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Concentrations of particulate matter in the North Frisian Wadden Sea

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ABSTRACT: The amount of particulate matter for different size classes was determined in the North Frisian Wadden Sea over a period of 10 months from November 1973 to August 1974. Particle volume, particulate organic carbon and phaeopigment concentrations decrease with advancing season, reaching minima in June. It is concluded that concentrations of particulate matter including chlorophyll *a* were sufficiently high throughout the study period to support the growth and reproduction of appendicularia which abundantly occur in the Wadden Sea.

INTRODUCTION

The amount and nature of particulate matter in the range of approximately 1 to 100 μm diameter largely determines the development and occurrence of herbivores and omnivores in the zooplankton community. Though particulate matter present has been measured in various ways (organic carbon, nitrogen, organic dry weight, chlorophyll *a*, particle volume, inverted microscope), the matter available has been most frequently expressed as a single parameter, for example carbon. This leaves open the important question of the relative proportions of living to non-living material. One recent effort dealt with the chemical, biological and volumetric determination of particulate matter from 2 to 150 μm diameter (Zeitzschel, 1970), but it was not known how much organic matter in the various size classes was present. Separation into size classes is necessary to determine the potential amount of food available to juvenile and adult copepods, but this information alone indicates only the volume, not the nature, of matter available (Mullin, 1965; Poulet, 1974, 1976).

Combining the measurement of several parameters expressing amount, size and nature of particulate matter is required to assess food value and availability to different groups of abundant zooplankton. The objective of this investigation was to study seasonal changes and relationships between different "food" parameters in the North Frisian Wadden Sea. Most of the particulate matter in the Dutch Wadden Sea (about 75 %) is thought to originate in the North Sea (De Jonge & Postma, 1974) where

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strong tidal currents keep much of the detritus suspended. The phytoplankton in the area of our collections consist regularly of pelagic and benthic species (cf. Drebes & Elbrächter, 1976) which indicates considerable turbulence.

MATERIAL AND METHODS

The part of the Wadden Sea north of Sylt covers an area of 410 km^2 at mean high and 240 km^2 at mean low tide. The only connection with the open North Sea is the Lister Dyb between the North Sea islands of Sylt and Rømø, a channel with a minimum width of about 3 km. The temperature minimum and maximum 1973/74 were 1.3 and 19.5° C. Salinity generally ranged from 28 to 32 ‰.

My investigations commenced in October 1973 and ended in August 1974. Samples were collected 2 days each week. The study location was about 500 m east of List Harbour (Island of Sylt, Federal Republic of Germany) where samples were collected by bucket just before or after high tide. The water column was always well mixed due to strong tidal currents (up to 5 knots). The seawater was analyzed immediately upon arrival at the laboratory.

Chlorophyll *a*, phaeopigments, particulate organic carbon and particulate nitrogen were determined on unfiltered material and on that passing through meshes of 30 and 180 μm. The seawater was gently filtered through each mesh. This screening procedure implies that all irregularly shaped particles smaller than 50 %, and all subspherical particles smaller than 80 % of the mesh size are not retained (Sheldon & Parsons, 1967a). In addition, breakage of unknown percentages of long chains mainly of the genera *Asterionella*, *Chaetoceros*, and *Thalassiosira* could not be avoided. The 30 μm mesh was selected to measure the particulate matter available to appendicularians as the filtering mechanism of *Oikopleura dioica* has a width of 30 to 40 μm. The particulate matter passing through a mesh of 180 μm should include almost all the material which can be ingested by copepods.

Chlorophyll *a* and phaeopigments were determined with a Turner fluorometer III using a high sensitivity door and a F4T.5. lamp, the method of Strickland & Parsons (1968). Particulate organic carbon (POC) and particulate nitrogen (PN) were determined using a Hewlett-Packard Model 185 CHN-Analyzer. Seawater samples from 25 to 200 ml were filtered at a vacuum of 150 mm Hg on precombusted Whatman GFC filters, rinsed twice with 2.5 ml distilled water, dried for 48 to 72 h at 60° C and stored in a desiccator until combustion. As distilled water rinses may cause a loss of organic matter, one test was carried out to compare samples with and without rinsing water (Table 1). The results indicated considerable losses in the 250 ml samples (24 % C and 29 % N lost). Most of the samples taken ranged from 25 to 150 ml. It should be noted that the retention by GFC-filters is not as high as that of the collection apparatus of *O. dioica* (0.1 × 0.8 μm mesh; Jørgensen, 1966).

