

## The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in arctic and temperate coastal ecosystems: A cross-latitude comparison

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### Abstract

We compared seasonal studies of ciliates and heterotrophic dinoflagellates conducted in Disko Bay (West Greenland, ~69°N) and the Kattegat (Denmark, ~56°N). In both systems, ciliates and heterotrophic dinoflagellates were important components of the plankton. Their biomass was minute in the winter (October to April) in Disko Bay compared to the Kattegat, but from May to August/September, the biomass and composition of the ciliate and heterotrophic dinoflagellate assemblages were similar in the two systems. The seasonal biomass pattern was unimodal and bimodal for Disko Bay and the Kattegat, respectively. To evaluate top-down versus bottom-up control, experimentally derived maximum estimates of protozooplankton growth rates and copepod predation capacities from the study sites were applied to biomass data. This analysis showed that the effect of copepods was significant but that ciliates and heterotrophic dinoflagellates could effectively exploit prey during periods when top-down pressure was relaxed. In Disko Bay, a high copepod biomass in spring is primarily caused by migration of an overwintering copepod population from deep waters into the photic zone prior to the spring bloom. We suggest that “regulation windows” for the protozooplankton are present even during the spring bloom when copepods occur at their peak levels because of food saturation. Bottom-up regulation occurred during the winter and occasionally when copepod predation pressure relaxed, but it was difficult to separate food limitation from the effect of temperature. Multiple regression analysis supports the notion that ciliate and heterotrophic dinoflagellate biomass changed seasonally according to both top-down and bottom-up regulation, as well as to temperature control. Protozooplankton growth estimates were also used to calculate the fraction of primary production processed by the ciliates and heterotrophic dinoflagellates. When assuming complete algalivory, 32–55% and 20–60% of the annual primary production was consumed by ciliates in Disko Bay and the Kattegat, respectively. Furthermore, because heterotrophic dinoflagellates were found to be as important grazers as ciliates in both systems, it was concluded that protozooplankton at high latitudes are also important in the cycling of primary production and should be considered if carbon and nutrient cycling in these systems is to be understood.

During the past decade it has been shown that ciliates and heterotrophic dinoflagellates are abundant in arctic marine waters; these protists have higher growth capacities than copepods from the genus *Calanus*, which traditionally have been considered the principal grazers associated with high latitudes (Andersen 1988; Nielsen and Hansen 1995; Hansen et al. 1996; Sherr et al. 1997; Levinsen et al. 2000a). Furthermore, adult and nauplii of the *Calanus* species have been shown to preferentially feed on ciliates and dinoflagellates (Barthel 1988; Ohman and Runge 1994; Levinsen et al.

2000b; Turner et al. 2001). Such results infer that ciliates and heterotrophic dinoflagellates play an important role in the cycling of pelagic primary production in arctic regions, similar to their role at temperate latitudes. However, no comparative studies have documented this point. Therefore, the objective of this paper is to compare the role of protozooplankton from two regions that adequately represent arctic and temperate coastal ecosystems.

Arctic regions are characterized by a short productive season. The annual pattern of primary production is unimodal, with a single burst coupled to the ice break (Smith and Sakshaug 1990). To cope with this environment, the dominant arctic copepods (*Calanus* spp.) overwinter most of the year in deep waters. Adult *Calanus* spp. only visit the euphotic layer from spring, when they ascend in time to match the vernal phytoplankton bloom, until midsummer, when they descend before the end of the productive season (Conover 1988; Diel and Tande 1992; Madsen et al. 2001). This copepod life strategy implies that the arctic winter-starved protozooplankton assemblages must initiate growth in spring during high biomass of their main predators. Later in the season, on the other hand, most predators disappear.

In stratified, temperate, shallow regions, the productive season is longer and includes a bimodal pattern with a larger winter/spring and a smaller late summer/autumn phytoplankton bloom. The dominant small neritic copepods have low overwintering biomass, and most of the community estab-

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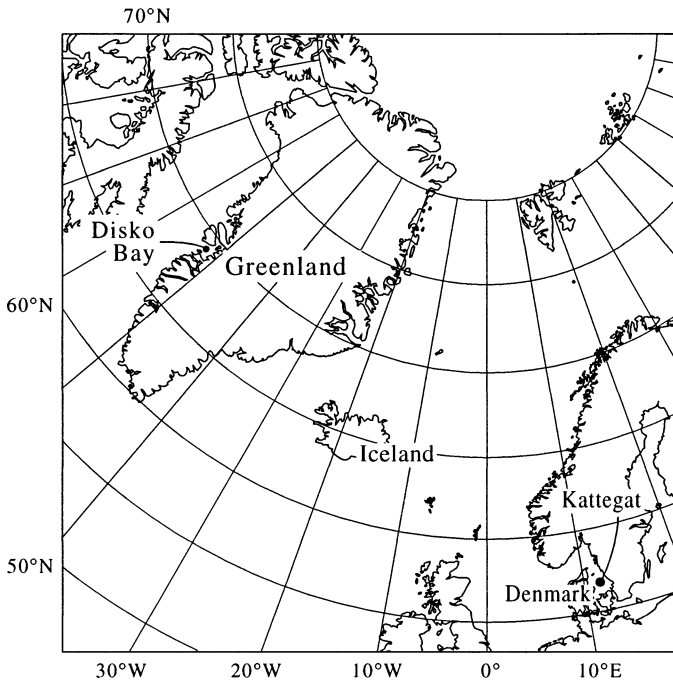


Fig. 1. Map showing Disko Bay, West Greenland, and Kattegat, Denmark (arrows).

lishes from resting eggs (Viitasalo 1992). Because the copepod community has to build up from eggs at the low temperatures, which prevails at the onset of the phytoplankton bloom, the copepod biomass lags the bloom considerably (Kjørboe 1991). For temperate protozooplankton, the mismatch between the spring bloom and copepods imply that their response on the bloom can occur in the almost absence of predators. This near-predator-free situation is followed by a period with increasing predator biomass during summer.

The main goals of this paper are to (1) compare regulation

of ciliate and heterotrophic dinoflagellate assemblages in arctic and temperate coastal regions and (2) estimate grazing effects by these assemblages on annual primary production in the two regions. These goals were addressed using published data from studies conducted in Disko Bay, West Greenland ( $69^{\circ}15'N$ ,  $53^{\circ}33'W$ ), and Kattegat, Denmark ( $56^{\circ}11'N$ ,  $12^{\circ}04'E$ ) (Fig. 1). The sites were selected based on where the authors have previously conducted plankton ecology studies. Regulation was analyzed by comparing potential growth rates of selected protozooplankton cell sizes versus the predation capacities of copepods on these cells, as determined from incubation experiments. In addition, regulation was addressed by conducting multiple regression analysis. The data cover a complete annual cycle of ciliates and heterotrophic dinoflagellates and their main prey (phytoplankton) and predators (copepods). Primary production, protozooplankton growth, and predation loss rates were obtained from the same studies.

