Vol. 117: 241–248, 1995 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published February 9

Heterotrophic dinoflagellates in the ecosystem of the Gulf of Gdańsk

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ABSTRACT: Quantitative studies on heterotrophic dinoflagellates were carried out in 1987 at 3 stations located in the Gulf of Gdańsk (southern Baltic) and differing in environmental conditions. Heterotrophic dinoflagellates were identified under an epifluorescence microscope and counted, using Utermöhl's technique, in Lugol-solution-treated samples. Two biomass peaks were recorded over the year: one in the spring, co-occurring with the spring phytoplankton bloom, and the other in autumn. Heterotrophic dinoflagellates were the dominant component of the protozooplankton, particularly in the eutrophic, highly productive Gulf waters where they made up almost half of the total zooplankton and dominated over the metazooplankton.

KEY WORDS: Heterotrophic dinoflagellates · Protozooplankton · Epifluorescence · Biomass changes · Baltic Sea

INTRODUCTION

Dinoflagellates (Dinophyceae) are a large taxon consisting of numerous species which inhabit different marine, brackish, and freshwater habitats. Dinoflagellates occur both in the water column, as a component of the plankton, and at the bottom of water bodies, where they belong to the benthos. The taxon reveals an unmatched diversity of trophic types, from pure autotrophs through mixotrophs and pure heterotrophs to parasites, each of the categories being represented by numerous species.

In the Gulf of Gdańsk, Ringer (1990) listed a total of 25 dinoflagellate species; the list is, however, far from complete. Most notably, it lacks small-sized species known to occur in the Gulf (Pliński et al. 1985, Bralewska 1992). Owing to difficulties inherent in their identification, numerous dinoflagellates have not yet been found in the Gulf of Gdańsk, and this is particularly the case with naked forms. Some dinoflagellate species belong to the most important phytoplankters and form blooms in certain seasons. Edler et al. (1984) listed a total of 117 dinoflagellate species in the entire Baltic Sea.

Despite their distinctly different functional character, heterotrophic dinoflagellates have been treated as phytoplankters in most routine algal studies. However, their contribution to the biomass (usually less than 10%) and abundance were not overly high compared to those of autotrophs. Furthermore, the taxon was disregarded for a long time in zooplankton studies, as its importance for the ecosystem was considered negligible. Smetaček (1981) was among the first workers to demonstrate that heterotrophic dinoflagellates were an important functional entity in the Baltic ecosystem. Studies on the trophic status of individual dinoflagellate species (Lessard & Swift 1986, Hansen 1991b) and on feeding mechanisms of heterotrophic dinoflagellates (Gaines & Taylor 1984, Gaines & Elbrächter 1987, Schnepf & Elbrächter 1992) have been initiated since then. However, many questions such as feeding preferences, energy budgets of individual species, and their role in the energy flow in the ecosystem still remain unanswered and require investigation.

This study was aimed at evaluating the importance of heterotrophic dinoflagellates in the ecosystem of the Gulf of Gdańsk by estimating their biomass and comparing it with the biomass of other plankters. It was frequently unclear whether a given species was an autor a heterotroph, and thus it was necessary to examine the cells for the presence of chlorophyll.

MATERIALS AND METHODS

Cells of individual dinoflagellate species were examined for the presence of chlorophyll under an Olympus IMT-2 inverted microscope with an IMT2-RFL epifluorescence attachment. The cells, live or fixed with a weak glutardialdehyde solution, were examined under blue excitation light obtained with a combination of BP490 and EY455 excitation filters, a DM500 dichroic mirror, and Y455 and B460 barrier filters. The photosynthetically active pigments produced red or orange autofluorescence, the cytoplasm itself fluorescing various shades of green. The cells were examined while fresh, within several hours of collection. The cell size, colour and intensity of fluorescence, arrangement of chloroplasts, and the presence of food remains, if any, were recorded. The fluorescence study was carried out in October 1989 on board a vessel operating in the southern Baltic and in May 1991 at the Sea Fisheries Institute laboratory, following collection of samples from the wharf near the Institute.