The particle volume of material passing through 30 μm mesh was determined using a Coulter Counter ZB with an orifice of 100 μm diameter. Material passing through 180 μm mesh was analyzed with a 100 and 400 μm diameter orifice. Sample volume for the 100 μm orifice was 0.55 ml, for the 400 μm orifice 23.32 ml using a

Table 1

Organic carbon (C) and nitrogen (N) content of one seawater sample washed through 30 μm mesh with and without being rinsed with distilled water ($\mu g/l$) on July 9, 1974

Seawater sample size	No dist. water C	N	Rinsed with 2 × 2.5 ml dist. water C	N
25 ml	532	104	532	104
100 ml	548	77	531	70
250 ml	603	90	458	64

Coulter Timer. The procedure allowed us to reliably measure particle diameters from 2 to 25 μm passing through 30 μm mesh and 2 to 63 μm passing through 180 μm mesh. The number of particles above 63 μm was too low for satisfactory statistical evaluation. To keep coincidence low the samples were often diluted to 2.5 to 20 % of their original volume using seawater filtered immediately before use through 0.45 μm millipore filters. The samples were counted at 22 different settings (Aperture Current, Amplification) with both orifices overlapping for certain particle sizes. This resulted in 15 different settings (7 with the 100, 8 with the 400 μm aperture) used for the calculation of the particle volume for sizes from 2 to 63 μm diameter.

The volume settings of 0.5 and 2.0 ml on the Coulter Counter ZB were calibrated several times. It was found that 0.55 ml and 2.24 ml, respectively, passed through an orifice at the above mentioned settings indicating that the original Coulter calibrations were not correct.

The volume of particulate matter from 2 to 63 μm diameter was computed using the data up to 10 μm diameter from the 100 μm orifice and those above 10 μm from the 400 μm orifice. Particle concentration in relation to size is presented according to Sheldon et al. (1972).

RESULTS

Most of the results are presented as monthly averages (Fig. 1). Each data point is the mean of 6 to 10 determinations, except that from August when only two measurements were made. The particle volume data indicate highest values during winter. The highest monthly average for the range 2 to 25 μm diameter was 19.48 ppm in December compared with the lowest average in June 1974 at 1.93 ppm. A comparison of monthly data for the small and large ranges shows significant correlations for all months except April (Table 2). A developing phytoplankton bloom changed the relation of both particle ranges during that month. Correlations (1) and (4) are of limited importance as the parameters in each correlation are not stochastically independent.

Particulate organic carbon (POC) values decreased in a manner similar to particle volume (Fig. 1), attaining minimum values during June. The fraction passing through 180 μm mesh was close to 90 % of the total from December through May, indicating that most of the POC was near or smaller than 100 μm in diameter (Table 3). During summer the POC passing 180 μm mesh dropped to 60 % of the total. From December

Table 2

Coefficients of correlation for several environmental parameters and their significant probabilities: (1) Particle volume 2 to 63 μm vs. particle volume 2 to 25 μm. (2) Particle volume 2 to 63 μm vs. POC passing 180 μm mesh. (3) Particle volume 2 to 25 μm vs. POC passing 30 μm mesh. (4) POC passing 180 μm vs. POC passing 30 μm. (5) Particle volume 2 to 63 μm vs. Chl *a* passing 180 μm mesh. (6) POC no mesh vs. chl *a* no mesh. (7) POC passing 30 μm mesh vs. Chl *a* passing 30 μm mesh. The number of determinations range from 6 to 10 each month excluding November 1973 through January 1974 when the available data were pooled. * significant at the 5 % level; ** significant at the 1 % level; *** significant at the 0.1 % level; ns not significant

Date	(1) r	(2) r	(3) r	(4) r	(5) r	(6) r	(7) r
Nov. 1973 through Jan. 1974	—	—	.932***	.966***	—	.805**	.929***
Feb. 1974	.955*	.971**	.992***	.995***	.954*	.973***	.986***
March	.992***	.971***	.939***	.983***	.551 ns	.374 ns	.745*
April	.253 ns	.766*	—.506 ns	.457 ns	.783*	.502 ns	.065 ns
May	.994***	.924***	.851**	.906***	.333 ns	.472 ns	.236 ns
June	.876**	.541 ns	.698*	—.061 ns	.491 ns	.762*	.887**
July	.921***	.961**	.961**	.972**	.890**	.646*	.912*