## Methods

*Sampling program and presentation of data*—Sampling was conducted at approximately weekly (Disko Bay) or 14-day (Kattegat) intervals around local noon. In addition, the Kattegat station was sampled almost daily during two 3-week sampling periods (March–April and August–September). In total, the 250-m-deep Disko Bay station was visited 46 times from April 1996 to June 1997, and the 28-m-deep Kattegat station was visited 54 times from January to December 1989. Exact sampling intervals are shown in Fig. 2. The sampling depths were determined according to the chlorophyll fluorescence profile of the water column and usually included water from above, within, and (for Disko Bay) below the fluorescence peak. These depths corresponded to sampling above, within, and below the pycnocline that was present throughout the summer. Water was collected us-

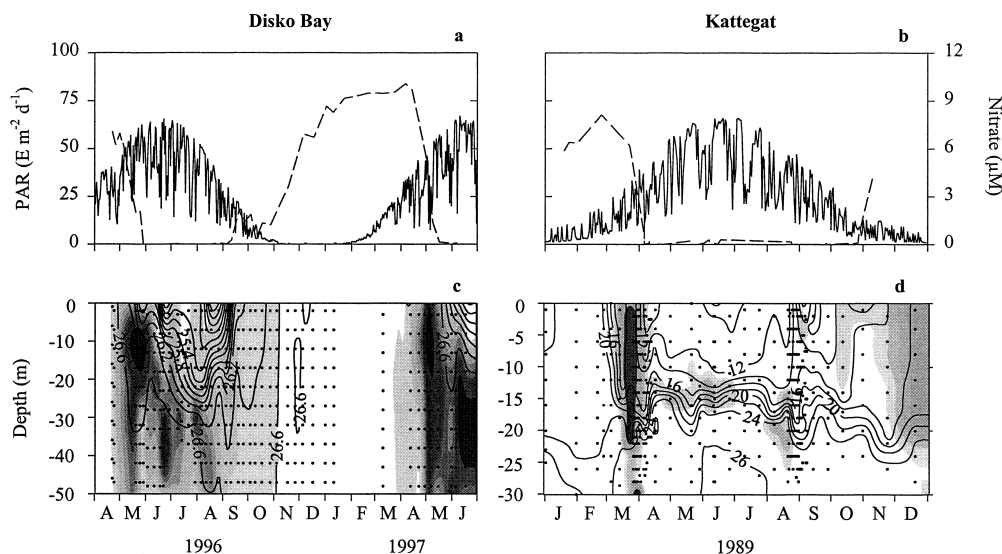


Fig. 2. (a, b) Seasonal variations in the daily mean of PAR (solid line) and the concentration of nitrate ( $\mu M$ , broken line). (c, d) Water density ( $kg + 1000 m^{-3}$ ) and chlorophyll concentration (arbitrary units, shaded areas) in the upper 50 m or the entire water column.

ing a Niskin water sampler and transferred to dark plastic containers. Subsamples were taken from these containers after mixing. For each sampling day, the biomass, determined from three to six discrete depths, was transformed (values  $\text{m}^{-2}$ ) by trapezoidal integration over the depth strata (0–28 m) (Nielsen and Bresta 1984). The 0–28-m depth-integrated water column corresponded to the euphotic zone in Disko Bay and represented the whole water column at the Kattegat site. Depth-integrated biomass of heterotrophic dinoflagellates in Kattegat was calculated from surface (2 m) and fluorescence maximum samples, as described for ciliates in Nielsen and Kiørboe (1994). Data on standing stocks are presented as monthly averages of 2–10 values, except for January in Kattegat when the station was only visited once. In the case of Disko Bay, data from 1996–1997 have been combined into one calendar year.

*Physicochemical measurements*—Vertical profiling of temperature, salinity and chlorophyll fluorescence was conducted as described in Kiørboe and Nielsen (1994) and Levinsen et al. (2000a). Solar irradiance was calculated as photosynthetically active radiation (PAR) from total global irradiance measured at Qeqertarsuaq by the Arctic Station of the University of Copenhagen (Disko Bay) or at Nakkehoved by the Danish Meteorological Institute (Kattegat). Samples for determination of nutrient concentrations were frozen immediately after sampling, and the concentration of nitrate was measured on an automatic nutrient analyzer following Grasshoff (1976).

*Primary producers*—Chlorophyll *a* (Chl *a*) was measured following extractions in 96% ethanol (Disko Bay; Levinsen et al. 2000a) or 90% acetone (Kattegat; Richardson and Christoffersen 1991).

The carbon content of the phytoplankton was calculated from Chl *a* using C/Chl *a* relations for Disko Bay of 38 (spring bloom), 44 (postbloom), and 109 (winter) (T. G. Nielsen et al. unpubl. data). For Kattegat, conversion factors were 29 (spring bloom) and 93 (late summer bloom); a linear increase in the C/Chl *a* ratio for the intervening summer period was applied (Olesen and Lundsgaard 1995). For the remaining winter period, we assumed a mean of the spring and late summer bloom C/Chl *a* ratios of 61.

Measurement of particulate primary production in Disko Bay was based on *in situ*  $^{14}\text{C}$  incubations at six depths in the upper 30 m (T. G. Nielsen et al. unpubl. data). Data on primary production from Kattegat, originating from Richardson and Christoffersen (1991), was based on  $^{14}\text{C}$  incubations in a natural light incubator at six photon flux densities.

*Ciliates and heterotrophic dinoflagellates*—Cells were preserved in 2% Lugol's and counted using inverted microscopy (Utermöhl 1958). Cell volumes were estimated from simple geometric shapes. Heterotrophic dinoflagellates <20  $\mu\text{m}$  were counted on proflavine-stained filter preparations of 1% glutaraldehyde-preserved water samples using epifluorescence microscopy (Haas 1982). The carbon content of cells was calculated from volume, applying a conversion factor of 0.13  $\text{pg C } \mu\text{m}^{-3}$  (Hansen et al. 1997). Ciliate and

heterotrophic dinoflagellate data from Disko Bay originates from Levinsen et al. (2000a). For the Kattegat, ciliate data originate from Nielsen et al. (1990) and Nielsen and Kiørboe (1994); heterotrophic dinoflagellates are from Hansen (1991).

Seasonal variations in growth rates of three selected sizes of ciliates, representing small (15  $\mu\text{m}$  equivalent spherical diameter [ESD]), medium (30  $\mu\text{m}$  ESD), and large (50  $\mu\text{m}$  ESD) species, were calculated using the equation describing size-dependent growth at 1.4°C in Disko Bay (Levinsen et al. 1999) or using the combined equation describing temperature and size-dependent growth of ciliates in Kattegat (Nielsen and Kiørboe 1994, NB erratum in *Limnol. Oceanogr.* 39(6): 1423). Growth capacities of similar-sized arctic, heterotrophic dinoflagellates were obtained from Levinsen et al. (1999) and unpublished results as explained in the figure text (Fig. 6), whereas the growth capacities of heterotrophic dinoflagellates in Kattegat were calculated from the size-growth equation provided by Hansen (1992).

*Copepods*—Depth-integrated zooplankton samples were collected by a submersible pump equipped with a 50- $\mu\text{m}$ -mesh net and were preserved in 2–4% formalin. In Disko Bay, 0–50-m samples were transformed to 0–28-m depth integrations by assuming equal distribution of copepods in the sampled water stratum. In the Kattegat, 0–28-m depth-integrated samples were collected. Biomass was determined using length-weight regressions (Kiørboe and Nielsen 1994; Madsen et al. 2001).

Copepod predation on protozooplankton in Disko Bay was computed as copepod biomass multiplied by the potential clearance, assuming weight-specific clearance capacities (at 3°C) of 1 and 4  $\text{ml } (\mu\text{g C})^{-1} \text{d}^{-1}$  on small (15  $\mu\text{m}$  ESD) and large (50  $\mu\text{m}$  ESD) ciliates, respectively (Levinsen et al. 2000b). For heterotrophic dinoflagellates, rates of 0.5 and 2  $\text{ml } (\mu\text{g C})^{-1} \text{d}^{-1}$  on the two cell sizes were applied (Levinsen et al. 2000b). Predation by the copepods in Kattegat was calculated similarly, using a clearance capacity (at 14°C) of 4 and 7  $\text{ml } (\mu\text{g C})^{-1} \text{d}^{-1}$  for small and large ciliates, respectively (Tiselius 1989); half of these values were applied for heterotrophic dinoflagellates assuming the same relative difference in clearance as determined in Disko Bay.

