.

In enrichment cultures, diatoms were prey for *Protoperidinium brevipes*, *P. conicum* and *P. pellucidum* during spring and large (> 20 µm) dinoflagellates for *P. divergens*, *P. pellucidum* and species of the *Diplopsalis* group in late summer. These dinoflagellates were not observed to prey on nanoflagellates present in the crude cultures, nor on the added cryptophyte *Rhodomonas baltica*. Two species belonging to the dinophysoids, *Dinophysis hastata* (= *D. odiosa*) and *D. rotundata*, were found. Both feed on the prostomatid ciliate *Tiarina fusus* by sucking out the contents of the prey through a peduncle (Hansen 1991).

The most abundant larger (> 20 µm) naked forms found in the Kattegat belonged to the genera *Amphidinium*, *Gymnodinium*/*Gyrodinium* and *Polykrikos*. One *Amphidinium* species was found: *A. cras-sum*, which preys on nanoflagellates with a peduncle. The species of other genera are all able to engulf entire

prey organisms. The prey included diatoms for *Gyrodinium dominans* and *G. spirale* during spring, nanoflagellates for *G. dominans* during summer and mixed microplankton for *Polykrikos schwartzii* in late autumn. The species *Gyrodinium* cf. *fusiforme* and *G. glaucum* were found throughout the year feeding mainly on nanoflagellates. In enrichment cultures incubated with the cryptophyte *Rhodomonas baltica*, *Amphidinium* sp. and all *Gyrodinium* spp. were observed to feed on this nanoflagellate and respond numerically.

The small (< 20 μm) heterotrophic dinoflagellates in the Kattegat were exclusively naked forms of the *Gyrodinium/Gymnodinium* type. Some of them engulf entire prey organisms and others suck out the prey through a peduncle. In the first case the food consists of nanoflagellates (which included *Rhodomonas baltica*) and in the second case diatoms or nanoflagellates.

Seasonal distribution of phytoplankton and heterotrophic dinoflagellates

The seasonal distribution of phytoplankton (estimated from chlorophyll *a*) was studied at 2.5 m depth and the depth of the pycnocline/max. fluorescence. Due to the similarity in the results obtained, only results from 2.5 m are presented in Fig. 1A. The phytoplankton biomass is low during winter, but in March and April a pronounced diatom spring bloom occurs. The dominant species are *Chaetoceros debilis*, *Chaetoceros* spp., *Thalassiosira nordenskiöldii*, *Thalassiosira* spp., *Thalassionema nitzschioides*, and *Skeletonema costatum*. Following the sedimentation of the spring bloom in April and until July the phytoplankton biomass was generally low and nanoplankton accounted for a large part of the biomass. During this period the maximum chlorophyll *a* level was found in the pycnocline. In August and September the pycnocline was partly disrupted and a bloom of dinoflagellates occurred (*Ceratium furca*, *C. fusus*, *C. tripos*, *C. longipes*, *Dinophysis norvegica*, *Dinophysis* spp., *Prorocentrum minimum*, *P. micans*). During the rest of the year the phytoplankton community consisted of a mixture of dinoflagellates, diatoms and silicoflagellates, but a diatom bloom occurred in December (*Rhizosolenia alata*).

The larger (> 20 μm) heterotrophic dinoflagellates (Figs. 1B & 2A, B) were especially abundant during 3 periods: March/April, August/September and November with standing stocks of 46, 42 and 163 $\mu\text{g C l}^{-1}$, respectively, at 2.5 m depth and 54, 38 and 159 $\mu\text{g C l}^{-1}$, respectively, at the pycnocline/max. fluorescence (not shown). These periods were all characterized by the dominance of large phytoplankton forms (diatoms,