To assess the importance of heterotrophic dinoflagellates in the ecosystem, samples collected in 1987 at 3 stations situated in the Gulf of Gdańsk (Fig. 1) were analysed. Samples were collected every 5 m down to 30 m, and every 10 m below that level; the samples were integrated over the depth intervals 0 to 15 m and 15 m to the bottom (about 35 m) at Stns 92A and R6, and over 0 to 15, 15 to 30, 30 to 60, 60 to 90, and 90 m to the bottom (about 105 m) at Stn G2. Collections were made every 2 to 3 wk between January 1987 and January 1988. Below 30 m depth at Stn G2, only 1 sample per month was analysed from September onwards. On each sampling event, other community components were sampled as well; the relevant data are reported elsewhere (Witek et al. 1993).

Samples were preserved in Lugol's solution, and heterotrophic dinoflagellates were identified and counted simultaneously with phytoplankton under an inverted microscope (Utermöhl 1958).

Dinoflagellate biomass was determined by measuring the individual cell volume and using conversion factors of 0.11 pg C μm^{-3} (naked forms) and 0.13 pg C μm^{-3} (thecate forms) (Edler 1979).

RESULTS

Fluorescence observations

Dinoflagellates examined for the presence of photosynthetically active pigments in cells, and the results of observations, are listed in Table 1.

The combination of filters used elicited a brilliant red fluorescence for chlorophyll *a* and a yellow-orange fluorescence for phycoerythrin and phycocyanin. The cytoplasm of heterotrophic dinoflagellates fluoresced green, probably due to the presence of some carotenoids (Lessard & Swift 1986, Schnepf & Elbrächter 1988, Laval-Peuto 1991). Thus the brilliant red fluorescence is a property of autotrophic dinoflagellate cells, while heterotrophic cells fluoresce green. The yellow-orange fluorescence may be associated with the presence of phycobilin-containing cyanobacterial or cryptophycean endosymbionts.

The 4 dinoflagellate species *Peridiniella catenata, Heterocapsa triquetra, Katodinium rotundatum* and *Prorocentrum minimum*, all autotrophic, gave off an intensely red fluorescence from their chloroplasts. The cytoplasm of heterotrophic dinoflagellates of the genus *Protoperidinium* and of the 'Diplopsalis group' fluoresced green. All the naked dinoflagellates examined turned out to be heterotrophic. The yellow, orange, or red granules occasionally visible inside them were most likely feeding vacuoles containing remains of phytal food. Large (about 15 µm in diameter), spherical luminous bodies emitting intensely red light were occasionally observed, most often in larger naked forms. The spheres were most likely cells of the Centrales diatoms that had been ingested whole and not yet digested.

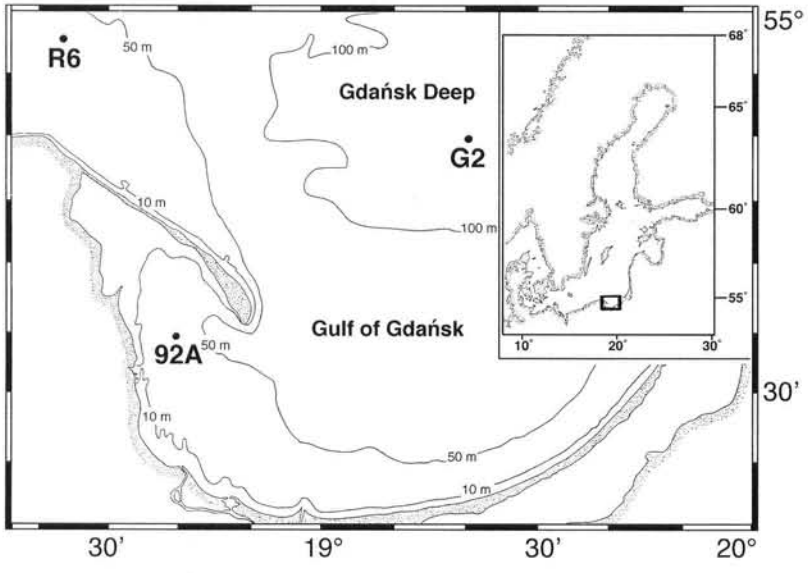

Fig. 1. Location of stations sampled in 1987 in the southern Baltic

Table 1. Dinoflagellates examined under epifluorescence microscopy for the presence of phytopigments. n: number of specimens examined