A  $Q_{10}$  of 2.8 was used to correct all growth, grazing, and predation rates for differences in temperature (Hansen et al. 1997).

*Statistical analysis*—To address which factors were most important in the regulation of the ciliate and heterotrophic dinoflagellate assemblages at the two study sites, multiple regression analyses were conducted. First, the biomass values were log-transformed to correct for nonnormal distributions. Then, in the multiple regression analysis, the most significant variables explaining the observed dynamics of the log-transformed ciliate and heterotrophic dinoflagellate biomass was identified using backward elimination in SAS/in-sight (type III test); that is, all potential explanatory variables were initially included and tested for significance at the 5% level. The variables in the resulting regression model that best explained the dynamics were ranked according to their significance level, 1 being most significant.

## Results

*Environmental conditions and water column structure*—In Disko Bay, the daily mean PAR fluctuated between zero during the 2 months of polar night and peaks of 65 mol photons  $m^{-2}$  during summer, when there was continuous light (Fig. 2a). Irradiance at the Kattegat position showed amplitude of similar magnitude, but irradiance was higher in the Kattegat than at Disko during the winter (Fig. 2b).

Sea ice developed in Disko Bay from February. Land fast sea ice covered the Bay in March–April, and drift ice was present until June (not shown). Ice was absent in Kattegat throughout the year considered.

The systems shared the stabilizing effects of receiving water with low salinity. In Disko Bay, seasonal stratification established in May at the time of ice break, when snow and ice melted, and strengthened over the summer because of solar warming. The fresh, warm surface layer influenced the upper 20–25 m of the water column (Fig. 2c). Associated with the decreasing day lengths, stratification weakened again, and in mid-September, the water column was mixed. Winter mixing persisted until the next ice-break. The Kattegat was almost permanently stratified with a halocline at 15–20 m because of constant outflow of brackish water from the Baltic Sea (Fig. 2d). From May to September, surface water heating strengthened the salinity-based stratification. Water temperatures ranged seasonally between 4 and 20°C. By comparison, temperatures in Disko Bay ranged from –1.8 to 6°C (Fig. 3a,b).

Nitrogen limited the primary production in both Disko Bay (Nielsen and Hansen 1995, 1999) and the Kattegat (Richardson and Christoffersen 1991). From a prebloom level of 8–10  $\mu M$  in the surface layer, nitrate was depleted to below the detection level after the spring bloom, until storms introduced nutrient-rich water (Fig. 2a,b). In Disko Bay, this episode occurred following destratification of the water column in September. In the Kattegat, mixing did not occur until the late winter.

*Seasonal plankton patterns*—Pelagic primary production in Disko Bay was zero during the polar night and low in spring when snow-covered ice reduced light penetration (Table 1). Break-up of the sea ice at the end of April increased production, and in the subsequent weeks, a bloom developed. In late May, a maximum primary production of 0.6–0.7  $g C m^{-2} d^{-1}$  occurred. The average for the month was  $\sim 0.3 g C m^{-2} d^{-1}$ . In June, mean primary production was  $\sim 0.2 g C m^{-2} d^{-1}$ , after which it declined to  $\sim 0.1 g C m^{-2} d^{-1}$  in July–September. Following autumn mixing, it declined further through October to reach undetectable levels in November. Annual estimated primary production was 26  $g C m^{-2}$  (T. G. Nielsen et al. unpubl. data).

Primary production was measurable throughout the year in the Kattegat (Table 1). The winter level was 0.1–0.2  $g C m^{-2} d^{-1}$ . In mid-March primary production increased, and at the end of the month, a maximum productivity of around 3.5  $g C m^{-2} d^{-1}$  was measured. The spring–summer monthly averages of primary production were 1.2–1.4  $g C m^{-2} d^{-1}$ , slowly declining in the autumn. Annual primary production

was estimated to 290  $g C m^{-2}$  (Richardson and Christoffersen 1991).

Phytoplankton biomass followed the patterns of primary production with distinct peaks in May (5  $g C m^{-2}$ ) and March (8  $g C m^{-2}$ ) (Fig. 3c,d). In Disko Bay, the diatoms *Thalassiosira* spp. and *Detonula confervaceae* were dominant bloom components. Prior to, and mixed with, these species were single cells and colonies of the prymnesiophyte *Phaeocystis* cf. *pouchetii*. (H. A. Thomsen unpubl. data). In the Kattegat, the spring bloom consisted of the diatoms *Chaetoceros* spp., *Thalassiosira* spp., *Thalassionema nitzschioides*, and *Skeletonema costatum* (Thomsen 1992). After the bloom, autotrophic flagellates, mostly nanoplankton, became abundant in both areas, but subsurface peaks of diatoms were observed throughout the postbloom period in Disko Bay (H. A. Thomsen unpubl. data) and regularly in Kattegat (Thomsen et al. 1992). Such dense subsurface concentrations of diatoms maintained a relatively high depth-integrated phytoplankton biomass during the summer (Fig. 3c,d). Besides small flagellates, the large mixotrophic dinoflagellates *Ceratium* spp. were occasionally important summer components in Kattegat. In August–September, they increased in abundance near and below the pycnocline and accounted for most of the phytoplankton biomass (Nielsen 1991). In contrast, *Ceratium* spp. were rare in Disko Bay.

Ciliates and heterotrophic dinoflagellates in Disko Bay showed a unimodal distribution with a pronounced seasonal peak (Fig. 3g,i). In the Kattegat, the distribution of heterotrophic dinoflagellates was bimodal, whereas ciliates showed minor seasonal changes (Fig. 3h,j). Ciliates from the Kattegat did not show a prompt numerical response to the phytoplankton bloom, as was otherwise characteristic for the protozooplankton in the two systems. Although ciliates and heterotrophic dinoflagellates in Disko Bay responded to the bloom by increasing to roughly the same level, ciliates in Kattegat obtained a mean biomass half that of the heterotrophic dinoflagellates. The responses in Disko Bay were initiated from winter levels that were 10-fold lower than in Kattegat. During the post-spring bloom period, the biomass of protozooplankton continued to increase in Disko Bay with peaks of ciliates (0.27  $g C m^{-2}$ ) and heterotrophic dinoflagellates (0.5  $g C m^{-2}$ ) in August. In Kattegat on the other hand, ciliates, but particularly heterotrophic dinoflagellates, declined after the spring bloom and remained at prebloom biomass levels until late summer, when a new increase was observed. The return to winter levels was much later than in Disko Bay.