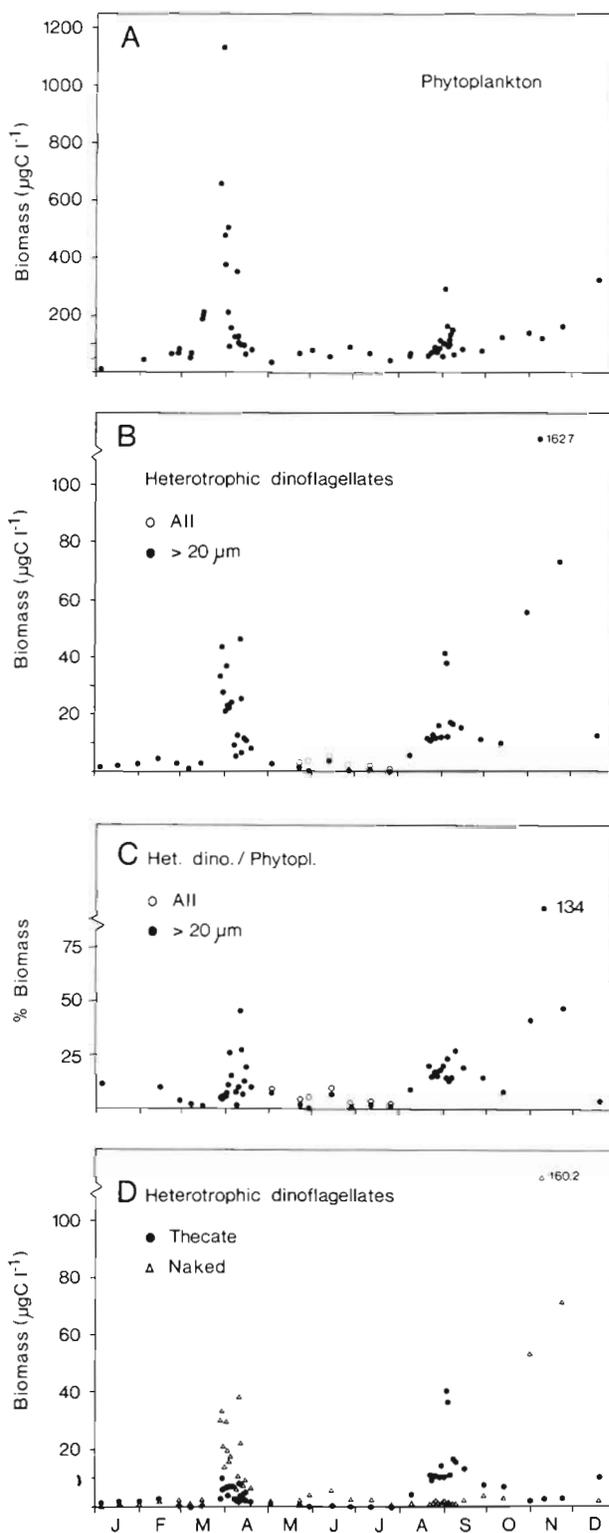


Fig. 1. Seasonal distribution of phytoplankton and heterotrophic dinoflagellate biomass in samples from 2.5 m depth. (A) Phytoplankton. (B) Heterotrophic dinoflagellates. (C) Heterotrophic dinoflagellates (biomass in % of phytoplankton biomass). (D) Biomass of naked and thecate heterotrophic dinoflagellates