Species or group	n	Cell size (µm) Length	Width	Fluorescence[a]	Interpretation
Peridiniella catenata (Levander, 1894, Kofoid, 1911b) Balech, 1977	20	25–36	30–32	1	Autotrophic
Heterocapsa triquetra (Ehrenberg, 1840) Stein, 1883	20	16–30	9–18	1	Autotrophic
Katodinium rotundatum (Lohmann, 1908) Loeblich III, 1965	10	12–14		1	Autotrophic
Prorocentrum minimum (Pavillard, 1916) Schiller, 1933	20	14–22	10–15	1	Autotrophic
Gonyaulax triacantha Jorgensen, 1900	9	46–56	36–41	3ab•	Endosymbionts
Dinophysis acuminata Claparede & Lachmann, 1858/59	5	41–45	25–31	3c	Endosymbionts
Dinophysis cf. *norvegica* Claparede & Lachmann, 1858/59	5	46–64		3a	Endosymbionts
Protoperidinium bipes (Paulsen, 1904) Balech, 1974	10	23–35	19–30	3	Heterotrophic
Protoperidinium brevipes (Paulsen, 1908) Balech, 1974	13	31–36	25–36	3	Heterotrophic
Protoperidinium pellucidum (Bergh, 1882) Schütt, 1895a	10	52–77	49–67	2	Heterotrophic
Diplopsalis group cf. *Oblea rotundata* (Lebour, 1922) Balech ex Sournia, 1973	8	26–34	26–34	3d	Heterotrophic
Form 1 — thecate dinoflagellates of *Cachonina*-like shape	3	23–28	23–26	3e	Heterotrophic
Form 2 — small, naked dinoflagellates of *Gymnodinium/ Gyrodinium* type	13	18–26	16–26	3f	Heterotrophic+h[b]
Form 3 — large, naked dinoflagellates of *Gyrodinium* type	5	101–120	34–38	3g	Heterotrophic
Form 4 — large, naked dinoflagellates of *Gymnodinium/ Gyrodinium* type	19	34–57	31–54	3gb	Heterotrophic+h
Amphidinium crassum Lohmann, 1908	4	23–26	11–21	3e	Heterotrophic
Ebria tripartita (Schumann, 1867) Lemmermann, 1900b	10	33–35	26–33	3	Heterotrophic

[a](1) intensely red, filling whole cell volume, (2) intensely green, filling whole cell volume, (3) pale green, filling whole cell volume, (a) with numerous orange bodies, (b) in some cases with yellow and/or red bodies, (c) with 2 orange bodies, (d) in some cases with orange shade, (e) with orange shade, (f) with single red and/or orange bodies, (g) with intensely green granules

[b]h: containing remnants of plant food

•See also text

Dinoflagellates of the genus *Dinophysis* and the species *Gonyaulax triacantha* contained inclusions emitting orange fluorescence. These were probably cyanobacterial or cryptophycean endosymbionts.

Field studies

The 3 sampling stations (Fig. 1) differed with respect to their environmental characteristics. Stn 92A, 35 m deep, is representative of sheltered and eutrophic Gulf waters, with a distinct seasonal thermocline and high primary production. Stn R6, of similar depth, represents open sea conditions, with a water column that is well mixed all the way down to the bottom almost throughout the year; primary production is less than half that in the Gulf. Stn G2 typifies the situation in the central part of the Gdańsk Deep, with over 100 m depth and permanent temperature and salinity stratification; the oxygen content is drastically reduced below the halocline.