Protozooplankton was dominated by athecate heterotrophic dinoflagellates (*Gymno-/Gyrodinium*, *Amphidinium* spp.) and naked oligotrichous ciliates (*Strombidium*, *Strobilidium* spp., *Lohmaniella oviformis*, *Laboea strobila*) at both sites (Fig. 4). The most striking differences were mass occurrence in Kattegat of the athecate dinoflagellate *Polykrikos schwartzii* in November and dominance of the thecate dinoflagellate species of *Protoperidinium* and *Diplopsalis* during the August–September bloom of *Ceratium* spp., when >75% of the total heterotrophic dinoflagellate biomass was thecate species. Generally, thecate heterotrophic dinoflagellates were more abundant in Kattegat than in Disko Bay, where their contribution always was minor. The autotrophic

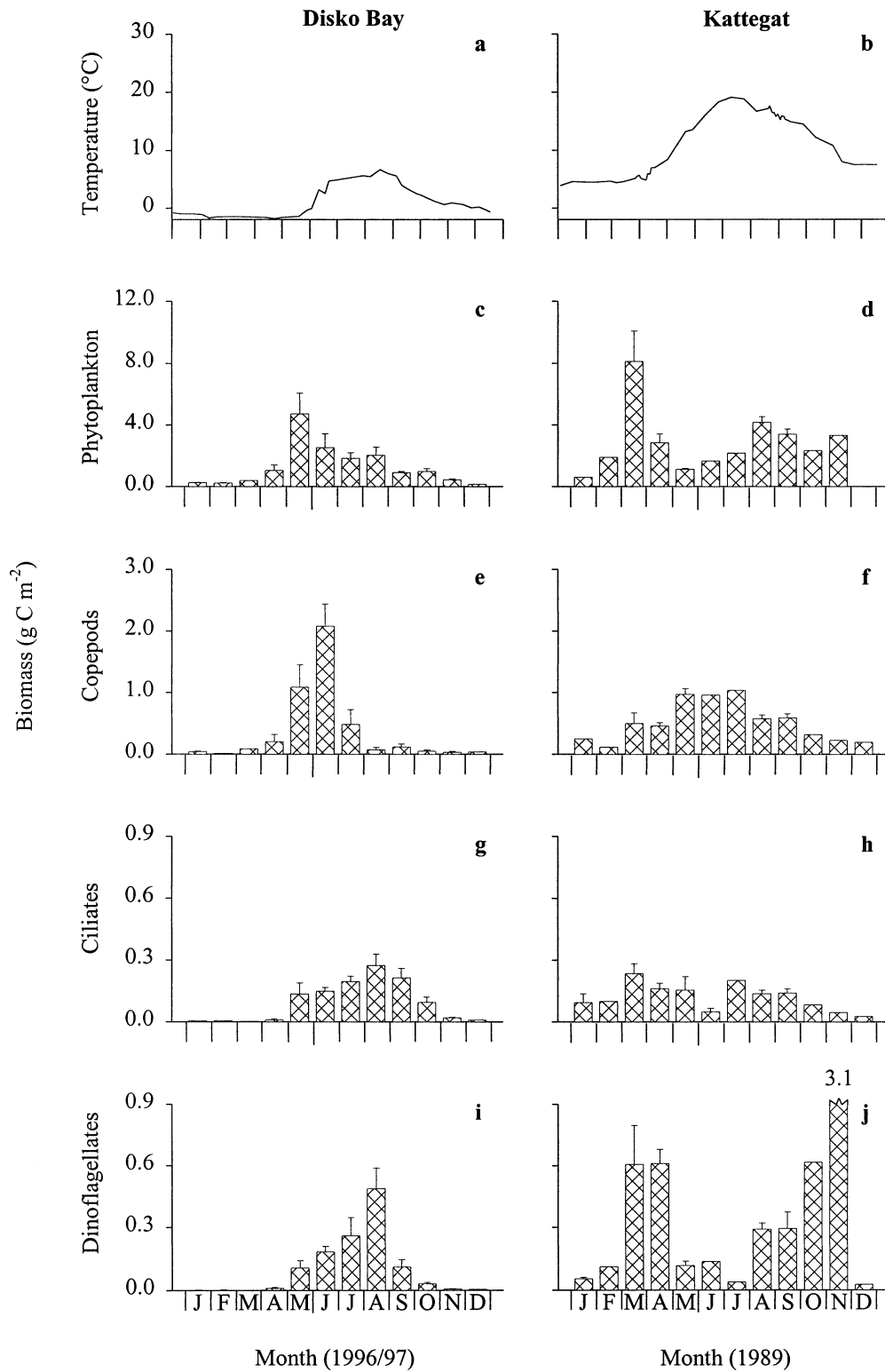


Fig. 3. (a, b) Surface water temperatures and depth-integrated monthly averages of the biomass of (c, d) phytoplankton, (e, f) total copepods, (g, h) ciliates excluding *Myrionecta rubra*, and (i, j) heterotrophic dinoflagellates throughout the year in Disko Bay, West Greenland, and Kattegat, Denmark. Bars denote standard errors. In December, the average copepod biomass of 1983–1996 from Ærtebjerg et al. (1998) has been used. No phytoplankton biomass was available for Kattegat in December. Note the different scales.

Table 1. Monthly averages ( $\pm$ SE) of primary production in Disko Bay and Kattegat calculated from T. G. Nielsen et al. (unpubl. data) and Richardson and Christoffersen (1991), respectively. Number of measurements are in parentheses; nd, no data.

	Primary production ( $\text{g C m}^{-2} \text{d}^{-1} \times 10^{-3}$ )	
	Disko Bay	Kattegat
Jan	1 (2)	100 (2)
Feb	1 (2)	223 (1)
Mar	9 (2)	2,932 $\pm$ 896 (6)
Apr	61 $\pm$ 43 (5)	1,341 $\pm$ 200 (8)
May	308 $\pm$ 93 (10)	1,183 $\pm$ 229 (3)
Jun	212 $\pm$ 70 (8)	1,436 (2)
Jul	97 $\pm$ 9 (4)	1,259 (2)
Aug	99 $\pm$ 21 (4)	nd (-)
Sep	85 $\pm$ 6 (4)	389 $\pm$ 64 (5)
Oct	34 $\pm$ 12 (4)	832 (1)
Nov	1 (1)	507 (1)
Dec	0 (1)	nd (-)

ciliate *Myrionecta rubra* (= *Mesodinium rubrum*) displayed a similar seasonal pattern at the two sites, but this species was more abundant in the Kattegat, forming >50% of the depth-integrated ciliate biomass in February–April compared to <35% in Disko Bay.

Copepod biomass in the sampled water stratum of Disko Bay was highest from late April to mid-July. At their peak in July, copepods obtained a biomass twice that of the Kattegat maximum (Fig. 3e,f). For the rest of the year, copepods were present at a low biomass level. The Kattegat experienced less pronounced seasonal variations in copepod biomass, with a pattern following the water temperature (Kjørboe and Nielsen 1994).

In Disko Bay, three species of *Calanus* (*C. finmarchicus*, *C. glacialis*, *C. hyperboreus*) contributed to >95% of the copepod biomass until they descended to the deep water in July and smaller species took over (Madsen et al. 2001). In the Kattegat, small neritic species of the genera *Acartia*, *Centropages*, *Temora*, *Oithona*, and *Pseudocalanus* were dominant throughout the year (Kjørboe and Nielsen 1994).