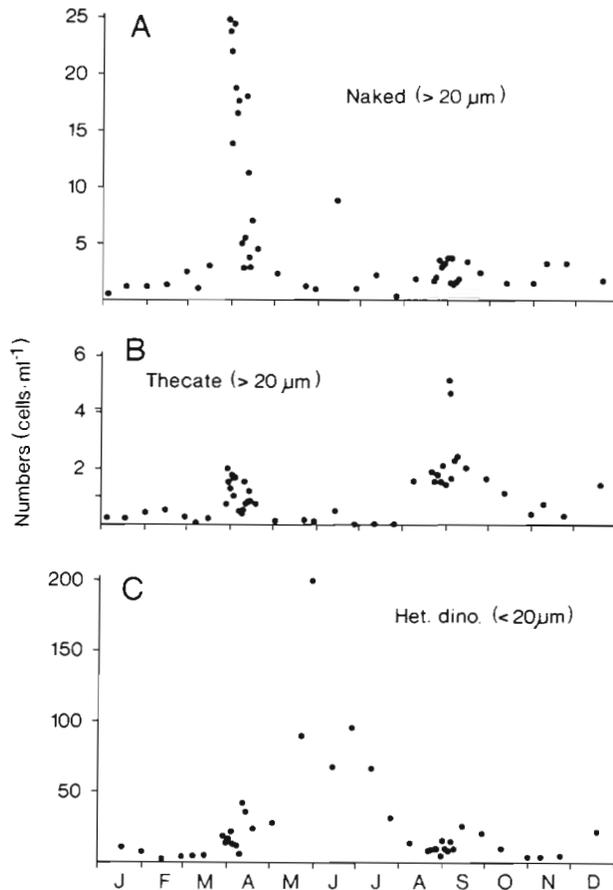


Fig. 2. Seasonal abundance of heterotrophic dinoflagellates in samples from 2.5 m depth. (A) Naked (> 20 μm). (B) Thecate (> 20 μm). (C) < 20 μm

dinoflagellates, silicoflagellates). During these periods, the heterotrophic dinoflagellates attained biomass levels corresponding to between 13 and 77 % of the phytoplankton biomass at 2.5 m (Fig. 1C) and between 17 and 61 % at the pycnocline (not shown). On one occasion the heterotrophic dinoflagellates accounted for as much as 134 % of the phytoplankton biomass (Fig. 1C).

The small (< 20 μm) heterotrophic dinoflagellates were most abundant during summer (May to July) representing a biomass of 0.5 to 3.7 μg C l⁻¹ at 2.5 m and 0.2 to 4.4 μg C l⁻¹ at the depth of the pycnocline/max. fluorescence, or 1 to 5 % of the phytoplankton biomass (Figs. 1C & 2C). Nanoplankton forms constituted a substantial part of the phytoplankton during this period. During the rest of the year the biomass of heterotrophic dinoflagellates < 20 μm made up less than 1 % of the phytoplankton biomass.

Among the larger (> 20 μm) heterotrophic dinoflagellates the naked forms were most abundant during March/April and again in November (Figs. 1C & 2A). The thecate forms were most abundant during March/

April and again in August/September (Figs. 1C & 2B). The seasonal succession of some important species is shown in Fig. 3.

Vertical distribution

The vertical distribution of phytoplankton (> 20 μm) and large (> 20 μm) heterotrophic dinoflagellates at the permanent station was studied at the peak of a dinoflagellate bloom on 2 September 1989 (Fig. 4). The phytoplankton biomass was largest in the surface layer of the water column (230 μg C l⁻¹), falling to a lower,