Among the heterotrophic dinoflagellates, species of the genera *Gyrodinium* and *Protoperidinium*, as well as a group called the 'naked dinoflagellates', dominated by organisms of the *Gymnodinium/Gyrodinium* type, provided most of the biomass. Additionally, *Ebria tripartita* periodically attained large biomass values.

Two peaks were characteristic in the pattern of annual biomass changes, one in the spring, when the thecate forms reached peak densities, and the other in autumn (Figs. 2 to 4), thus indicating that heterotrophic biomass was related to phytoplankton dynamics. At Stn 92A, both peaks were very pronounced within the 0 to 15 m and 15 m to bottom layers, the maximum biomasses in the lower layer being higher than those in the upper one. The autumn peak at Stn R6 was less pronounced, and at Stn G2 it occurred within the 15 to 30 m layer.

The heterotrophic dinoflagellate biomass changes showed a very interesting depth-related pattern at Stn G2 (Fig. 4). In the upper layer, the biomass peak occurred in late April–early May and showed a time

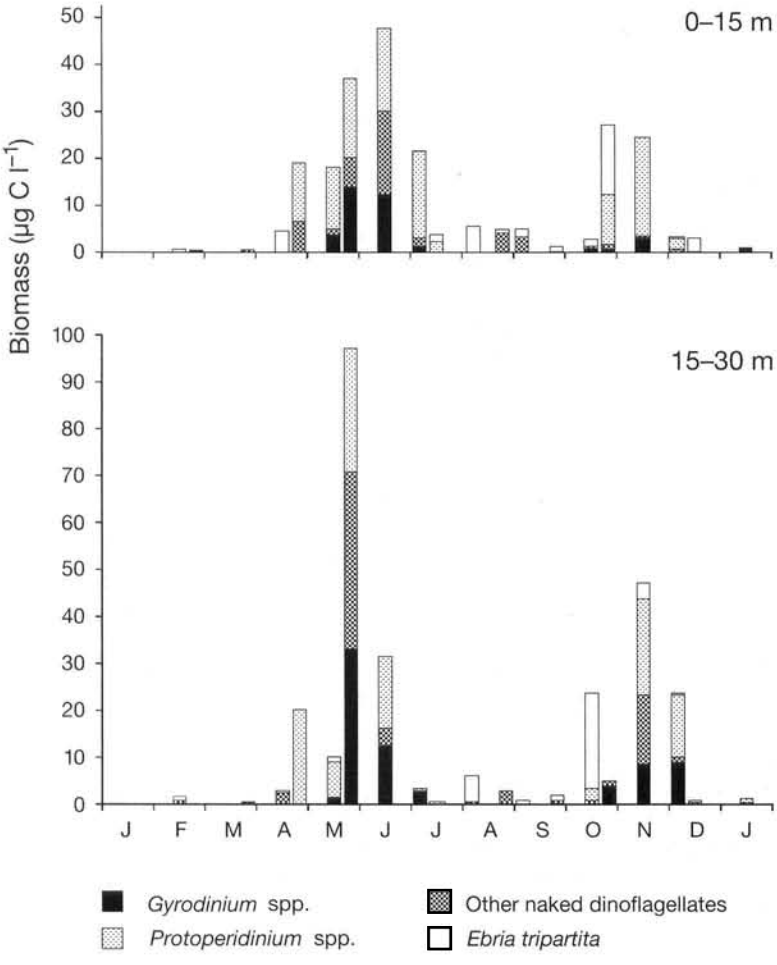

Fig. 2. Biomass of heterotrophic dinoflagellates at Stn 92A

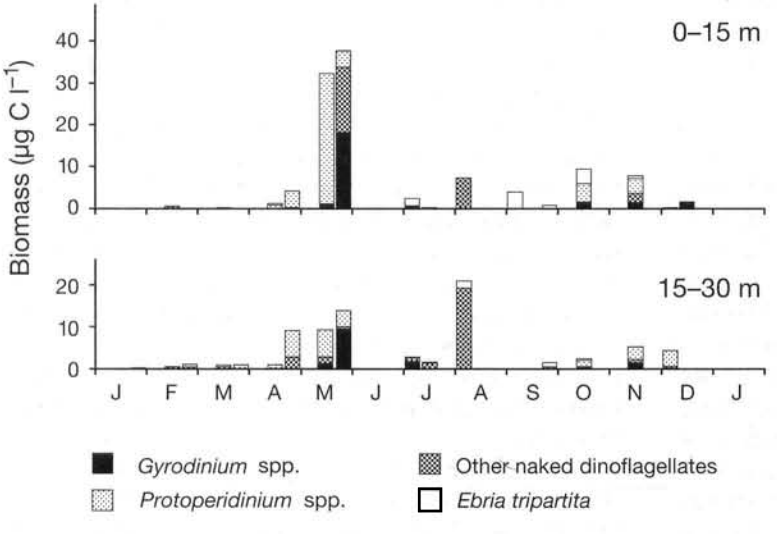

Fig. 3. Biomass of heterotrophic dinoflagellates at Stn R6

lag progressing with depth. The maximum biomass within the deep (60 to 90 m) layer occurred almost 2 mo after the peak had been recorded near the surface. Heterotrophic dinoflagellates failed to form dense concentrations below 90 m. Below 30 m, heterotrophic dinoflagellates were dominated by species of the genus *Gyrodinium*.

DISCUSSION

Fluorescence observations

