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THE RELATIVE IMPORTANCE OF NANNOPLANKTON IN THE NORTH SEA PRIMARY PRODUCTION*

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The South Bight of the North Sea has been investigated for the photosynthetic capacity of net- and nannoplankton, the fractional filtration method being used simultaneously with the C14 technique. The water appeared to be well mixed so that no important variations occurred along the vertical profile. The horizontal distribution of net-/nannoplankton ratios showed, however, a zonation pattern with netplankton-dominant activity near to the coast and nannoplankton-dominant activity further off. The interference of the River Scheldt has also been demonstrated. The various implications of the 'metabolic structure' of the phytoplankton community demonstrated by the fractionation method are discussed.

The existence of a major group of phytoplankton with cells of small size (below 50 μm) that are not retained by the finest mesh nets is well established (although many ecologists still study only netplankton). Since Lohman (1903) gave this group the name nannoplankton, its relative significance has been emphasised by Birge & Juday (1922), Riley (1941), Harvey (1950), Atkins & Parke (1951), Atkins (1953), Wood & Davis (1956), Steemann Nielsen (1938), Steemann Nielsen & Aabye Jensen (1957), Yentsch & Ryther (1959), Texeira (1963), Holmes & Anderson (1964), Saijo & Takesue (1965), Anderson (1965) and Semina (1969).

Preserved phytoplankton samples indicate that a proportion of the nannoplankton is made of very small diatoms but the majority of it consists of flagellates (belonging to several different algal classes) which are difficult, and in many cases impossible, to preserve (Bernhard, Rampi & Zattera, 1967). The electron microscope and the development of single cell isolations and culture techniques has allowed the ultrastructure and the systematics of some of these organisms to be thoroughly investigated. More recently, the global metabolism of nannoplankton has been investigated and higher productivity indexes demonstrated (Malone, 1971a, 1971b; Curl & Small, 1965; Mommaerts, 1972) for nannoplankton cells as could be expected from their high surface-area-to-volume ratio (Zeuthen, 1970; Odum, 1956).

In this paper the results are given of our first investigations on nannoplankton and netplankton production in the South Bight of the North Sea.

MATERIAL AND METHODS

Netplankton and nannoplankton photosynthetic capacities were estimated from water samples collected at the sampling stations shown in Figs 1–3 at about local apparent noon from a range of depths corresponding to 100%, 10% and 1% of surface irradiance. Four light and two dark bottles were drawn from each sample, inoculated with 4 μCi of $NaHC^{14}O_3$ and incubated under fluorescent light (about 0·055 lx/min^{-1}) for 3–4 h at sea surface temperature.

* Contribution to the Belgian programme of research and development on the physical and biological environment.

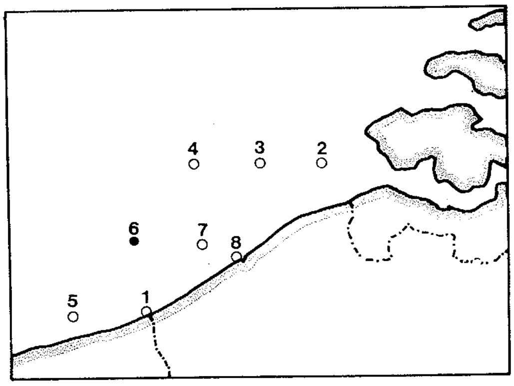

FIG. 1. Sampling stations off the Belgian coast at cruise 0 (January 1971). Black circle indicates a comparatively high net-/nannoplankton ratio, white circles indicate a comparatively low ratio.