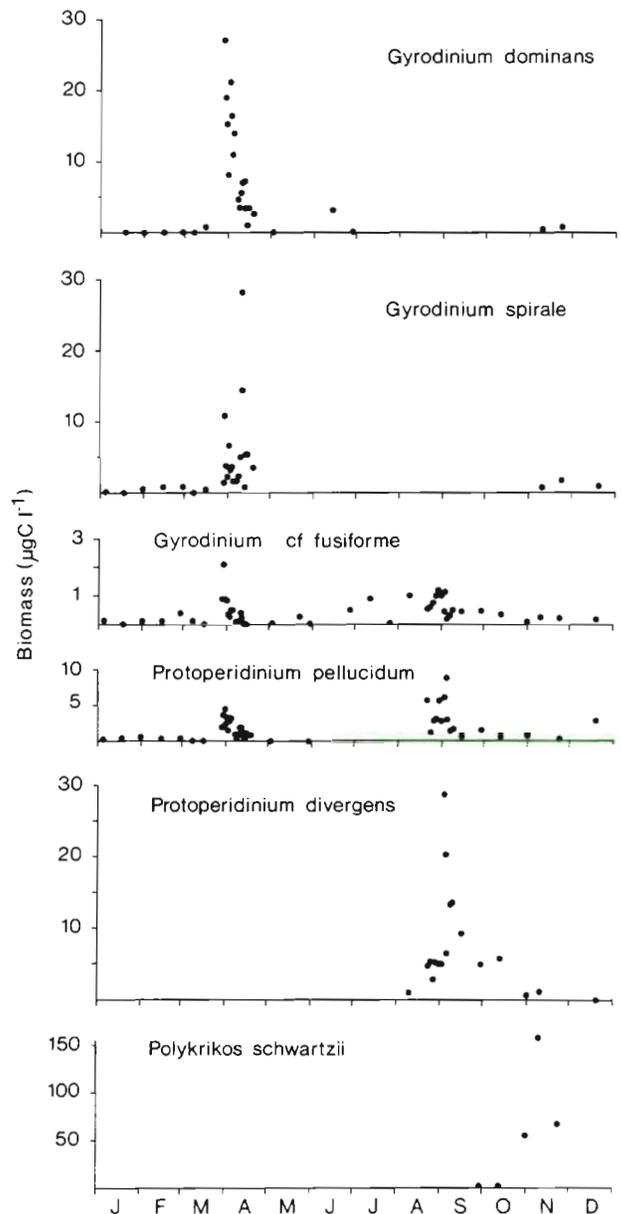


Fig. 3. Seasonal distribution of some important species of heterotrophic dinoflagellates

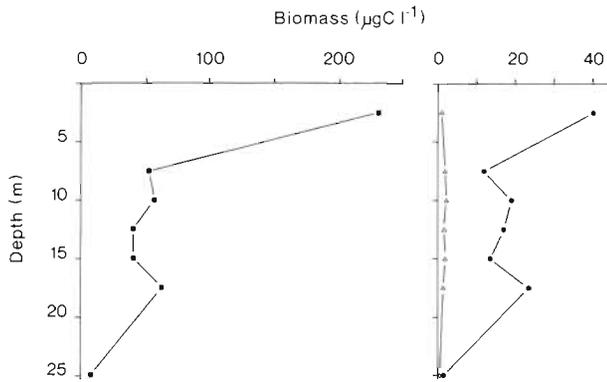


Fig. 4. Vertical biomass distribution of phytoplankton ($> 20 \mu\text{m}$) and heterotrophic dinoflagellates ($> 20 \mu\text{m}$) during the peak of a *Ceratium* bloom (2 September 1989). Left: phytoplankton. Right: heterotrophic dinoflagellates; (●) thecate forms; (△) naked forms

fairly constant level at depths between 7.5 and 17.5 m (42 to $63 \mu\text{g C l}^{-1}$). Near the bottom (25 m) the biomass was very low ($8 \mu\text{g C l}^{-1}$). The dinoflagellates *Ceratium furca*, *C. fusus*, *C. tripos* and *C. longipes* accounted for more than 90 % of the phytoplankton biomass.

The vertical biomass distribution of larger ($> 20 \mu\text{m}$) thecate heterotrophic dinoflagellates resembled that of the phytoplankton: $40 \mu\text{g C l}^{-1}$ in the surface layer, 12 to $23 \mu\text{g C l}^{-1}$ in the largest part of the water column and $1.5 \mu\text{g C l}^{-1}$ in the bottom waters. Altogether the biomass of the heterotrophic dinoflagellates was 17 to 42 % of phytoplankton biomass $> 20 \mu\text{m}$. The dominant species were *Protoperdinium divergens*, *P. pellucidum* and *Diplopsalis* spp. The biomass of the larger ($> 20 \mu\text{m}$) naked heterotrophic dinoflagellates was low (0.45 to $2.2 \mu\text{g C l}^{-1}$) and fairly uniform throughout the water column.