Table 3

Average monthly concentrations of particulate organic carbon, chlorophyll *a* and phaeopigments passing 180, 95 and 30 μm mesh expressed as mg/l and as percentage of the NO MESH concentration and particle volume from 2 to 26 and 2 to 63 μm diameter (SD = standard deviation). The open spaces indicate that no determinations were carried out during that particular period Number of determinations range from 6 to 10 each month

Date	Particulate organic carbon (mg/l)				Chlorophyll *a* (μg/l)				Phaeopigment (μg/l)				Particle volume mm³/l	
	No mesh	through mesh of 180 μm	95 μm	30 μm	No mesh	through mesh of 180 μm	95 μm	30 μm	No mesh	through mesh of 180 μm	95 μm	30 μm	2 to 25 μm	2 to 63 μm diameter
Nov. 1973	—	—	—	—	4.51	3.98	—	2.08	2.68	2.68	—	2.03	13.65	—
SD					± 1.59	± 1.73		± .94	± 1.77	± 1.71		± 1.16	± 9.64	—
					100 %	88 %		46 %	100 %	96 %		73 %		
Dec. 1973	2.66	2.57	—	1.93	2.50	2.25	2.06	1.55	2.44	2.20	2.00	1.78	19.47	—
SD	± .79	± .75		± .57	± .99	± .57	± .52	± .67	± .96	± .77	± .74	± .58	± 6.45	—
	100 %	97 %		75 %	100 %	86 %	79 %	59 %	100 %	90 %	82 %	73 %		
Jan. 1974	2.44	2.26	—	1.58	2.30	2.28	1.95	1.36	2.43	2.20	2.21	1.45	18.07	—
SD	± 1.56	± 1.65		± 1.09	± 1.58	± 1.61	± 1.45	± 1.08	± 2.15	± 1.86	± 1.88	± 1.41	± 11.99	—
	100 %	94 %		65 %	100 %	99 %	85 %	59 %	100 %	91 %	91 %	60 %		
Feb. 1974	1.96	1.82	—	1.36	2.04	1.80	1.73	1.10	1.37	1.28	1.26	.97	13.98	29.29
SD	± 1.18	± 1.10		± .71	± 1.52	± 1.06	± 1.01	± .57	± .98	± .92	± .90	± .62	± 9.00	± 18.38
	100 %	93 %		69 %	100 %	88 %	85 %	54 %	100 %	93 %	92 %	71 %		
March 1974	1.71	1.58	1.52	1.13	3.42	3.03	2.93	1.55	.87	.92	.91	.77	13.78	26.76
SD	± .67	± .65	± .63	± .42	± 1.69	± 1.56	± 1.38	± .69	± .60	± .51	± .59	± .36	± 6.59	± 13.26
	100 %	92 %	88 %	66 %	100 %	88 %	83 %	39 %	100 %	106 %	105 %	89 %		
April 1974	1.79	1.62	1.47	.83	19.71	18.19	16.84	3.56	.63	.32	.30	.26	7.47	20.88
SD	± .41	± .42	± .41	± .27	± 10.28	± 10.09	± 9.44	± 1.17	± 1.38	± .74	± .62	± .48	± 3.23	± 5.49
	100 %	98 %	87 %	48 %	100 %	93 %	87 %	18 %	100 %	50 %	46 %	41 %		
May 1974	.98	.86	—	.47	5.06	4.01	2.91	.92	.51	.44	.38	.31	3.46	10.21
SD	± .59	± .50		± .29	± 3.17	± 2.63	± 1.71	± .30	± .53	± .50	± .32	± .32	± 3.54	± 9.47
	100 %	88 %		48 %	100 %	79 %	58 %	18 %	100 %	82 %	73 %	59 %		
June 1974	.70	.428	—	.237	2.76	1.75	1.30	.78	.35	.18	—	.15	1.94	4.95
SD	± .19	± .156		± .06	± 2.46	± 1.41	± .62	± .32	± .29	± .09		± 0.7	± .51	± 1.65
	100 %	61 %		34 %	100 %	63 %	47 %	28 %	100 %	51 %	—	43 %		
July 1974	1.21	.738	—	.406	4.25	3.40	2.99	1.63	.52	.49	—	.25	4.06	12.10
SD	± .34	± .39		± .19	± 1.94	± 2.41	± 2.07	± .95	± .43	± .36		± .17	± 2.67	± 9.00
	100 %	63 %		34 %	100 %	80 %	70 %	41 %	100 %	94 %		48 %		
Aug. 1974	—	—	—	—	3.98	3.77	2.87	1.56	.21	.22	—	.19	3.15	8.16
SD					± .13	± .16	± .23	± .03	± .29	± .32		± .27	± 1.47	± 2.84
					100 %	95 %	72 %	39 %	100 %	105 %		91 %		

