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SEDIMENTING PHYTOPLANKTON AS MAJOR FOOD SOURCE FOR SUSPENSION AND DEPOSIT FEEDERS IN THE ØRESUND

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ABSTRACT

The chlorophyll and phaeopigment content of the sediment, and in *Abra nitida, Nuculoma tenuis, Chlamys opercularis* (Mollusca, Bivalvia) and *Anobothrus gracilis* (Annelida, Polychaeta) from a depth of 30 m in the Øresund, Denmark, was measured together with seasonal changes in weight and reproduction of the animals. Sedimentation from the spring phytoplankton bloom was the main regulating factor for weight increases and development of reproductive tissue of the bottom invertebrates, including deposit feeders, and the importance of bacteria/detritus for these is questioned. The sedimenting phytoplankton was successively exploited by species feeding from the water, from the sediment surface, and from below the sediment surface. Compared to deposit feeders, suspension feeders had only a short period available for exploiting the sedimenting material. The results are compared with similar results from the Clyde Sea, Great Britain, and seem to be valid in those neritic sediment communities of the temperate zone, which are not exposed to light.

INTRODUCTION

In boreal waters the seasonal variations in light and temperature impose changes on the quantitative relationship between phytoplankton and grazing zooplankton (Franz & Gieskes 1984), with considerable effects on the quality and quantity of sedimenting organic material. Rates of sedimentation, normally are measured in fixed collectors (e.g. Webster *et al.* 1975, Smetacek *et al.* 1978) and provide valuable information on the average supply to the bottom for larger areas. But, for obvious reasons, organic material sampled in collectors, cannot represent the supply to organisms, that actively catch and sort food material. Nor does it represent very well the supply to a particular area of the sediment surface, as sedimentation depends on the local surface structure and topography. Estimates based on collectors, therefore, may be of little value for estimates of the importance of sedimentation for individual species of the benthos, at least in areas dominated by strong horizontal water movements, as in the Øresund, between Denmark and Sweden.

Recent investigations have focused on the importance for the benthic system of sedimentation events. Graf *et al.* (1982, 1983 and 1984) observed in the Kiel Bight

an immediate increase in bacterial activity following sedimentation, and a delayed increase in meiofauna biomass, but they found their results inconclusive regarding the macrofauna. Earlier results from the Clyde Sea, Great Britain, suggested marked macrofaunal responses to the sedimentation of phytoplankton (Ansell 1974a, b, and c).

In the present work we have avoided the use of indirect monitoring (collectors) in an evaluation of the importance of sedimenting phytoplankton for the benthic macrofauna. Instead, we have used the sediment, and the macrofauna itself as monitors. We have analysed the seasonal changes in phytogenous material in the sediment, and in the food of selected suspension and deposit feeding species of the macrofauna, and we relate these changes to variations in growth and reproduction of the invertebrates.

Our work is part of a larger research project, describing the primary production, and the fate of the primary produced material in the Øresund.

We wish to express our thanks to the crew of the vessel OPHELIA, and to the technical staff of the Marine Biological Laboratory in Helsingør, for their assistance and for the interest they took in our work.

METHODS

Samples of *Nuculoma tenuis, Abra nitida, Chlamys opercularis* (Mollusca, Bivalvia) and of *Anobothrus gracilis* (Annelida, Polychaeta) were dredged with time intervals of 10-40 days, between February 1983 and January 1984 at a station in the Øresund, about 8 km SE of Helsingør, and with a water depth of 30 m. The sampling station (12°42.5'E, 55°58.9'N) was situated in the bottom current of North Sea water flowing towards the Baltic area, and having a salinity of 30-34‰. The maximum light compensation depth at the station is 19-20 m. No attempts were made to collect the animals quantitatively, nor to collect quantitatively all size groups of the population. Since large individuals alone were used in the measurements, the results are representative only for these. The species sampled were treated in slightly different ways:

Nuculoma tenuis. Following collection, the animals were left overnight in running sea water to allow the mantle cavity to be cleared of sediment. A sample of 30 animals, about 8 to 11 mm in length, were used for the determination of length and of 'total wet weight', which was the weight of the washed and dry-blotted bivalve, including the water retained between the valves. A few individuals opened their valves during the weighing procedure, with a resulting loss of intervalve water. These were discarded and replaced by new specimens. The maximum shell length was measured using an eye piece micrometer.