When pelagic grazers were pooled, they showed two distinct annual patterns. In Disko Bay a unimodal pattern was

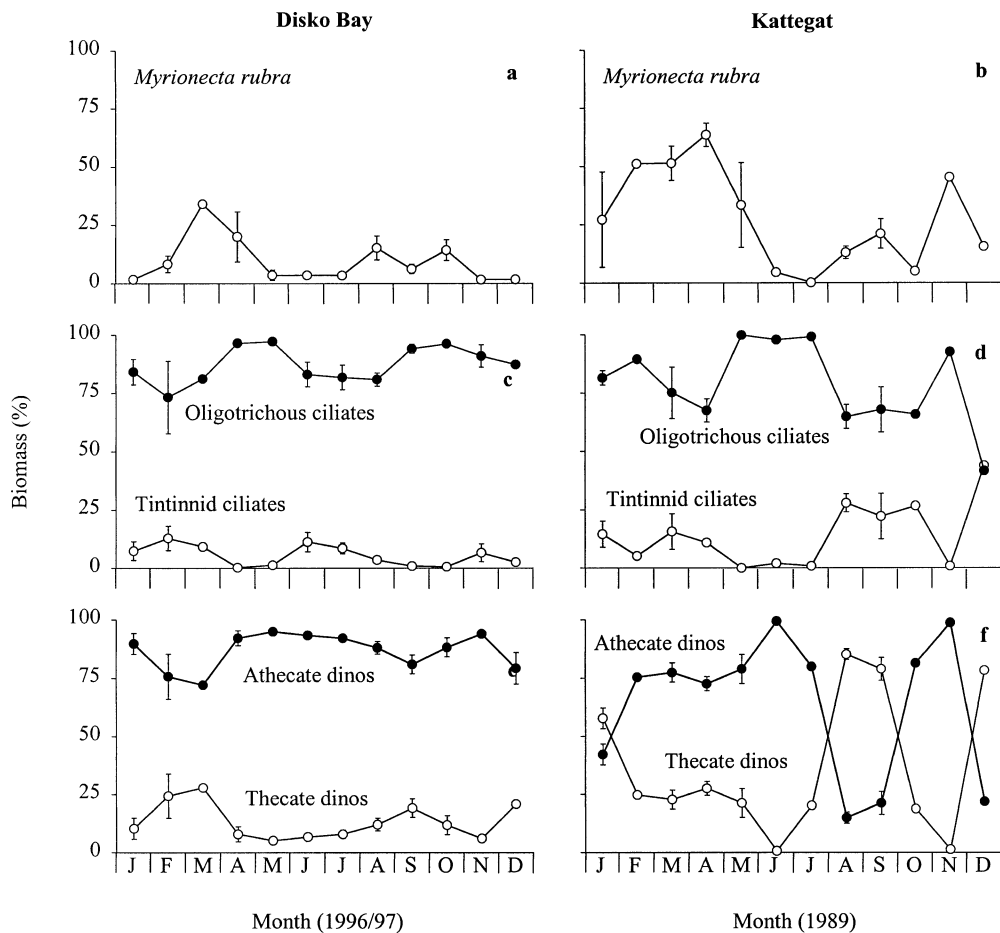


Fig. 4. Seasonal variations in the contribution (% of biomass) of (a, b) *Myrionecta rubra* to total ciliates, (c, d) tintinnid and oligotrichous ciliates to total ciliates excluding *M. rubra*, and (e, f) athecate and thecate heterotrophic dinoflagellates to total heterotrophic dinoflagellates. Bars denote standard errors.

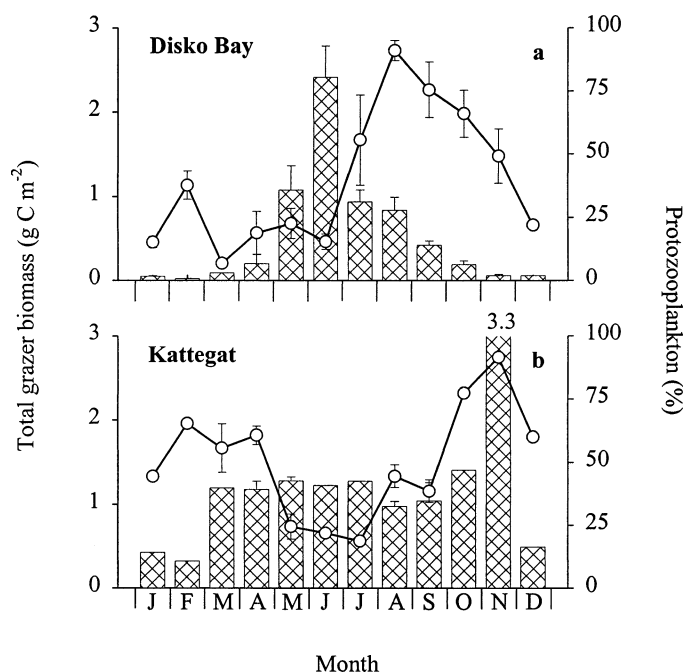


Fig. 5. Depth-integrated monthly averages with standard errors of total (ciliates + heterotrophic dinoflagellates + copepods) grazer biomass (bars) and protozooplankton (%) of total grazer biomass (line) in (a) Disko Bay and (b) Kattegat.

evident with a pronounced summer peak. In contrast, there was a relatively constant level of grazers in the Kattegat (Fig. 5). In relative terms, Disko Bay experienced a midsummer shift from a dominance of copepods to a dominance of protozooplankton. Before this shift, the fraction of protozooplankton was 15–20% of total grazer biomass. In July, the fraction increased to 56%, and in August, it increased further to 90%. During the autumn, the protozooplankton contribution decreased again until December, when they constituted 22%. In the Kattegat, shifts in the seasonal pattern of the two groups' relative contribution to total grazer biomass was also clear. Protozooplankton dominance from January to April was followed by a reduction of their importance in May–July, when copepods contributed ~75% to the total grazer biomass. Then, from late summer to early autumn, protozooplankton dominated again.

**Seasonal regulation and growth capacities of ciliates and heterotrophic dinoflagellates**—In Disko Bay, copepod clearance capacity on ciliates and heterotrophic dinoflagellates closely reflected the seasonal vertical migration of *Calanus* spp. The highest predation pressure was in May–June when the capacity of copepods exceeded growth of all but the smallest ciliates (Fig. 6a). From mid-July, the predation capacity declined to levels below the growth of even the largest ciliates. At this time, a peak of large species, like *Laboea strobila* and *Strobilidium spiralis*, was observed (Levinsen et al. 1999, 2000a). During the winter, top-down regulation of ciliates was further relaxed because of the low copepod stock. Throughout the year and even at their peak capacity, copepod clearance could not match the growth of small ciliates. The seasonal pattern of heterotrophic dinoflagellates

was similar to that of ciliates, but their growth rates were consistently higher compared to clearance than observed for ciliates (Fig. 6b).

In the Kattegat, predation capacity reflected the later establishment of the copepod community. Ciliate growth exceeded copepod clearance in the spring, but during summer, clearance equaled or surpassed growth of the larger ciliates (Fig. 6c). As in Disko Bay, predation was unable to match the growth of small ciliates. Heterotrophic dinoflagellates experienced a predation pressure exceeding their growth potential from May to July (Fig. 6d). Thereafter, the copepod predation capacity was reduced, although it was still, on average, similar to the potential growth of larger dinoflagellates. Throughout the year, small dinoflagellates could potentially outgrow copepod predation.

## Discussion

**Length of the productive season and the effect of temperature**—Irradiance and temperature, major driving forces on productivity and the cycling of phytoplankton-fixed carbon, change with latitude. In Disko Bay, no, or low, irradiance and ice cover delayed the spring bloom by about 2 months compared to Kattegat, and wind mixing terminated the productive season much earlier. Despite the much later bloom development, the temperature at the bloom onset was 5°C lower in Disko Bay (−1.5°C) compared to the Kattegat (4°C). Neglecting adaptations to temperature (*but see* Levinsen et al. 1999), the rates of specific growth, grazing, and predation would be predicted to be a factor of about two lower in Disko Bay. At the respective annual temperature peaks, these rates would differ by a factor of about four, and this trend of higher rates in the Kattegat would always apply because Disko Bay (<6°C) generally is colder than Kattegat (<20°C). However within a system, temperature likely influences planktonic grazers equally (Hansen et al. 1997). Temperature per se is thus not central in, for example, determining the importance of the “microbial” versus the “classical” grazers in permanently cold waters (Rivkin et al. 1996); it influences the rate at which the primary production is cycled.