to March the majority of POC was in the fraction passing 30 μm mesh, decreasing evenly until June when it made up only one third of the total. Particle volume (2 to 63 μm Φ) correlated significantly with POC passing the 180 μm mesh except in June when both parameters reached minima. Plots of POC passing through 180 μm mesh against that passing through 30 μm mesh were not significant in April and June.

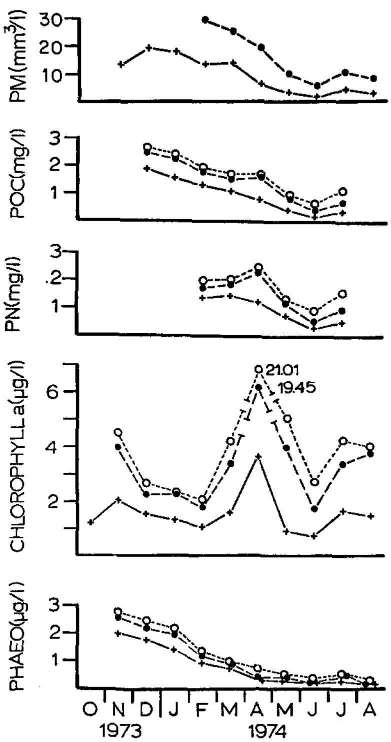

Fig. 1: Monthly averages of particulate matter (PM) measured in mm³ of particulate matter per liter of seawater, particulate organic carbon (POC), particulate nitrogen (PN), chlorophyll *a* and phaeopigments (Phaeo.). Symbols: + = particulate matter passing through 30 μ mesh; o = passing through 180 μ mesh; o = no mesh used

A spring phytoplankton bloom began toward the end of March and ceased in mid-May. Most of the bloom species occurred as chains which did not pass through the 30 μm mesh. The high amounts of chlorophyll *a* in unfiltered water and that passing through 180 μm mesh in April coincided with increases in PN but did not alter the POC values which were similar to those from March. The majority of the POC in April as in earlier months was non-living. POC (unfiltered) did not correlate with chlorophyll *a* during the months of high chlorophyll. POC (passing 30 μm mesh) correlated significantly with chlorophyll *a* of the same size group except in April and May. It appeared that the phytoplankton carbon was a rather even fraction of the total POC during each month of relatively low phytoplankton concentration.

Table 4

Average monthly concentrations of particulate nitrogen and carbon : nitrogen ratio (SD = standard deviation)

Date	PN mg/l No mesh	PN mg/l through mesh of 180 μm	PN mg/l through mesh of 30 μm	C : N No mesh	C : N through mesh of 180 μm	C : N through mesh of 30 μm
Feb. 1974	.198	.173	.136	9.90	10.52	10.00
SD	± .109	± .081	± .067			
	100 %	87 %	69 %			
March 1974	.207	.186	.148	8.26	8.49	7.64
SD	± .059	± .062	± .050			
	100 %	90 %	72 %			
April 1974	.252	.239	.128	6.82	7.00	6.53
SD	± .055	± .050	± .025			
	100 %	95 %	50 %			
May 1974	.134	.123	.078	7.31	6.99	6.03
SD	± .061	± .053	± .043			
	100 %	92 %	58 %			
June 1974	.095	.057	.034	7.40	7.51	6.97
SD	± .028	± .014	± .008			
	100 %	60 %	36 %			
July 1974	.159	.097	.056	7.51	7.71	7.25
SD	± .045	± .047	± .019			
	100 %	61 %	35 %			

Data available for particle volume from each month are plotted against POC in Figure 2, which shows considerable variation.