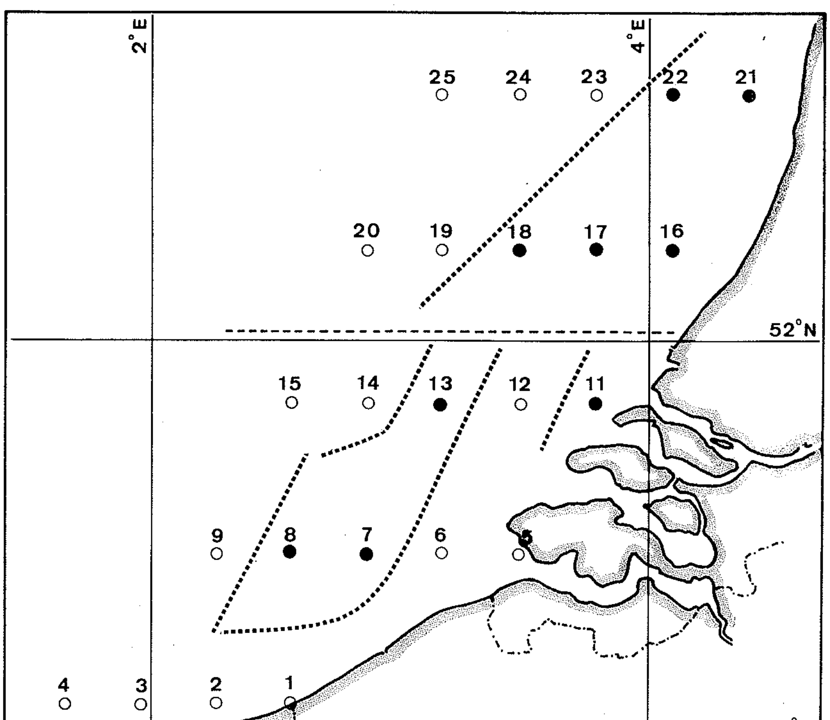

FIG. 2. Sampling stations off the Belgian and the Dutch coast. (A) Under the horizontal dashed line: cruise 1 (June–July 1971); (B) above the horizontal dashed line: cruise 2 (August 1971). Black circles indicate a comparatively high net-/nannoplankton ratio, white circles indicate a comparatively low ratio.

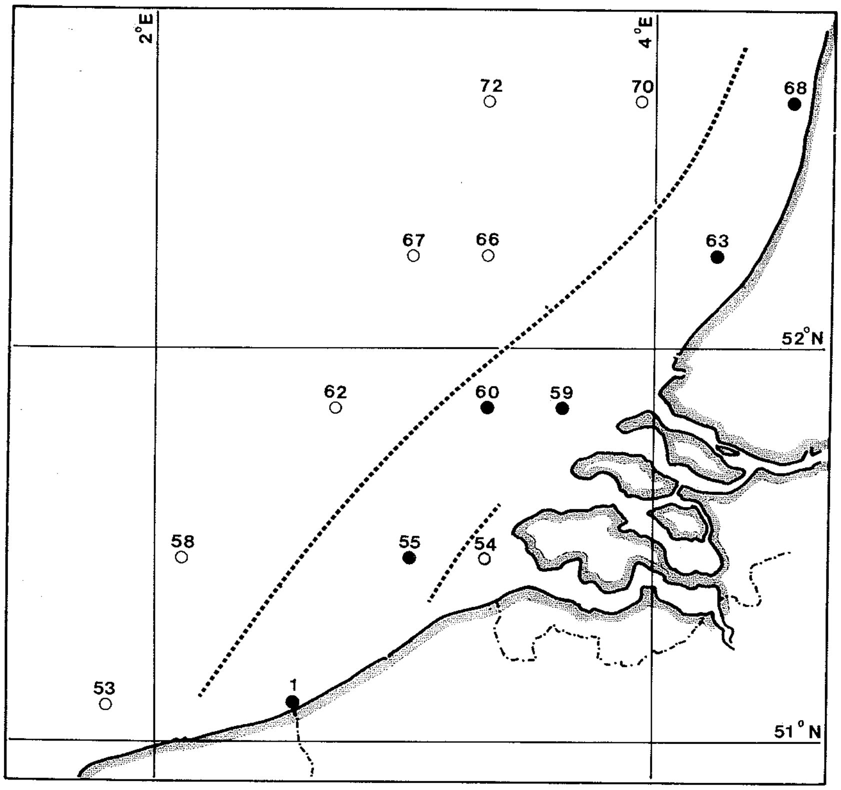

FIG. 3. Sampling stations off the Belgian and the Dutch coast at cruise 3 (September 1971). Black circles indicate a comparatively high net-/nannoplankton ratio, white circles indicate a comparatively low ratio.