**Composition of the protozooplankton assemblages**—The Arctic and temperate protozooplankton assemblages were similar; athecate heterotrophic dinoflagellates and oligotrichous ciliates were abundant, and thecate dinoflagellates and tintinnids were less abundant. This composition of protozooplankton >10 μm is typical for coastal and oceanic waters at various latitudes (Verity et al. 1993; Stoecker et al. 1995; Strom and Strom 1996). The most obvious difference between the systems was the relation between thecate and athecate dinoflagellates. Low abundance of thecate dinoflagellates in Disko Bay (Nielsen and Hansen 1995; Levinsen et al. 1999, Levinsen et al. 2000a), Canadian Arctic (Bursa 1961), and northeast Greenland (Rysgaard et al. 1999) suggests that it is characteristic for arctic waters.

**Top-down regulation**—Two periods were defined in Disko Bay based on the presence or absence of late stage *Calanus* spp. in the euphotic zone. In the “*Calanus* period,” con-

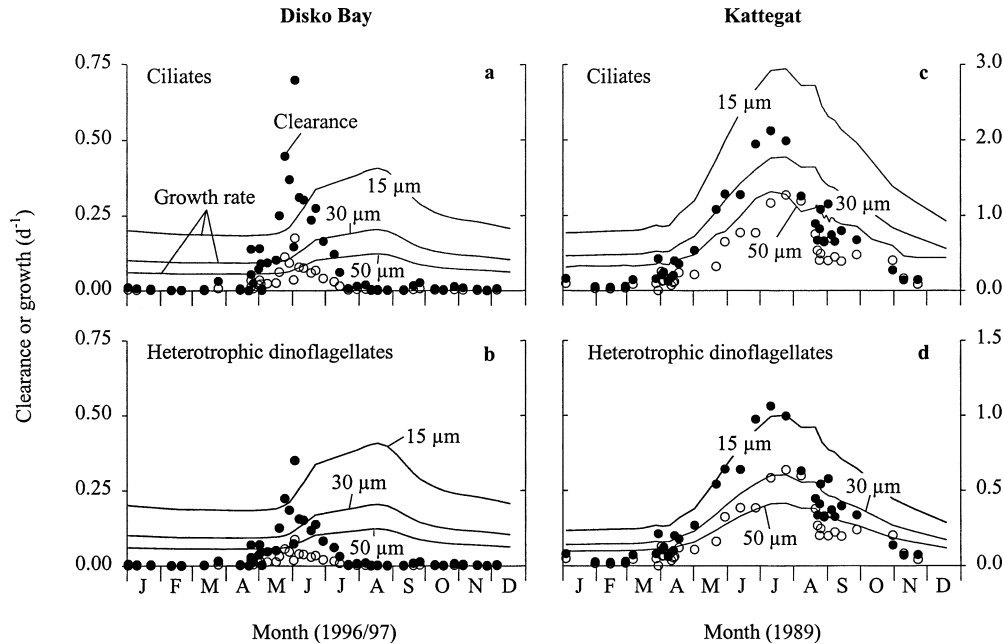


Fig. 6. Copepod clearance capacity (fraction of water cleared  $d^{-1}$ ) on  $15 \mu\text{m}$  ESD (open dots) and  $50 \mu\text{m}$  ESD (closed dots) of (a, c) ciliates and (b, d) heterotrophic dinoflagellates, and the growth potential (lines) of different sizes ( $15$ ,  $30$ , and  $50 \mu\text{m}$  ESD) of ciliates and heterotrophic dinoflagellates calculated as explained in the text. Corrections were made to the volume–growth rate relationship established for heterotrophic dinoflagellates in Disko Bay by Levinsen et al. (1999) because a less size-dependent growth (scaling factor of  $-0.16$ ) than usually reported indicated that large species had divided independently of growth. Thus, the volume-specific growth of a particular large species was probably somewhat overestimated when determined from changes in cell abundance and assuming constant cell volume. To determine growth of  $30$  and  $50 \mu\text{m}$  ESD-sized cells we therefore applied the common scaling factor of  $-0.25$  to a calculated mean growth rate for  $\sim 15 \mu\text{m}$  ESD dinoflagellates obtained by data from Levinsen et al. (1999) and additional unpublished values.

sisting of the phytoplankton spring bloom and the early post-bloom period, covariation of ciliates and heterotrophic dinoflagellates suggests that they were regulated by the same factor (Tables 2, 3). Copepods appeared to be obvious candidates as this controlling factor because of their high biomass and a clearance capacity that equaled or exceeded the

potential growth of protozooplankton (Fig. 6). However, contrary to expectation, top-down regulation was less important. Two observations support low predation effects during the first part of the *Calanus* period. First, buildup of ciliate and heterotrophic dinoflagellate biomass was exponential and occurred at instantaneous rates of around  $0.1 d^{-1}$

Table 2. The most significant variables explaining the observed variation of the ciliate biomass\* in Disko Bay and Kattegat identified by multiple regression analysis. PP, primary production; Phyto-C, phytoplankton biomass in carbon units;  $\pm$  *Calanus*, presence or absence of *Calanus* spp. in the euphotic zone. Model  $r^2$  in bold.

Ranking	Disko Bay			Kattegat Full year
	Full year	+ <i>Calanus</i>	- <i>Calanus</i>	
1	Chl <i>a</i>	H-dinoflagellates	Temperature	H-dinoflagellates
2	H-dinoflagellates			Phyto-C ( $>11 \mu\text{m}$ )
3	Phyto-C (total)			Temperature
4	$\pm$ <i>Calanus</i>			Phyto-C (total)
5	PP			PP
6				Copepods
$r^2$	<b>0.93</b>	<b>0.95</b>	<b>0.87</b>	<b>0.80</b>

\* The biomass values were log-transformed to assure normal distribution. Full-year Disko Bay data are from 22 Apr 1996 to 19 Jun 1997; + *Calanus* Disko Bay data are from the period between ascendance and descendance of *Calanus* spp. (24 Apr–14 Jul); - *Calanus* Disko Bay data are from the period after *Calanus* spp. left the euphotic zone (22 Jul) until ascendance again the following year (14 Apr).

Table 3. The most significant variables explaining the observed variation of the heterotrophic dinoflagellate biomass\* in Disko Bay and Kattegat identified by multiple regression analysis (abbreviations as in Table 2).

Ranking	Disko Bay			Kattegat Full year
	Full year	+ <i>Calanus</i>	− <i>Calanus</i>	
1	± <i>Calanus</i>	Ciliates	Temperature	Chl <i>a</i>
2	± <i>Calanus</i> × PP		Phyto-C (total)	Phyto-C (<11 μm)
3	Phyto-C (>11 μm)			
4	Copepods			
5	Ciliates			
<i>r</i> <sup>2</sup>	<b>0.83</b>	<b>0.95</b>	<b>0.97</b>	<b>0.63</b>

\* The biomass values were log-transformed to assure normal distribution. Full-year Disko Bay data are from 22 Apr 1996 to 19 Jun 1997; +*Calanus* Disko Bay data are from the period between ascendance and descendance of *Calanus* spp. (24 Apr–14 Jul); −*Calanus* Disko Bay data are from the period after *Calanus* spp. left the euphotic zone (22 Jul) until ascendance again the following year (14 Apr).