One mm^3 of particulate matter (range 2 to 63 μm diameter) contains 51 μg C in material passing through a 180 μm mesh (see also Sheldon, 1974). During April (diatom bloom) the carbon to volume ratio was higher and during June lower than the average. The intercept at 0.302 mg C could be attributed to particulate matter smaller than 2 and larger than 63 μm being sampled on the filters but not included in the volume determination (Zeitzschel, 1970).

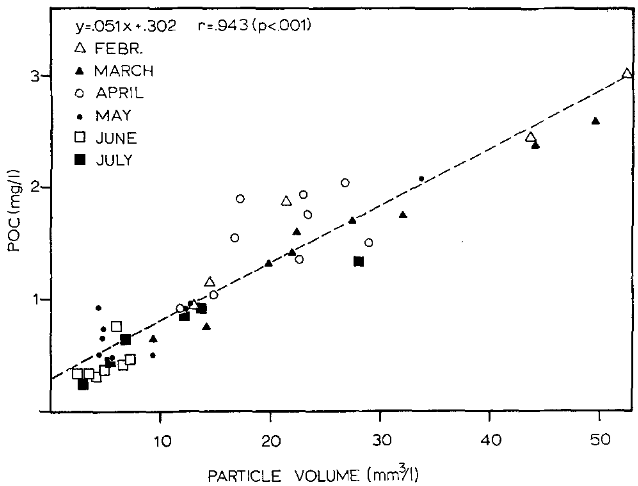

Fig. 2: Particle volume as determined with a Coulter Counter ZB (2 to 63 μm ∅) vs. particulate organic carbon passing through 180 μm mesh

Phaeopigments decreased evenly with proceeding season and did not change considerably after April. In several samples in late spring and summer the values were registered as zero when they amounted to less than 10 % of chlorophyll *a* and phaeopigments combined.

Particulate nitrogen (PN) concentrations correlated with POC when monthly average values (data obtained from passing through 180 and 30 μm mesh) were compared as a percentage of that in unfiltered material (Tables 3 and 4). The C : N ratio of each size range decreased from February to April and showed little change in the following months. This indicated that the percentage of living matter increased from February to April, assuming even values thereafter.

During June and July the amount of POC and PN passing through the 30 μm mesh dropped from 75 to 34 % of the total; that passing through 180 μm mesh decreased sharply from 95 to about 61 %, signifying a considerable increase in the amount of larger (> 180 μm) and decrease of smaller particulate matter (Table 3).

Particle size spectra were derived from the counts of a total of 22 different settings of the Coulter Counter with the 100 and 400 μm orifices overlapping. Spectra characteristic of certain parts of a month and which showed the spectral changes occurring during various periods are presented. Four spectra are plotted together for better comparison (Fig. 3).

From February 27 to March 21 the volume in almost all of the 15 size ranges dropped with volume peaks in the range from 10 to 14 μm. With the onset of the spring bloom (end of March) the spectrum peaks shifted toward larger volumes