Of the 30 *N. tenuis*, 20 animals were used for the determination of dry weight. The soft tissues were removed under a dissection microscope, weighed on aluminium foil dishes, and reweighed after drying overnight. The soft tissues of the remaining 10 animals were placed in 10 ml of 90 % acetone for the extraction of

plant pigments. The shells of all the 30 *N. tenuis* were dried and weighed. The sex of each animal was recorded when possible under a dissection microscope, and the number of sexable animals was used as an estimate of the degree of development of the gonads in the population. No significant differences were found between males and females in the total wet weight, dry weight or pigment content, so the values for the two sexes were combined in the calculations.

Assuming the mantle cavity cleared of sediment, the space between the two valves is occupied by ex- and internal water, and by body organic material and minerals. During growth of the soft parts, particularly of the gonads, that fraction of the intervalve space which is occupied by water will decrease. Therefore, the ratio of the body dry weight to the total wet weight or to the length, may be used as an estimate of the general condition of the animal. We calculated the seasonal variation in the general condition of a 'standard' *N. tenuis*, having a total wet weight of 150 mg, as well as in a standard animal defined by length (9 mm). Both gave similar results. The calculations were based on regressions, made for every sample, of 1) total wet weight, of 2) dry weight, and of 3) shell weight, on length, all following double logarithmic transformations (Table 1).

Table 1. Nuculoma tenuis. Estimates with 95% confidence limits of total wet weight, body dry weight, shell weight and phaeopigment content of a 9 mm long animal. (Confidence limits based on logarithmic regressions result in different confidence intervals above and below the estimates. Only the larger (upper) intervals are given.)

Date	Total wet weight, mg	Body dry weight, mg	Shell weight, mg	Pigment content, μg
21.02.1983	142.9 ± 8.6	12.1 ± 0.8	53.6 ± 6.5	4.9 ± 1.0
03.03.1983	142.5 ± 10.9	10.7 ± 1.5	53.9 ± 6.5	3.5 ± 0.7
14.03.1983	146.6 ± 10.1	10.7 ± 0.9	59.1 ± 8.1	4.9 ± 0.9
23.03.1983	145.6 ± 8.4	11.8 ± 0.7	51.8 ± 4.6	6.5 ± 1.4
28.03.1983	153.5 ± 9.4	13.7 ± 0.8	58.3 ± 7.7	9.9 ± 2.4
06.04.1983	132.9 ± 10.1	12.8 ± 0.5	48.4 ± 5.3	18.3 ± 2.4
13.04.1983	157.5 ± 8.8	14.7 ± 0.7	63.7 ± 7.5	23.9 ± 5.4
25.04.1983	138.1 ± 8.0	14.2 ± 0.7	53.0 ± 5.6	20.8 ± 4.4
16.05.1983	153.8 ± 10.0	16.9 ± 1.0	59.4 ± 7.8	15.4 ± 4.9
13.06.1983	137.4 ± 12.5	15.7 ± 0.6	58.0 ± 8.0	13.7 ± 3.1
28.06.1983	172.1 ± 10.8	19.6 ± 0.8	67.1 ± 8.2	10.0 ± 3.2
17.08.1983	148.8 ± 10.7	17.4 ± 1.1	55.3 ± 7.0	6.9 ± 1.3
29.09.1983	139.5 ± 7.2	15.2 ± 0.7	54.2 ± 5.2	3.8 ± 0.3
13.10.1983	147.4 ± 13.1	14.9 ± 1.5	59.5 ± 11.3	2.4 ± 0.4
07.11.1983	135.0 ± 7.2	13.8 ± 0.7	54.2 ± 7.1	2.6 ± 0.7
14.11.1983	159.7 ± 10.8	17.0 ± 1.3	62.8 ± 9.4	2.1 ± 0.4
29.11.1983	128.1 ± 9.4	13.4 ± 1.0	48.8 ± 8.1	3.1 ± 0.8
19.12.1983	147.6 ± 9.9	12.8 ± 1.2	56.7 ± 7.4	4.5 ± 1.4
25.01.1984	145.7 ± 8.4	12.2 ± 0.9	58.9 ± 8.9	3.9 ± 1.1

Pigment content was related to length (Table 1) as well as to total wet weight, both giving similar results. In presenting the results the weight and pigment content of a standard animal of 150 mg total wet weight was used. The standard animal was defined by total weight, and not by length, in order to reduce the effect of any seasonal variation in shell length and -weight on the dry weight, and the pigment content estimates.