For two of the light bottles and one dark bottle, all planktonic organisms above 50 μm (i.e. netplankton and zooplankton) were eliminated by filtering the water through fine-mesh net. Following incubation, the contents of the bottles were filtered through Sartorius 0·2 μm membrane filters under pressure. The filters were washed with about 20 ml filtered seawater and dried. Their activity was measured at the International Agency for C14 determination, Charlottenlund, Denmark. The results are expressed as mg $Cm^{-3}h^{-1}$ Netplankton photosynthetic capacity is computed by subtracting nannoplankton photosynthetic capacity from that of total phytoplankton.

Drawbacks of the fractionation method

The interpretation of the results is not always simple. (1) The activity measured in the non-filtered sample reflects the balance of total phytoplankton production and possibly grazing by the zooplankton also present in the sample. (2) The production of the filtered sample is mainly that of nannoplankton but can also be that of a small proportion of netplankton that has passed through the fine-mesh net (e.g. diatoms with small cross-section).

In most instances these interferences seem to be negligible as suggested by direct examination of the water under a microscope.

TABLE I. Photosynthetic capacities (mg $Cm^{-3}h^{-1}$) of samples collected at 3 optical depths (fractions of surface irradiance), weighted means and ratios for net and nannoplankton sampled in cruises 0, 1, 2, 3 and 5

Station	Date	100% irrad. net-nanno	10% irrad. net-nanno	1% irrad. net-nanno	Weighted mean net-nanno	Ratio net/nanno
Cruise 0						
1	230171	1·57–2·40	0·91–2·33	1·31–2·43	1·17–2·37	0·49
2	280171	(0)–2·61	—	0·65–3·06	0·32–2·83	0·11
3	300171	1·60–2·02	1·15–2·49	1·24–2·31	1·28–2·32	0·55
4	310171	0·74–1·23	0·96–1·08	0·93–1·00	0·89–1·09	0·81
5	020271	1·11–1·24	1·27–1·20	0·63–1·25	1·07–1·22	0·87
6	040271	2·02–1·04	2·38–1·07	2·66–1·24	2·36–1·10	2·13
7	050271	1·06–3·56	—	—	1·06–3·56	0·29
8	020271	(0)–7·18	—	—	0–7·18	0
Cruise 1						
6	230671	3·70–18·12	—	8·54–19·40	6·12–18·76	0·32
9	240671	(0)–5·47	(0)–3·92	(0)–6·53	(0)–4·96	0
7	250671	9·73–2·93	9·99–2·92	9·72–3·53	9·85–3·07	3·20
1	280671	4·25–16·74	11·41–15·56	8·0–16·8	9·08–16·17	0·56
4	290671	5·7–2·48	0·07–3·86	(0)–3·98	1·46–3·54	0·41
2	300671	2·61–3·30	0·30–3·30	0·28–3·21	0·89–3·27	0·27
3	010771	0·07–3·74	0·52–4·46	0·88–4·18	0·49–4·21	0·11
5	020771	3·12–13·95	—	11·55–9·2	7·33–11·57	0·63
8	050771	1·73–1·76	3·75–2·43	2·08–1·62	2·82–2·06	1·37
11	070771	1·68–0·95	1·91–1·95	6·27–1·99	2·90–1·70	1·70
12	080771	1·22–2·21	0·22–3·72	0·28–3·0	0·48–3·16	0·15
13	080771	1·08–1·74	2·60–1·74	—	1·84–1·74	1·05
14	090771	—	2·15–2·89	2·07–2·93	2·11–2·91	0·72
15	090771	0·06–1·65	0·11–3·19	0·76–2·25	0·26–2·57	0·10
Cruise 2						
16	170871	14·52–2·17	41·72–3·32	30·25–6·0	31·88–3·66	8·70
17	170871	13·10–0·75	13·42–2·15	13·89–1·35	13·47–1·61	8·34
18	180871	19·15–4·08	41·90–3·38	30·79–3·40	33·79–3·53	9·55
19	180871	0·92–3·67	2·58–4·51	2·63–3·97	2·17–4·16	0·52
20	190871	1·34–4·19	1·68–5·44	0·93–5·51	1·39–5·17	0·27
25	240871	1·69–0·95	2·28–1·14	1·45–2·49	1·92–1·43	1·34
24	240871	1·68–0·95	(0)–2·41	—	0·84–1·68	0·50
23	250871	1·34–2·96	3·14–3·89	5·8–4·2	3·35–3·73	0·89
22	250871	13·18–2·54	13·79–2·34	15·05–3·31	14·01–2·65	5·27
21	260871	25·02–8·93	40·23–11·11	56·52–15·87	39·28–11·48	3·41
Cruise 3						
1	070971	13·12–5·75	16·97–5·06	29·07–6·72	18·58–5·62	3·30
53	080971	1·05–5·45	1·62–6·44	1·34–5·99	1·41–6·09	0·23
58	090971	0·86–2·69	0·92–2·75	0·14–3·20	0·71–2·84	0·24
62	100971	0·38–3·70	0·69–3·04	1·24–2·78	0·75–3·14	0·23
55	130971	13·69–7·62	21·52–9·99	16·28–8·36	18·33–9·01	2·03
67	140971	3·37–3·28	1·94–2·89	2·56–3·72	2·45–3·19	0·76
66	140971	1·39–5·63	0·24–5·76	0·75–5·39	0·65–5·63	0·11
72	150971	0·88–1·99	0·37–2·63	1·36–2·67	0·74–2·48	0·30
60	160971	8·45–3·37	14·65–4·15	13·53–5·46	12·82–4·28	2·99
54	200971	7·37–7·49	3·16–14·56	8·55–15·95	5·56–13·14	0·42
59	210971	21·71–9·67	12·85–9·50	19·05–14·74	16·54–10·99	1·50
63	220971	11·47–15·25	14·90–13·16	11·25–15·10	13·12–14·16	0·92
68	230971	26·81–13·04	16·22–16·59	36·81–21·03	24·20–16·96	1·42
70	230971	(0)–9·67	(0)–9·54	1·95–2·67	0·38–8·22	0·04