DISCUSSION

Dinoflagellate feeding mechanisms

Table 1 summarizes what is known on feeding mechanisms and prey of heterotrophic dinoflagellates. Peduncle feeding is found among thecate as well as naked forms. Engulfment of particles is restricted to some naked forms, while pallium feeding is only found among thecate forms. In evolutionary terms the type of feeding mechanism seems to be a conservative feature shared by all species belonging to a given genus. Apparent exceptions are constituted by the genera *Gyrodinium* and *Gymnodinium*. In these genera, species are found which engulf food particles, as well as species which possess a peduncle. However, the distinction between genera in the order Gymnodiniales is primarily based on the location and displacement of

the girdle. A taxonomic revision of the 2 genera will probably show that this species complex involves 3 or more genera.

A large majority of phagotrophic dinoflagellates found so far lack chloroplasts. There are reports on photosynthetic dinoflagellates which take up food particles. However, this subject needs further attention in order to determine how common this phenomenon is and whether the food particles are used as carbon source or as a source of vitamins (see Gaines & Elbrächter 1987 for discussion). Recently, Larsen (1988) reported on 'chloroplast symbiosis' (retention of functional chloroplasts deriving from prey organisms) in an *Amphidinium* species feeding on cryptophytes, but the photosynthetic competence of these chloroplasts was not investigated. In addition to dinoflagellates, mixotrophy is found in some representatives of other flagellate classes: Prymnesiophyceae, Cryptophyceae and Chrysophyceae (Fenchel 1982, Bird & Kalff 1986, Sanders & Porter 1988, Anderson et al. 1989, Tranvik et al. 1989).

Trophic role of heterotrophic dinoflagellates

Prey particle size spectra for heterotrophic dinoflagellates have not been studied in detail. However, the co-occurrences of certain species with high concentrations of a given type of prey species implies food preferences. Three such periods were found during this study: the diatom bloom in spring, the nanoflagellate-dominated summer period and dominance of large thecate dinoflagellates in late summer.

Large ($> 20 \mu\text{m}$) naked and thecate heterotrophic dinoflagellates formed a high biomass in response to the diatom spring bloom. Smetacek (1981) found the same response of both naked and thecate forms in Kiel Bight (German Baltic Sea), while others have demonstrated a dominance of thecate forms in association with diatom blooms in other coastal areas (Jacobson 1987, Lessard 1991). Bursa (1961) found a naked heterotrophic dinoflagellate in association with diatoms in the Arctic. This demonstrates that both naked and thecate forms are able to respond numerically to diatom blooms, even when these are dominated by colonial and spiny forms.

Only naked heterotrophic dinoflagellates were present during the nanoflagellate-dominated summer plankton, of which a substantial proportion was $< 20 \mu\text{m}$. A similar observation was made by Bjørnsen & Kuparinen (1991) in the Weddell Sea. The relatively large thecate forms are apparently unable to compete with naked forms for small food particles. This is supported by laboratory studies in which the cryptophyte *Rhodomonas baltica* ($10 \mu\text{m}$) was added to water sam-

Table 1. Feeding mechanisms in heterotrophic dinoflagellates (non-parasites)