Abra nitida was treated in the same way as *N. tenuis*, but the shell weight of this species was not determined (Table 2), as the fragile shells often were destroyed during handling. The animals used were from 10 to 14 mm in length. Dry weight and pigment content of a standard *A. nitida* of 150 mg total wet weight, were calculated.

The relatively clear growth rings on the shells of *A. nitida* offered the possibility to study seasonality in the rate of shell growth. It was necessary, however, to establish which rings were true annual rings, and which were disturbance rings, assumed to be connected with spawning. To do this, the total length of the shell, as well as the lengths at all the growth rings, were measured on all animals collected between April 1983 and January 1984 (N = 245). The measurements were made

Table 2. Abra nitida. Estimates with 95% confidence limits of total wet weight, body dry weight and phaeopigment content of a 12 mm long animal. Confidence limits: See Table 1.

Date	Total wet weight, mg	Body dry weight, mg	Pigment content, µg
10.02.1983	154.2 ± 7.8		0.55 ± 0.25
21.02.1983	166.6 ± 8.4	10.4 ± 0.9	0.41 ± 0.12
03.03.1983	159.3 ± 5.8	10.1 ± 0.7	0.33 ± 0.08
14.03.1983	157.1 ± 7.4	10.1 ± 0.5	1.29 ± 0.61
23.03.1983		10.9 ± 1.0	4.14 ± 1.33
28.03.1983		11.8 ± 1.1	5.67 ± 1.80
06.04.1983	160.4 ± 6.8	13.2 ± 1.2	8.02 ± 2.46
13.04.1983	161.8 ± 8.5	13.6 ± 1.3	5.59 ± 1.45
25.04.1983	161.3 ± 6.8	14.3 ± 1.3	6.83 ± 2.63
16.05.1983	173.3 ± 8.5	16.5 ± 0.8	2.17 ± 0.63
13.06.1983	168.3 ± 9.1	17.8 ± 2.9	2.15 ± 0.92
28.06.1983	186.8 ± 7.2	18.2 ± 1.3	2.17 ± 0.26
17.08.1983	138.2 ± 8.1	11.9 ± 1.5	1.04 ± 0.19
29.09.1983	158.4 ± 5.3	14.0 ± 0.7	1.26 ± 0.27
13.10.1983	151.4 ± 7.8	13.1 ± 0.9	0.95 ± 0.20
07.11.1983	147.0 ± 6.7	12.6 ± 1.2	0.70 ± 0.17
14.11.1983	160.2 ± 5.5	13.6 ± 1.9	0.63 ± 0.13
29.11.1983	147.9 ± 4.7	13.1 ± 1.2	1.13 ± 0.18
19.12.1983	165.4 ± 7.3	13.5 ± 0.7	0.41 ± 0.08
25.01.1984	171.6 ± 7.1	14.2 ± 0.7	0.45 ± 0.12

Table 3. Chlamys opercularis. Estimates with 95 % confidence limits of body dry weight, gonad dry weight and stomach phaeopigment content of a 60 mm long animal. Confidence limits: See Table 1.