TABLE I continued

Station	Date	100% irrad. net-nanno	10% irrad. net-nanno	1% irrad. net-nanno	Weighted mean net-nanno	Ratio net/nanno
Cruise 5						
1	030172	0·34–3·94	8·39*	3·49*		0·86
3	040172	(0)–3·26	3·62	3·25		0
4	040172	0·15–1·12	1·85	—		0·13
25	050172	0·21–1·57	1·49	3·03		0·13
24	050172	(0)–1·33	1·86	1·74		0
23	060172	1·20–1·17	2·22	2·30		1·02
22	060172	0·29–1·95	1·97	1·98		0·14
8	070172	0·21–2·05	2·42	2·92		0·10
7	070172	(0)–4·41	4·84	3·20		0
5	100172	(0)–4·44	3·72	2·55		0
20	110172	0·07–0·76	0·64	—		0·09
19	110172	(0)–1·7	1·75	0·91		0
18	120172	0·41–1·28	1·79	1·67		0·32
17	120172	0·04–1·97	2·26	2·40		0·02
21	130172	0·11–1·39	1·31	1·35		0·07
16	130172	0·47–1·79	2·02	2·58		0·26
9	140172	(0)–3·72	2·52	1·97		0

* Total photosynthetic capacity.

OBSERVATIONS

Vertical profiles of photosynthetic capacity and local abnormalities

In most instances, the total photosynthetic capacity was basically the same at all sampling depths (Table I) or at least of the same order of magnitude. Moreover, no important changes occurred in the ratio netplankton/nannoplankton throughout the euphotic region.

Exceptions to this rule (involving the passage to another order of magnitude) were few and concerned mostly surface water or sampling depths very near to the bottom. This indicates that the phytoplankton was rather homogeneously distributed in the water column.

In some cases [sampling stations 9 and 4 (cruise 1), 24 (cruise 2), 70 (cruise 3) and 3, 24, 7, 5, 19 and 9 (cruise 5)], the filtered samples had a higher photosynthetic capacity than the non-filtered samples.

Horizontal distribution of net- and nannoplankton

The distribution and evolution of primary production (mg $Cm^{-2}d^{-1}$) in the South Bight of the North Sea will be discussed in a future paper, but it already appears from our results that the photosynthetic capacity of a sample (mg $Cm^{-3}h^{-1}$) is mainly related to the distance from the coast, with the highest figures near to the coast.