| Genera/species (no. of species) | Feeding mechanism | Prey type | Source |
|--|-------------------|--|-------------|
| Order Dinophysiales <i>Dinophysis</i> (2) | Peduncle | Ciliates (<i>Tiarina</i>) | 1 |
| Order Gonyaulacales <i>Cryptothecodinium cohnii</i> | Peduncle | Nanoflagellates | 2 |
| Order Peridinales <i>Peridinopsis beroliense</i> | Peduncle | Flagellates | 3 |
| <i>Protoperidinium</i> (19) | Pallium | Diatoms, dinoflagellates | 4, 5, 6 |
| <i>Diplopsalis</i> group (4) | Pallium | Diatoms, dinoflagellates (nanoflagellates) | 4, 6 |
| Order Gymnodiniales <i>Amphidinium</i> (2) | Peduncle | Nanoflagellates | 4, 7 |
| <i>Gymnodinium</i> (8) | Engulfment | Diatoms, dinoflagellates, ciliates, nanoflagellates | 2, 8, 9 |
| <i>Gymnodinium</i> (= <i>Katodinium</i>) <i>fungiforme</i> | Peduncle | Nanoflagellates, injured ciliates | 10 |
| <i>Gymnodinium</i> -'like' sp. | Peduncle | Diatoms | 4 |
| <i>Gyrodinium</i> (6) | Engulfment | Diatoms, dinoflagellates, ciliates, nanoflagellates | 2, 4, 8, 11 |
| <i>Gyrodinium lebouriae</i> | Peduncle | Nanoflagellates | 12 |
| <i>Gyrodinium vorax</i> ^a | Peduncle | Dinoflagellates | 2 |
| <i>Nematodinium partitum</i> | Engulfment | Dinoflagellates | 8 |
| <i>Polykrikos</i> (2) | Engulfment | Dinoflagellates, silicoflagellates | 4, 8, 13 |
| <i>Warnowia vocaris</i> | Engulfment | Dinoflagellates | 8 |
| Order Noctilucales <i>Noctiluca scintillans</i> | Engulfment | Almost anything of appropriate size | 8, 14 |
| <i>Pratjetella medusoides</i> | Engulfment | Silicoflagellates | 15 |
| <i>Incertae sedis</i> <i>Oxyrrhis marina</i> | Engulfment | Nanoflagellates, diatoms | 16, 17 |

^a This species has been reported as having 'regressed' chromatophores
1, Hansen (1991); 2, Biecheler (1952); 3, Wedemayer & Wilcox (1984); 4, this study; 5, Gaines & Taylor (1984); 6, Jacobson & Anderson (1986); 7, Larsen (1988); 8, Kofoed & Swezy (1921); 9, Irish (1979); 10, Spero (1982); 11, Bursa (1961); 12, Lee (1977); 13, Carreto et al. (1986); 14, Hofker (1930); 15, Cachon & Cachon (1969); 16, Barker (1935); 17, Droop (1966)

ples containing thecate as well as naked heterotrophic dinoflagellates. It was always the naked dinoflagellates which responded and became the dominant predators. Small thecate heterotrophic dinoflagellates such as *Oblea rotunda* (size 20 µm) have been reported to feed on prasinophytes (10 µm) (Jacobson & Anderson 1986), but when observed in large quantities in nature, it has been in association with the dinoflagellate *Heterocapsa triquetra* (size 30 µm) and diatoms (Jacobson 1987, Les-sard 1991).

Phytoplankton in the late summer was dominated by large thecate dinoflagellates. The fraction of phytoplankton > 11 µm accounted for about 75% of the phytoplankton biomass, mainly *Ceratium* spp. (Nielsen

1991). During this period the only heterotrophic dinoflagellates of quantitative importance were large thecate forms. The naked dinoflagellates present were so small that they were unable to graze these large species. During a *Ceratium* bloom in Kiel Bight, Smetacek (1981) found equal amounts of large naked and thecate forms. It is unclear why no large naked heterotrophic dinoflagellates were present during the *Ceratium* bloom in the Kattegat. During 1989 the zooplankton biomass was fairly high in the Kattegat until late October (Nielsen 1991, T. G. Nielsen & T. Kjørboe pers. comm.) but had already declined in late September in Kiel Bight (Smetacek 1981). Perhaps the absence of large naked heterotrophic dinoflagellates

was due to copepod grazing, since the zooplankton are more efficient grazers of naked than of thecate forms. Nielsen (1991) studied the grazing of *Ceratium* species by copepods and found that the dominating copepods were unable to graze *Ceratium* due to the latter's heavy theca. If this explanation is correct it may also explain why the large naked heterotrophic *Gyrodinium* spp. in the spring and *Polykrikos schwartzii* in November can form large populations as copepod populations are low during those periods.