Date	Body dry weight, mg	Gonad dry weight, mg	Pigment content, µg
21.02.1983	829 ± 70	47.9 ± 17.0	16.4 ± 2.3
03.03.1983	859 ± 47	40.8 ± 13.8	21.2 ± 1.7
14.03.1983	894 ± 61	30.5 ± 7.3	22.3 ± 3.0
23.03.1983	939 ± 74	37.4 ± 7.2	228.3 ± 52.5
28.03.1983	963 ± 68	38.9 ± 8.2	207.0 ± 84.1
06.04.1983	1012 ± 102	32.3 ± 3.8	139.5 ± 16.9
13.04.1983	1009 ± 77	33.9 ± 5.6	105.7 ± 12.9
25.04.1983	965 ± 87	38.4 ± 8.0	98.5 ± 17.4
16.05.1983	862 ± 66	36.5 ± 6.2	55.2 ± 7.2
13.06.1983	1017 ± 64	60.0 ± 10.3	150.8 ± 10.8
28.06.1983	967 ± 80	45.7 ± 14.7	117.6 ± 14.7
17.08.1983	939 ± 74	50.7 ± 11.3	99.7 ± 8.8
29.09.1983	948 ± 60	102.6 ± 18.5	188.8 ± 11.0
13.10.1983	913 ± 57	96.4 ± 22.0	53.8 ± 6.1
01.11.1983	934 ± 54	93.9 ± 9.8	204.9 ± 33.4
07.11.1983	1041 ± 62	125.6 ± 15.3	182.8 ± 11.8
14.11.1983	1065 ± 87	104.8 ± 10.6	103.1 ± 13.8
29.11.1983	1049 ± 59	104.4 ± 21.5	156.0 ± 15.7
19.12.1983	1091 ± 54	58.7 ± 9.2	57.0 ± 6.8
25.01.1984	1138 ± 81	67.9 ± 23.5	57.0 ± 14.1

under a dissection microscope, using an eye piece micrometer. In the period before the onset of spawning, the shell increment was calculated as the mean difference between the total length of the shell, and the length at the last growth ring. After spawning had commenced an increasing number of animals became spent, and a new ring was laid down in their shells. In these individuals the difference between the total length and the length at the next to the last growth ring, was used for the calculation of mean shell increment.

The lengths of the *Chlamys opercularis* used were between 50 and 70 mm, which is close to the maximum size in the Øresund. Since *C. opercularis* can not completely seal the shells, variable amounts of water drained off from the animals, when they were removed from the water, and therefore length alone was used in defining the standard animal. The lengths (i.e. the longest dimension of the shell parallel to the hinge line) of 20 individuals were measured with a slide caliper, and the animals were opened by cutting the adductor muscle close to the valve. Animals with sediment in the mantle cavity were discarded. The gonad was removed by cutting close to the foot, and weighed separately. The stomach was removed and cleared of all external, non-stomach tissue, weighed and transferred to 25 ml of

90% acetone, after being cut into small pieces. Comparisons of the efficiency of pigment extraction in cut stomachs and in homogenized stomach tissue, revealed no significant difference. The remaining body (hereafter referred to as 'body') was weighed, and the dry weights of gonad and body were determined after drying for 48 hours. The shell weight was not determined due to varying amounts of epifauna growth on the upper valve.

Mean weights of the gonad and body were calculated for each sample, and regressions were made of gonad dry weight, body dry weight and stomach pigment content on length after double logarithmic transformations (Table 3). The weight and pigment content of a standard animal (60 mm) were calculated.

Anobothrus gracilis. 20 large individuals were removed from their tubes, washed and immediately placed in 5 ml 90% acetone. After the extraction of pigments, the polychaetes were transferred to preweighed aluminium foil dishes, dried overnight and weighed. For each sample, the mean pigment content per gram dry weight of the acetone treated animals was calculated.

Bottom cores were taken from the same station with a HAPS sampler (Kanneworff & Nicolaisen 1973), normally on the same day as the dredging of the animals. To reduce the effect of any disturbance of the bottom surface by the sampler, only cores covered by completely clear water were used. From each of 6 cores, 2 subsamples of sediment were scraped from the surface 1-2 mm, and another 2 from about 10 mm down in the sediment. The dry weight and pigment content were measured on the sediment subsamples. Sediment surface temperature was measured onboard, in newly collected cores.

All drying for dry weight determinations took place in an oven at 105 °C. Plant pigment content was determined fluorometrically (Holm-Hansen *et al.* 1965). Less than 10% of the pigments in the animals was chlorophyll-*a*, and as the fluctuations in the chlorophyll content paralleled those of the phaeopigments, only the last mentioned was used in the calculations.