(Levinsen et al. 2000a). Second, field studies showed a low predation pressure on protozooplankton in Disko Bay when the concentration of phytoplankton was high (Levinsen et al. 2000b). We suggest that copepod feeding was saturated at high phytoplankton concentrations (Kiørboe et al. 1985; Kiørboe and Nielsen 1994), and the clearance on protozooplankton was reduced. Calanoid copepods are also able to switch between feeding modes whether feeding on motile (e.g., ciliates) or immobile (diatom) prey, depending on the relative abundance of prey types (Jonsson and Tiselius 1990). During the spring, protozooplankton accounted for only 5% of total protist biomass. Thus, *Calanus* spp. likely fed primarily as suspension feeders on diatoms. We conclude that protozooplankton, growing at rates approaching the temperature-limited maximum, took advantage of excess food concentrations for their abundant predators and, in this way, were able to reach summer levels while the temperature was still <0°C.

In the second part of the *Calanus* period, coincident with the summer minimum of phytoplankton, three lines of circumstantial evidence suggest that copepods exerted a heavy top-down pressure on protozooplankton: (1) regulation capacity was still pronounced (Fig. 6); (2) protozooplankton biomass was substantially reduced (this decrease in biomass occurred during late June to the beginning of July and was, therefore, not evident from the monthly averages in Fig. 3, but see Levinsen et al. 2000a); and (3) phytoplankton were not sufficiently abundant to support *Calanus* spp. egg production (Madsen et al. 2001).

In the Kattegat, Nielsen and Kiørboe (1994) argued for top-down control of the ciliate assemblage based on measured near-maximum growth rates of the dominant species in size-fractionated water samples. The multiple regressions conducted in the present study do not support this (Tables 2, 3), but the importance of copepods in Kattegat is indicated in the regression model of the ciliates; when copepods are eliminated from this model, a lower *r*<sup>2</sup> (=0.2) was obtained. The analysis might not be able to deal with species-specific differences in copepod grazing, which could obscure trends at the applied assemblage level (Tiselius and Jonsson 1990). Support for top-down regulation using regression also could have been blurred by regulation processes prevailing during seasons other than the four summer months, when copepod

regulation capacity exceeded ciliate growth (Fig. 6). In fact, all but the largest ciliates could outgrow copepod predation throughout most of the year. Cross-latitude differences in top-down regulation, as expected from the contrasting biomass development of copepods, were thus not found. The seasonal regulation pattern from the Kattegat resembles that of Disko Bay, with the heaviest top-down pressure in mid-summer, although the time of top-down pressure relative to the spring bloom is much lagged in the Kattegat. Top-down regulation in the Kattegat also persisted longer because a large copepod assemblage was present throughout the summer.

*Bottom-up regulation*—Differences in the annual cycles of primary production were responsible for a shorter protozooplankton growth season in Disko Bay than in Kattegat. Thus, food controlled the overall seasonal patterns of ciliates and heterotrophic dinoflagellates. Food limitation during winter was revealed by the fast response triggered by the phytoplankton spring bloom. For Disko Bay, winter starvation was also demonstrated by considerations of prey availability and threshold food concentrations for protozooplankton growth (Levinsen et al. 2000a).

Was bottom-up regulation in Disko Bay also important during other periods? In the post-*Calanus* period, after the predation pressure relaxed because of the downward migration of *Calanus* spp. in mid-July, the protozooplankton increased again to peak values in August (Fig. 3). Although specific growth rates exceeded copepod clearance capacity for the rest of the year (Fig. 6), the biomass thereafter declined to winter levels. Growth could not keep up with loss rates at the decreasing temperatures. Only heterotrophic dinoflagellates were secondarily correlated with phytoplankton, whereas both groups of protozooplankton were strongly correlated with temperature (Tables 2, 3). This suggests that food was not the most important limiting factor when top-down regulation by *Calanus* spp. relaxed; rather, temperature limited growth of the protozooplankton during the post-*Calanus* period in Disko Bay. The linear increase in surface Chl *a* concentration in the beginning of October from 0.2 to 0.8 μg L<sup>−1</sup> supports a temperature-initiated decoupling of primary production and grazing during the last part of the growth season.

By comparison, using stepwise regression analysis to resolve the interactive effects of temperature and food concentration, Verity (1986) found that Chl *a* accounted for the largest source of variance in the community growth rates of tintinnid ciliates in Narragansett Bay, Rhode Island. However, he also found that the largest fraction of variance in the maximum growth rate was attributed to temperature. In the Kattegat, Nielsen and Kiørboe (1994) found that temperature explained 75–97% of the variation in measured ciliate growth rates; the near-maximal growth rates were independent of various measures of food availability. Extrapolating these results to Disko Bay implies that ciliates were growing at temperature-limited maximum rates and were not bottom-up regulated. This is corroborated by the growth rates measured in late summer 1994 with water collected from the same station in Disko Bay (Levinsen et al. 1999). These rates were close to maximum rates for several dominant species. Regulation of large heterotrophic dinoflagellate was different from that of the ciliates. They possibly experienced food limitation before the ciliates, supported by (1) a biomass decline ~3 weeks earlier (Levinsen et al. 1999, 2000a), (2) dominance of phytoplankton cells <11  $\mu\text{m}$  (70–80% of total Chl *a*), which are suboptimal as food, and (3) correlation with phytoplankton (Table 3).

In the Kattegat, low abundance of small phytoplankton cells during the summer suggests food limitation of heterotrophic dinoflagellates at a time when they further had to compete for resources with their abundant copepod predators. It appeared that heterotrophic dinoflagellates in the Kattegat, in contrast to ciliates, were usually food limited (Table 3). Small heterotrophic dinoflagellates that feed on nanoplankton were correlated with the phytoplankton size fraction <11  $\mu\text{m}$  (Hansen 1991). They thus constitute an exception to the general pattern of seasonal changing regulation factors (e.g., coupled to the development of copepods), as indicated by the multiple regression analysis: the best model describing the annual development of protozooplankton includes several variables.

**Regulation windows**—The significant biomass of protozooplankton in Disko Bay is ascribed to the regulation “window” created by the spring bloom, when the copepods become food saturated, and to the window created by the migration of late stage *Calanus* spp. to the deep water. We suggest that ciliates and heterotrophic dinoflagellates are also important grazers in other arctic pelagic ecosystems when such windows are present. In contrast, protozooplankton should play a minor role in these systems when regulation windows are absent. Support for the latter is found in Young Sound, a fjord in northeast Greenland, where the ciliate and heterotrophic dinoflagellate assemblages were modest compared to copepods that were able to consume total pelagic primary production (Rysgaard et al. 1999). In this high arctic fjord, *Calanus* spp. did not make a downward migration during the very short productive season (10 months of ice cover), and the spring bloom concentration of Chl *a* was low (<2  $\mu\text{g L}^{-1}$ ). Copepods controlled both phyto- and protozooplankton during the entire productive season.

In the Kattegat, the protozooplankton, as in Disko Bay, experienced two windows: one in the spring before estab-

Table 4. Annual production by ciliates and heterotrophic dinoflagellates and their ingestion of primary production (PP) in Disko Bay, West Greenland, and Kattegat, Denmark, calculated using near-maximum growth rates ( $\mu_{\text{max}}$ , Disko Bay: Levinsen et al. 2000a; Kattegat: Nielsen and Kiørboe 1994) or a clearance of  $10^5$  body volumes (BV)  $\text{h}^{-1}$  at 20°C corrected to ambient temperature applying a  $Q_{10}$  of 2.8.