Jacobson (1987) and Lessard (1991) speculated that heterotrophic dinoflagellates and ciliates may occupy different niches with regard to prey, due to the inability of ciliates to feed on large diatoms. Ciliates were also quantified in the samples which were the basis for this study (T. G. Nielsen & T. Kjørboe pers. comm.). The ciliates were not found to respond numerically to the spring bloom of diatoms or to the late summer bloom of *Ceratium*. Marine planktonic ciliates (e.g. oligotrichs and tintinnids) ingest particles with a maximum size of 45% of the oral diameter (Spittler 1973, Heinbokel 1978b, Jonsson 1986). This indicates that the maximum prey size for the largest ciliate found (*Favella ehrenbergi*, oral diameter 80 μm) is about 35 μm and this is why the ciliates do not respond to the spring bloom of colonial diatoms or to the late summer bloom of large dinoflagellates. However, some ciliates (prostomatids) do exist which are able to ingest larger particles due to their flexible cytostome (Smetacek 1981, Hansen 1991, Nielsen 1991), but they were of little quantitative importance in the present investigation (Nielsen 1991, T. G. Nielsen & T. Kjørboe pers. comm.).

Quantitative importance

Heterotrophic dinoflagellates were especially important in the spring, late summer and autumn with mean biomasses representing 15, 21 and 69%, respectively, of the phytoplankton biomass. The biomass of small species (< 20 μm) was generally much lower than that of larger ones. Only during the summer did small and large species represent biomasses of similar magnitude. Smetacek (1981) obtained similar results in Kiel Bight. He found that large forms reached maximum biomasses during spring and autumn, representing 10% of that of the phytoplankton.

Among other protozoa the ciliates represent the major competitor for food. In the Kattegat the relative biomass of heterotrophic dinoflagellates and ciliates [expressed as $\text{het.dino.}/(\text{het.dino.} + \text{ciliates})$] fluctuated between 7.5 and 99%. Jacobson (1987) and Lessard (1991) made similar observations in other coastal areas. In Kiel Bight, Smetacek (1981) found that the 2 groups attain comparable biomass levels.

There are few reports on grazing and growth experiments with heterotrophic dinoflagellates in the literature. Maximum growth rates have been estimated to be 0.035 h^{-1} for *Protoperidinium hirobis* (size 20 μm) and 0.029 h^{-1} for *Oxyrrhis marina* (size 15 \times 30 μm) at 20°C (Jacobson 1987, Goldman et al. 1989). The paucity of grazing and growth rates for heterotrophic dinoflagellates makes it difficult to estimate the exact grazing impact on the phytoplankton.

The maximum growth rate of ciliates is a function of cell size and temperature (Fenchel 1968, Heinbokel 1978a). According to these data a 20 μm ciliate has on average a growth rate of 0.17 to 0.23 h^{-1} at 20°C. Growth experiments with similar sized heterotrophic dinoflagellates yielded a maximum growth rate of 0.029 to 0.035 h^{-1} (Jacobson 1987, Goldman et al. 1989). These data suggest that the heterotrophic dinoflagellates have lower maximum growth rates.

In conclusion, heterotrophic dinoflagellates are abundant in the Kattegat, as well as in other coastal seas, during periods characterized by large phytoplankton forms. Maximum growth rates of the heterotrophic dinoflagellates seem to be lower than those of ciliates – their main protozoan competitor. The seasonal distribution of ciliates in the Kattegat differs from that of heterotrophic dinoflagellates, suggesting differential preferences for prey sizes: the prey/predator relationship for dinoflagellates is close to 1:1 rather than 1:10, which has been shown for ciliates (Fenchel 1986).

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