Epifluorescence microscopy allows chlorophyll- and other phytopigment-containing cells to be precisely distinguished from those lacking pigments. The technique, however, is difficult to apply in routine algal studies. For this reason, attempts should be made to examine all dinoflagellate species for the presence or absence of phytopigments and provide this information in identification keys or disseminate it in checklists, as Lessard & Swift (1986) did for several NW Atlantic dinoflagellate species. Nevertheless, epifluorescence microscopy still seems to be a valuable supplementary method in cases when identification of dinoflagellates, particularly naked forms in preserved samples, is very problematic and when some species may be facultative heterotrophs.

The genus *Dinophysis* and *Gonyaulax triacantha* proved to be a difficult group as the pale green cytoplasm of the former contained orange inclusions, while brilliant yellow-orange to pale-red granules, varying in numbers but never filling the entire cell volume, were observed in the latter. In some older papers (Schiller 1933, Drebes 1974) these dinoflagellates were classified as autotrophs. In light of the present study and the work reported by Lessard & Swift (1986), however, the dinoflagellates in question seem to contain cyanobacterial or cryptophycean endosymbionts. Dinoflagellate cell ultrastructure, observed under electron microscope by Schnepf & Elbrächter (1988), led those workers to conclude that the chloroplasts present in *Dinophysis* individuals resembled those

of cryptophyceans. Without similar observations it is difficult at the moment to elaborate on the nature and origin of phycobilins in *G. triacantha*. The species requires further study, which should include an analysis of its ultrastructure. The question of the endosymbiont impact on dinoflagellate feeding remains unsolved as well. Does the symbiosis meet the energy demand of the hosts or does it merely supplement heterotrophic feeding? Many dinoflagellate species are known to switch from autotrophic to heterotrophic feeding mode, only a few being strictly autotrophic (Gaines & Elbrächter 1987, Schnepf & Elbrächter 1992).