Location		Ciliates		Heterotrophic dinoflagellates	
		$\mu_{\text{max}}$	$10^5$ BV	$\mu_{\text{max}}$	$10^5$ BV
Disko Bay	Production (g C $\text{m}^{-2} \text{yr}^{-1}$ )	5	3	5	3
	Ingestion (% PP $\text{yr}^{-1}$ )	55	32	55	37
Kattegat	Production (g C $\text{m}^{-2} \text{yr}^{-1}$ )	57	19	—	55
	Ingestion (% PP $\text{yr}^{-1}$ )	60	20	—	57

lishment of the copepod assemblage and a second in late summer–early autumn when the copepod community declined because of elevated mortality (Kiørboe and Nielsen 1994). The only exception to this pattern was the dinoflagellates <20  $\mu\text{m}$ . Small heterotrophic dinoflagellates in the Kattegat obtained peak abundances coincident with the largest regulation capacity of the copepods and the summer minimum of heterotrophic dinoflagellates >20  $\mu\text{m}$  (see fig. 2 in Hansen 1991). They were able to exploit the feeding niche that occurred when the large species were in low abundance, supported by growth rates that could exceed copepod clearance capacity (Fig. 6). Nonetheless, although copepods exerted a strong predatory effect, food may have generally been the primary controlling factor of the heterotrophic dinoflagellate assemblage during this period (see “Bottom-up regulation”).

**Production and grazing**—Based on the distribution of total grazer biomass (Fig. 5), much of the annual primary production was potentially grazed by protozooplankton, which have specific ingestion capacities an order of magnitude greater than those of copepods (Hansen et al. 1997 and references therein). Quantitatively, the importance of protozooplankton grazing was supported by calculations based on their growth and by clearance rates assumed to be  $10^5$  body volumes  $\text{h}^{-1}$  (at 20°C; Table 4).

In Disko Bay, net growth rates calculated from exponential increase in biomass from winter to summer levels (Levinsen et al. 2000a) were used to estimate protozooplankton production and grazing, assuming that these rates represent typical growth during the productive season. Applying growth rates of 0.11  $\text{d}^{-1}$  for ciliates (excluding *M. rubra*) and 0.10  $\text{d}^{-1}$  for heterotrophic dinoflagellates resulted in almost equal production of the two protozooplankton assemblages of 3–5 g C  $\text{m}^{-2} \text{yr}^{-1}$  (Table 4). This production is approximately an order of magnitude lower than the estimated ciliate production in the Kattegat of 19–57 g C  $\text{m}^{-2} \text{yr}^{-1}$  (Nielsen and Kiørboe 1994) and in other temperate coastal waters (Verity 1987, Montagnes et al. 1988, Leakey et al. 1992), but it is more than 10-fold higher than in Young

Sound, northeast Greenland (Rysgaard et al. 1999). The same applies for heterotrophic dinoflagellate production (Table 4). Thus, although the levels of protozooplankton biomass in arctic and temperate regions are similar, productivity differs. The magnitude of production reflects temperature, which perhaps is the principal factor controlling the different flows of carbon through ciliates and heterotrophic dinoflagellates, but the magnitude is also reflected by the light regime, which determines the length of the productive season.

The annual production by ciliates in Disko Bay would require a consumption of 9–15 g C m<sup>-2</sup> assuming a growth yield of 0.33 (Hansen et al. 1997). This corresponds to 32–55% of the primary production of 27 g C m<sup>-2</sup> yr<sup>-1</sup> and is similar to the 20–60% estimated for the Kattegat. Likewise, the grazing impact by heterotrophic dinoflagellates accounted for 37–55% (Disko Bay) and 57% (Kattegat) of the annual primary production. This means that despite the difference in absolute production, protozooplankton were able to annually cycle similar fractions of primary production in the two systems.

Heterotrophic dinoflagellates preferably ingest prey near their own size (10–50 μm) (Hansen et al. 1994). They, therefore, reduce phytoplankton sedimentation and contribute to the retention of material in the euphotic zone by grazing on diatoms. Compared with mesozooplankton, heterotrophic dinoflagellates can respond quickly to episodic diatom blooms. In Disko Bay, heterotrophic dinoflagellates were estimated to graze 7–18% of the diatom bloom. Using the same data for the Kattegat as presented in this paper, Lundsgaard and Olesen (1997) suggested that heterotrophic dinoflagellate ingestion was 21% of the spring bloom primary production. By comparison, the potential grazing of copepods during the same period was 20 to >100% (Disko; Madsen et al. 2001) and 8% (Kattegat; Lundsgaard and Olesen 1997) of the primary production.

*Regulation of biomass versus production in the two ecosystems*—The similar size of the ciliate and heterotrophic dinoflagellate assemblages in Disko Bay and Kattegat during the productive season suggests temperature-independent biomass distributions (Fig. 3). Support for this statement can be established by the Lotka–Volterra model to describe predator–prey dynamics. According to the model, fluctuations in prey biomass (phytoplankton) can be expressed by the differential equation

$$dB/dt = \mu B - \alpha BP$$

where  $B$  is phytoplankton biomass,  $\mu$  is the phytoplankton growth rate,  $\alpha$  is clearance on phytoplankton by protozooplankton, and  $P$  is protozooplankton biomass. Similarly, the Lotka–Volterra predator (protozooplankton) equation is

$$dP/dt = \alpha YBP - mP$$

where  $Y$  is yield and  $m$  is mortality of predators. If we assume steady state (i.e.,  $dB/dt$  and  $dP/dt = 0$ ), which is an approximation that might not be too different from prevailing conditions during much of the productive season, the concentrations of protozooplankton and phytoplankton become:  $P = \mu/\alpha$  and  $B = m/\alpha Y$ , respectively. Because there are no reasons a priori to believe that  $\mu$ ,  $\alpha$ , and  $m$  depend

differently on temperature, this is indicative of a temperature-independent biomass of  $B$  and  $P$ .

However, if temperature does not regulate ciliate and heterotrophic dinoflagellate biomass, then what does? It is reasonable to assume that the total phytoplankton biomass produced in a system is ultimately limited by nutrients and that protozooplankton are ultimately limited by food availability. From this it follows that the total protozooplankton biomass produced is determined by resource limitation of their phytoplankton prey; the equal biomass levels observed are due to similar winter concentrations of nitrate in the two ecosystems (Fig. 2a,b). When nutrients and biomasses are the same and production varies 10-fold between the systems, then the growth rate must vary by a factor of 10 because production equals biomass times community growth rate. In Disko Bay, the lower growth rate of phytoplankton might be the result of both light and temperature, but for the protozooplankton, the lower growth must be due to temperature.

*Summary*—This study shows the equal composition, biomass, and trophic roles of protozooplankton in arctic and temperate regions. Previously published papers have documented the importance of bacteria in Disko Bay (Nielsen and Hansen 1995, 1999; Møller and Nielsen 2000, Thingstad et al. in press); bacteria production is 37% of the annual primary production (Nielsen et al. pers. comm.). Because protozooplankton are linking bacteria–flagellates to the “classical” food web, similar-sized bacteria and protozooplankton assemblages imply similar importance of microbial food webs. Remarks such as “Microbial food webs operate at high latitudes, but do not seem as quantitatively important as in temperate neritic environments” (Grebmeier et al. 1995, p. 235) are, therefore, incorrect. The seasonal biomass patterns of the ciliates and heterotrophic dinoflagellates primarily reflect the length of the productive period. However, regulation windows with reduced copepod predation are important as well because copepods have a large structuring effect on the protozooplankton assemblage. It is further suggested that the size of the assemblage is ultimately set by the limiting resource for their phytoplankton prey; winter levels of this resource (inorganic nitrogen) are similar in the two systems. Temperature causes productivity in the arctic and temperate system to differ, but on a relative basis this is unimportant; despite an order of magnitude difference in grazing capacity, protozooplankton are equally important in the cycling of pelagic primary production.

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