RESULTS

Sediment

Fresh plant material was found in the surface of the sediment, in March and April (Fig. 1A). The surface concentration of chlorophyll-*a* increased during March to 7 times, and was in April still about 3 times the winter level. During the rest of the year the concentration remained at about 5 μg chlorophyll-*a* per g dry weight of sediment. 10 mm down in the sediment the chlorophyll content was about 2 μg/g, and showed only minor variations, which paralleled the variations at the surface.

Dead plant material, measured as phaeopigment concentration, was present at the sediment surface (20-50 μg/g) during the whole year (Fig. 1B). Increased values occurred simultaneously with the spring maxima in chlorophyll-*a*, but high

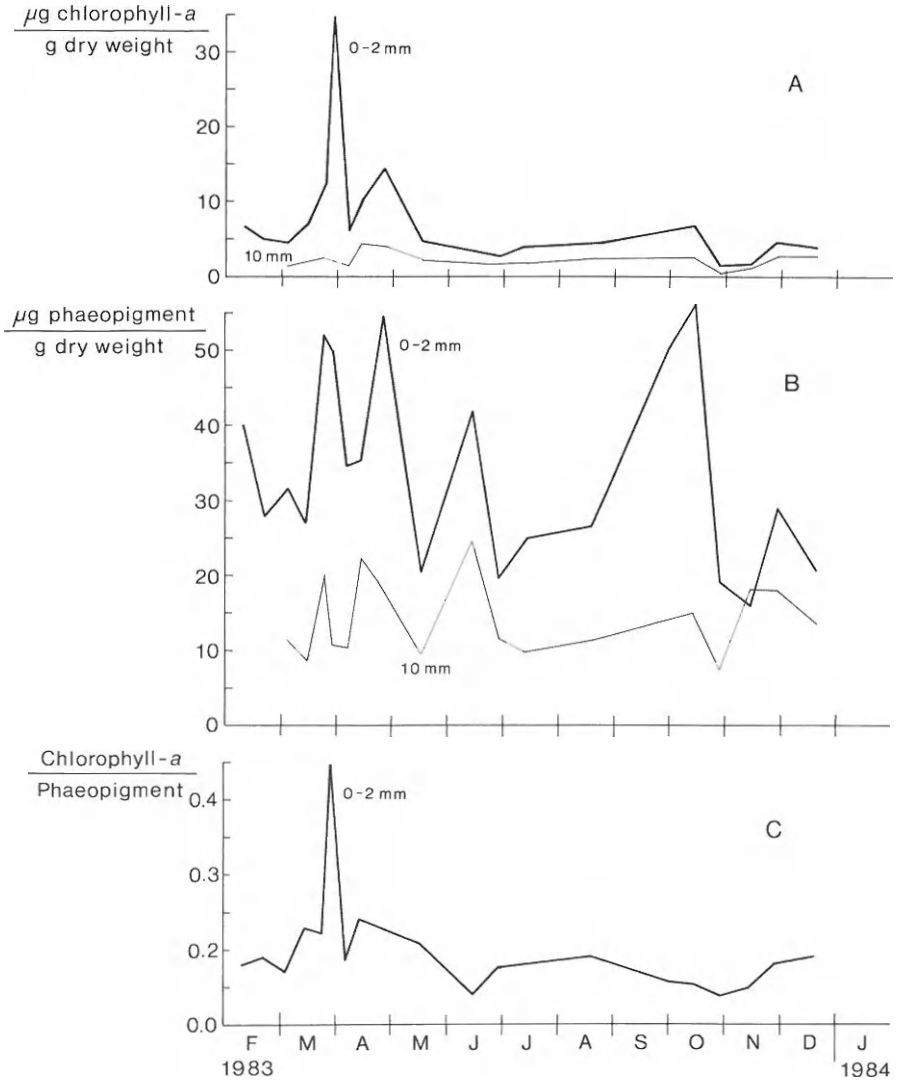

Fig. 1. Seasonal variation in pigment content of the sediment. A, μg chlorophyll-*a* per g dry weight of sediment. B, μg phaeopigment per g dry weight of sediment. C, ratio of chlorophyll to phaeopigment. —— denotes the top 2 mm of the sediment. —— a depth of 10 mm in the sediment.

values were observed also in June and in September-October. At a depth of 10 mm in the sediment the phaeopigment concentration was 10-20 μg/g, and the variations were damped compared to the surface.