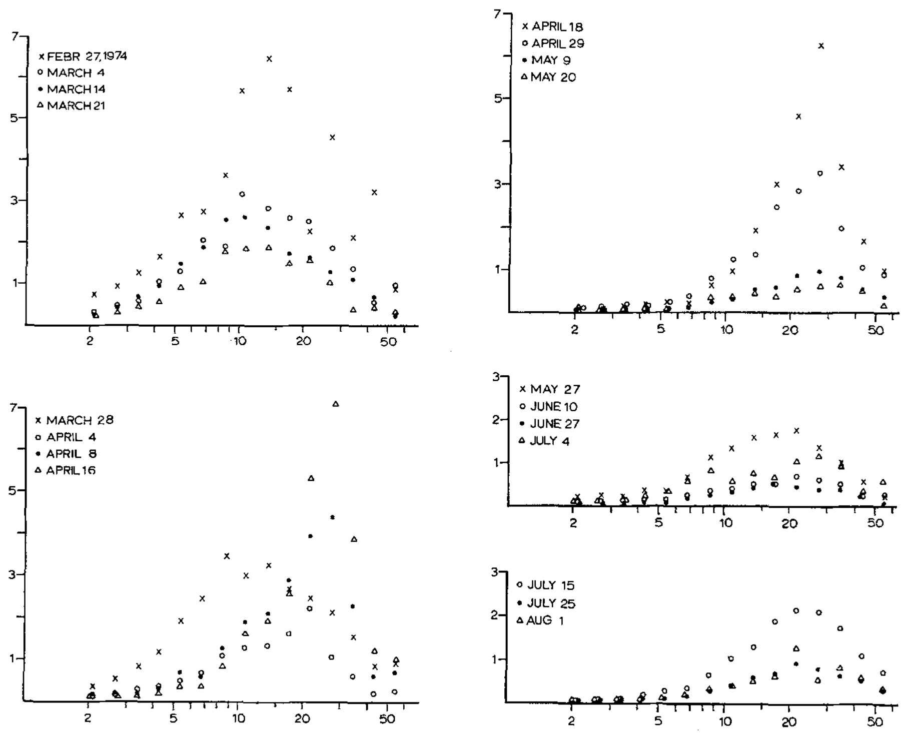

Fig. 3: Particle spectra from the North Frisian Wadden Sea determined with 100 μm and 400 μm diameter orifices of a Coulter Counter

(28 μm diameter). There the peak remained until May 20, coinciding with the phytoplankton bloom. Highest particle volumes were reached on April 16 to 18; also, on those days the highest chlorophyll *a* concentrations were measured, and from then on the volumes decreased gradually until May 20. From May to August maxima were in the range from 9 to 28 μm diameter. The amount of particulate matter from 2 to 6 μm diameter decreased with the advancing season and changed little after mid-April.

Varying wind velocities affected the total amount of particulate matter in the water column. Strong winds led to an increase of suspended benthic material. Except in March ($\gamma = .781$, $P < .01$) no significant correlation could be found between wind speed and particle volume.

DISCUSSION

A variety of studies have been carried out on the amount, size and size distribution of particulate suspended matter in the sea. For instance, in the Gulf of California Zeitzschel (1970) found significant correlations between particle volume (2–150 μm diameter), seston, phytoplankton carbon, POC, PN and chlorophyll *a*. One mm^3 of particles contained 220 μg C, one mm^3 of phytoplankton 42 μg C. One mm^3 of particulate matter in the study area of the Wadden Sea had an average of 51 μg C. During April the μg C · mm^{-3} increased to 64 when the phytoplankton were characterized by blooms of *Asterionella glacialis, A. kariana* and *Skeletonema costatum* (G. Drebes, personal comm.). For comparative purposes one mm^3 of *S. costatum* has an average carbon content of 115 to 200 μg. During phytoplankton blooms in the Straits of Georgia (Canada) the suspended matter contained 52 μg C · mm^{-3} (Parsons et al., 1967; Sheldon & Parsons, 1967b). Significant correlations were found between particle volume, nanoplankton carbon, microplankton carbon and chlorophyll (Parsons, 1969). Most of these data must be interpreted with caution as the Coulter Counter does not measure all particles accurately (Ilmavirta, 1974 Leslie et al., 1975). The significant relationship between particle volume and POC is attributed to non-living matter being far more abundant than living matter in all samples, resulting in low variability.

Seasonal variations in particle volume (1.6 to 144 μm particle diameter) were observed in Bedford Basin, Nova Scotia (Poulet, 1974). Minima were found between December and February (near 1 ppm) maxima in March (18 to 40 ppm). The volume of particulate matter in the size range of 3 to 120 μm diameter was determined during four cruises from March to November in the southern North Sea (Gieskes, 1972). Near-shore concentrations ranged from 3.8 to 5.8 ppm (early March) to a maximum of 9.0 to 19.6 ppm (early September) falling again to 3.2 to 5.1 ppm in early November. In the North Frisian Wadden Sea near Sylt, concentrations of particulate matter (2 to 63 μm diameter) decreased from 29.3 ppm (February) to 5.67 ppm (June). The decrease in POC and particle volume in the different size ranges from winter to early summer could be attributed to changes in meteorological conditions and to increases in benthic and planktonic feeding with increases in temperature and in grazer density, which will be discussed later.

Phaeopigment concentrations above 1 μg·l^{-1} were repeatedly observed in Narragansett Bay from May to November (Durbin et al., 1975). From December through April concentrations were below 0.8 with one exception. Concentrations in the North Frisian Wadden Sea decreased from 2.8 to about 0.5 μg · l^{-1} between November to April remaining even through summer. The high amounts of phaeopigments from November to April are considered to be caused by degrading processes and continued transport of particulate matter from the open North Sea into the Wadden Sea (DeJonge & Postma, 1974).