Field studies

Seasonal changes in heterotrophic dinoflagellate biomass in the Gulf of Gdańsk were similar to those observed in Kiel Bight (Smetaček 1981) and in the Danish sounds (Hansen 1991b); moreover, they even resembled those recorded in such distant parts as the waters off southern California, USA (Kimor 1981). In all the areas mentioned, 2 biomass peaks were observed, the first one in the spring, overlapping the spring phytoplankton bloom. Initial phases of the heterotrophic dinoflagellate peaks in the Gulf of Gdańsk, both in spring and in autumn, coincided with mass development of diatoms. In the spring, however, the heterotrophic dinoflagellates reached their peak biomass at a time when the phytoplankton was dominated by autotrophic dinoflagellates (Fig. 5). According to Smetaček (1981), low protozooplankton biomass in summer results from intensive grazing by the metazooplankton, present in high densities at this time. Metazooplankton biomass decreases in autumn, and a second protozooplankton biomass peak is then observed. This pattern was evident in the Gulf of Gdańsk (Fig. 6). At the shallow Stns 92A and R6, the spring and autumn peaks of heterotrophic dinoflagellate biomass coincided with low metazooplankton biomass, while in summer low heterotrophic dinoflagellate biomasses occurred together with the metazooplankton biomass maximum. The relationship was apparently masked at the deep station G2 by the high biomass of heterotrophic dinoflagellates recorded there in late June, which coincided with high metazooplankton biomass. It should be borne in mind, however, that the high biomass values of heterotrophic dinoflagellates recorded in late June occurred deeper in the water column, with a maximum between 60 and 90 m, while metazooplankton biomass at that time was concentrated within the upper 30 m (Witek et al. 1993).