The composition of the phytoplankton community as it appears from the photosynthetic capacities exhibited in filtered (50 μm) and non-filtered samples varies seasonally in accordance with our microscopical observations. Netplankton populations (mostly neritic diatoms) developed from spring to late summer (cruises 1, 2 and 3) and were more abundant near to the coast. In such periods and areas the nannoplankton production was somewhat overshadowed by the netplankton production but was seldom nonexistent. Actually, nannoplanktonic production varied mostly in the same way as total production so that one could find more nannoplankton near to the coast (despite its low relative significance).

Nannoplankton was dominant everywhere in the winter (cruises 0 and 5) and also just after the spring bloom (cruise 7, results not yet complete).

Elongated areas with similar properties appeared from the comparison of net-/nannoplankton ratios (Figs 2, 3). These areas were parallel to the coast and to the tidal streams in the North Sea. The transition between these areas could be abrupt (especially in cruise 2).

The mouth of the River Scheldt and the area below it (along the Belgian coast) were often characterised by particularly low net-/nannoplankton ratios (sampling stations 2, 8, 7 of cruise 0; sampling stations 5, 6, 1 of cruise 1; sampling station 54 of cruise 3).

DISCUSSION

The use of fractional filtrations in primary production measurements allows a better understanding of the 'metabolic structure' of the phytoplankton community. For the same standing crop, the nannoplankton is more efficient (high specific production) than the netplankton. It seems also to be a better food for zooplankton. All this means that in nannoplankton-dominant areas the turnover of biogenic elements is quicker. The persistence of a nannoplankton-dominant patch for a long time would mean a reinforced effect on the environment. It would thus be interesting to compare the stability (*sensu* MacArthur, 1955) of a nannoplankton-dominant community with that of a netplankton-dominant community.

Vertical and horizontal distributions of photosynthetic capacities and net-/nannoplankton ratios have been investigated. For most sampling stations, the great homogeneity of results along the vertical profile indicate that the water was well mixed. This could be expected above the continental shelf, especially in the shallow area investigated (about 25 m deep). This was especially so from cruise 0 which was made in very bad weather. Cruise 1 showed exceptions to this rule where surface water was concerned (sampling stations 5, 8, 13 and 4). Excepting station 5, where the difference exhibited could be accounted for by the vertical stratification of water in the Scheldt river, no explanation could be found for these examples.

In some cases, the photosynthetic capacity of non-filtered seawater was lower than that of filtered (50 μm) seawater. This could be explained by the grazing activity of zooplankton enclosed in the experimental bottle (see the review of the possible drawbacks of the fractionation method in Material and Methods). This suggestion however vanished in most of these instances as the 'grazing figures' could be explained by the variability of the replicates. Only sampling station 70 (cruise 3) and perhaps 24 (cruise 2) exhibited a marked enough difference between filtrated and non-filtrated water (differences amounting respectively to 48% and 28% of the highest figure). The occurrence of an important population of Rotifera at sampling station 70 suggests that the difference could be due to grazing. This would be a typical case where grazing is directly detectable. No information, however, appears from these results on the absolute value of grazing. Actually nothing indicates that grazing was more important in this particular case than in any others; there is just the initial ratio of net-/nannoplankton to go on.

As neritic and benthic diatoms are normally very significant near to the coast, an important netplankton production in this area was expected from springtime to fall. This was readily demonstrated by the fractionation method. Analogue results were recorded by Malone (1971a) who found a mean neritic net-/nannoplankton ratio of about 0·5, significantly higher than that observed in oceanic waters (down to 0·01).

Besides the 'metabolic structure' involved in the patterns demonstrated, the possible coincidence with the actual phytoplankton communities was considered. However, this possibility disappeared when the phytoplankton was examined under the microscope. Moreover, there was no absolute relation between production levels and structural properties.

Such patterns have been related by several authors (see discussion in Malone, 1971a) to grazing indices, the grazing pressure against netplankton being less effective in neritic waters.

Other environmental characteristics are revealed by the fractionation technique: the influence of the River Scheldt is emphasised by relatively low ratios (implying a very high nannoplanktonic activity). The abundance of nannoplankton has been demonstrated for most estuaries and been related to eutrophic properties of the water and to the flushing pattern of the estuary. The more heterogeneous pattern of horizontal distribution of net-/nannoplankton ratios in cruise 1 could be explained by the marked influence of the River Scheldt off the Belgian coast at this time of the year.

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