The relative amount of organic matter and chlorophyll (percentage of the total) in previous reports was highest for particles smaller than 30 μm. Particles from 1 to 33 μm accounted for 77 % of the organic carbon of particulate matter ranging from 1 to 500 μm diameter (Mullin, 1965). Particles smaller than 8 μm accounted for 60 %

of total living carbon in two eastern Canadian Bays throughout one year (Sutcliffe, 1972). Chlorophyll *a* passing through 35 μm mesh accounted for 61.5 to 100 % of the chlorophyll *a* passing through 163 μm mesh in Chesapeake Bay (McCarthy et al., 1974). In the North Frisian Wadden Sea the relationships differ as the amount of chlorophyll *a* passing through 30 μm mesh decreased from 59.2 % of the total in December to 17.6 % in April. The low percentages coincide with a bloom of chain-forming diatoms which do not usually pass through 30 μm mesh. POC passing through 30 μm mesh followed a different pattern, decreasing from 74.5 % of the total in December to near 34 % in June and July. The relatively large amounts of POC and PN not passing through 180 μm mesh during June and July (near 40 % of the total) could be partly attributed to large colonies of *Phaeocystis pouchetii* (Künne, 1952, and personal observations).

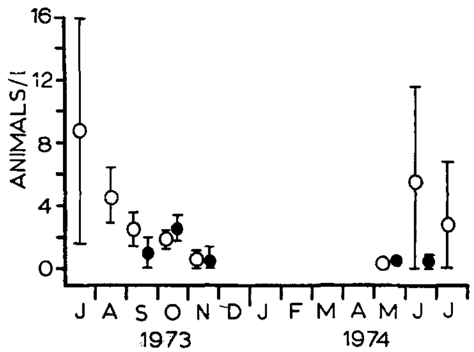

Fig. 4: Average monthly concentrations of *Oikopleura dioica* (o) and *Fritillaria borealis* (•) in the North Frisian Wadden Sea. The 95 % confidence limits are presented for all months except May 1974 when samples were taken on only 2 occasions. (Modified after Paffenhöfer, 1976)

Particle spectra from 3 to 120 μm size from the southern North Sea near the Netherland coast (stations 3 and 7) were characterized by 2 or more peaks from March through summer (Gieskes, 1972; Eisma & Gieskes, 1977). Non-living matter, as found off Sylt from November through March, dominated the March and November samples. In April flagellate blooms developed followed by diatom blooms in late summer. Particle spectra from Bedford Basin (Nova Scotia, Canada) varied considerably from January to November (Poulet, 1974) ranging from high concentrations near 2 μm diameter to others between 30 and 60 μm. Particle spectra from the North Frisian Wadden Sea were rather uniform being characterized by singular, mostly broad peaks often indicating high particle concentrations (> 0.3 ppm) in each of the ten size classes from 6 to 60 μm diamter, thereby implying that the majority of the particulate matter over most of the year is available to calanoid copepods such as the abundant *Pseudocalanus elongatus* and *Temora longicornis*.

The only zooplankton group which has been quantified reliably for a longer period of time are the appendicularia (Paffenhöfer, 1976). Appendicularia have at times been found in abundance in the Wadden Sea (Künne, 1952) and are considered to be the major food of the larvae of plaice and sand-eel in the Southern Bight (Ryland, 1964). They consume particulate matter in the range from approximately 0.1 to 30 μm diameter (Jørgensen, 1966; Paffenhöfer, 1976).

Bucket samples collected over a period of 13 months (Paffenhöfer, 1976) show that appendicularian densities were highest when POC and particle concentrations were lowest (Figs. 1 and 4), indicating that food was not limiting. The particulate matter passing through 30 μm mesh was thought to be available as food. The occurrence of both species of appendicularians seemed to be regulated by temperature (Paffenhöfer, 1976). No "crashes" of appendicularian populations as reported by Seki (1973) were observed. The continuous occurrence of a population of O. *dioica* during the warmer months is attributed not only to an adequate food supply but also to continuous losses of appendicularians (by mortality) thus avoiding bloom conditions which might fatally deplete the food resource. Data on the body length of O. *dioica* showed that the average size changed little during 48 to 72 hours (range of x = 331 to 488 μm). This points towards continous removal of O. *dioica* as their generation time at 16° C is short (6 days). The high particle concentrations in Wadden Sea waters lead to the assumption that the majority of non-carnivorous zooplankton is not food-limited during the entire year.

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