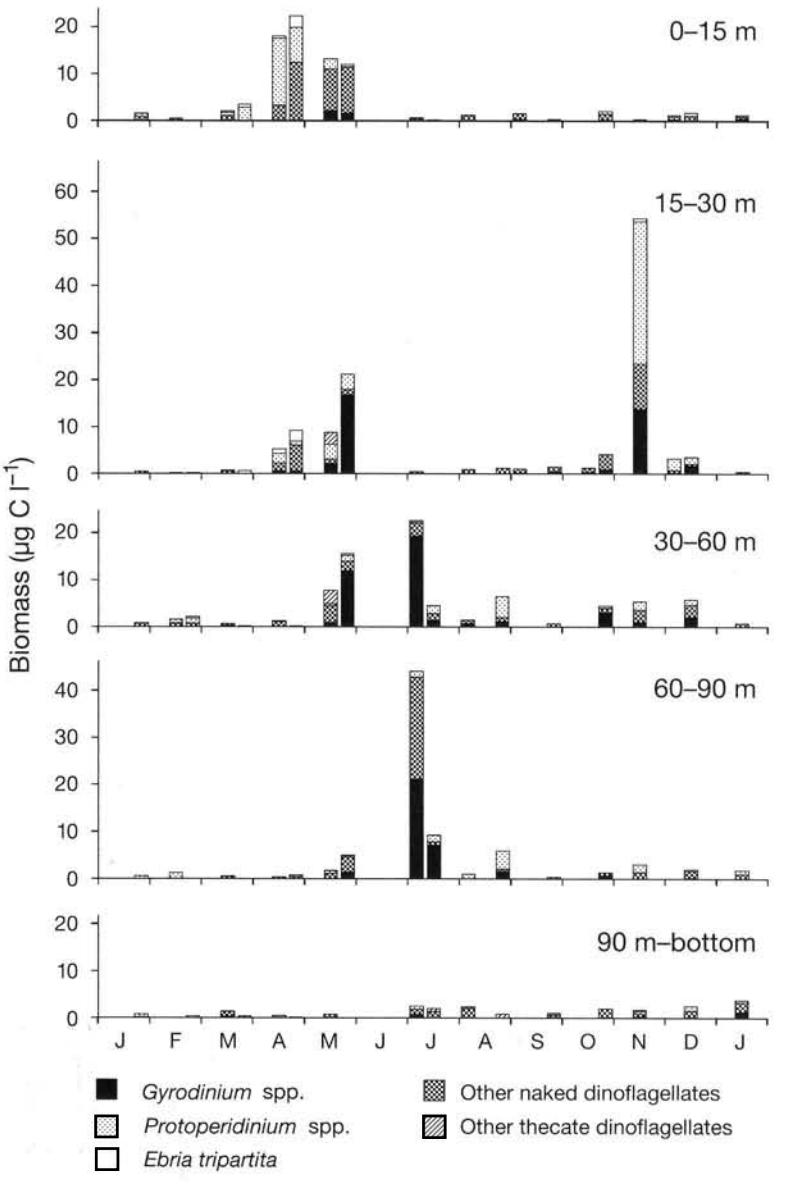

Fig. 4. Biomass of heterotrophic dinoflagellates at Stn G2

The heterotrophic dinoflagellate biomass values recorded in this study can be compared with biomasses of other zooplankters (Table 2), which were calculated during concurrent studies on other components of the Gulf of Gdańsk ecosystem (Mackiewicz 1991, Witek et al. 1993). The comparison shows the heterotrophic dinoflagellates to be a dominant compo-

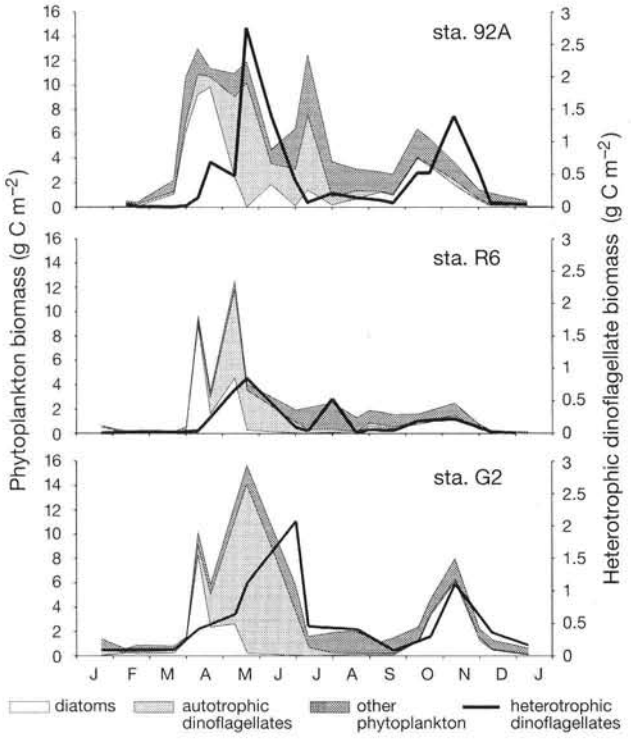

Fig. 5. Biomass of heterotrophic dinoflagellates and phytoplankton in the Gulf of Gdańsk. Phytoplankton data from Bralewska (1992)

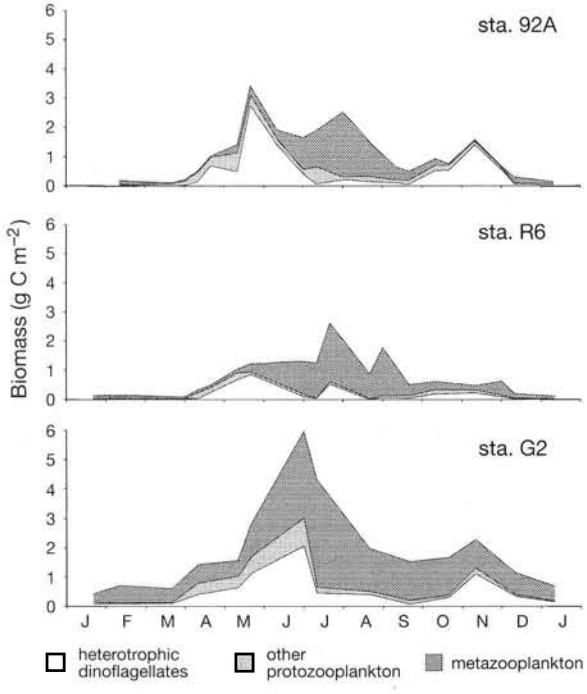

Fig. 6. Biomass of heterotrophic dinoflagellates and other zooplankton components in the Gulf of Gdańsk. Protozooplankton and metazooplankton data from Witek et al. (1993)

Table 2. Mean annual biomass (mg C m^{-2}) of the major zooplankton components at Stns 92A, R6 and G2 (after Witek et al. 1993)

	Station 92A	R6	G2
Protozooplankton			
Nanoplanktonic zooflagellates	43	20	32
Heterotrophic dinoflagellates	461	162	440
Ciliates	96	42	115
Metazooplankton			
Copepods	237	355	1088
Other mesozooplankton	76	62	184
Macroplankton	39	19	42

nent of the protozooplankton. At the stations located in the open sea, they made up almost one-fourth of the annual mean biomass of the total zooplankton, while at Stn 92A, typical of the highly productive (primary production in 1987: 436.6 g C m^{-2} yr^{-1}; Witek et al. 1993) inner waters of the Gulf of Gdańsk, these dinoflagellates contributed almost half of the total zooplankton biomass and dominated over the metazooplankton.

Conclusions

The results obtained in this work show that heterotrophic dinoflagellates are one of the major components of the Gulf of Gdańsk ecosystem and play an important role in the ecosystem's energy flow. Thus our understanding of the pelagic community's trophic structure in the Gulf, as derived from previous descriptions of the structure and functioning of the ecosystem in the area (Ciszewski et al. 1986, Pliński 1989, Wiktor 1990) which ignored the heterotrophic dinoflagellates, must be fundamentally amended. Heterotrophic dinoflagellates have not been given much attention in the 'microbial loop' descriptions of Pomeroy (1974), Azam et al. (1983), Fenchel (1988), and others who focused mainly on nanoplanktonic zooflagellates and ciliates. The position of heterotrophic dinoflagellates in the microbial loop is probably similar to that of ciliates, although recent studies (Gaines & Taylor 1984, Jacobson & Anderson 1986, Gaines & Elbrächter 1987, Hansen 1991a, 1992) show that large particles (e.g. algae, other dinoflagellates, ciliates) not much smaller, and occasionally even larger, than the heterotrophic dinoflagellates themselves are important food items for the latter. This would mean that the heterotrophic dinoflagellates' role in the ecosystem is that of an energy dissipator rather than an energy transfer link.

If the contribution of heterotrophic dinoflagellates to the planktonic biomass increases with the growing fertility of the habitat, which seems to be the case in the

area studied, the increase in primary production due to eutrophication will not necessarily result in a commensurate increase in the production of higher trophic levels, i.e. the metazooplankton, benthos, and/or fish. As primary production increases, a larger and larger proportion of the energy it provides will be consumed and dissipated by heterotrophic dinoflagellates at the very beginning of the food chain.

The developmental cycle of heterotrophic dinoflagellates in the deep layer below the halocline is different from that near the surface. Organisms living in deeper water depend not only on a supply of organic matter from the euphotic zone but also on ambient oxygen conditions, which, as a result of the bacterial decomposition of sinking organic matter, may deteriorate over a prolonged period of stagnation to such an extent as to wipe out all but anaerobic organisms. On the other hand, under favourable oxygen conditions, bacteria may be an important food source for protozooplankton. In the deep water layer, high densities of nanoplanktonic zooflagellates (Mackiewicz 1991) and ciliates (Witek 1994) have been observed, their annual patterns of biomass change being similar. We may thus believe that the layer in question is inhabited by a separate community, the development of which is controlled by factors different from those controlling the epipelagic biocoenosis.

Finally, it is worth mentioning that heterotrophic dinoflagellates may be important for benthic communities as well. The protozoobenthos in the Gulf of Gdańsk has not been sufficiently studied yet, but in the bottom sediments of other areas, e.g. Danish sounds (Fenchel 1967), heterotrophic dinoflagellates were observed to occur at high densities comparable to those of ciliates.

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This article was submitted to the editor

Manuscript first received: January 25, 1994
Revised version accepted: October 13, 1994