The difference in composition of the plant material in the main periods of high pigment content in the sediment, is evident from the ratio of chlorophyll to phaeo-

pigment (Fig. 1C). This ratio clearly demonstrates the living or fresh nature of the plant material in March (0.7), compared to the degraded material in June and September-October (0.1).

The animals

Nuculoma tenuis. The seasonal variation in phaeopigment and body weight is summarized in Fig. 2 and Table 1. In the period 3 March to 23 March the phaeopigment content of the standard *N. tenuis* increased slowly from 4 to 6 μg. A very rapid increase followed, leading to a maximum of 24 μg on 13 April. A slow and steady decrease took place during the late spring and summer, and minimum values of 2-3 μg were found in October-November.

From mid-March to early June the dry weight of the soft tissues of the standard *N. tenuis* increased from 11 mg to a maximum of about 17 mg, and it remained at this level through August. The building up of gonadal tissue took place in May and June. Spawning started in October, but the main spawning period occurred in December. The dry weight decreased in a pattern parallel to the spawning.

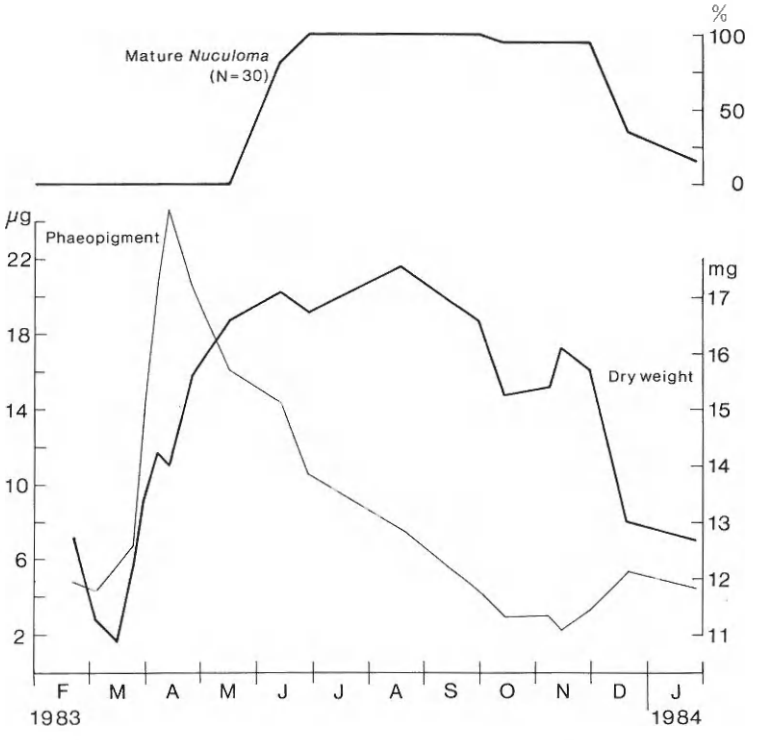

Fig. 2. Nuculoma tenuis. Seasonal changes in percentage of sexually mature individuals, in tissue dry weight and in phaeopigment content of a standard animal.

The shell weight varied between 48 and 67 mg for the standard animal, showing no seasonal trend. Erosion of, and deposits on the shells both contributed to this variation. The shells are heavily eroded at the umbones and extensively covered by a yellowish metal deposit, which despite careful cleaning could only be partly removed.

Abra nitida. From 3 March to 6 April 1983 the phaeopigment content increased from a winter value of 0.3 μg to a maximum of 8.0 μg (Fig. 3, Table 2). The spring maximum was followed by an abrupt decline in May, and by a slow and steady decrease during the summer and autumn, to reach the winter level in December.

The dry weight of the standard animal increased from 10 mg in March to 16.5 mg in the middle of May. The maximum dry weight (18 mg) occurred in June simultaneously with the maximum in gonadal development of the population.

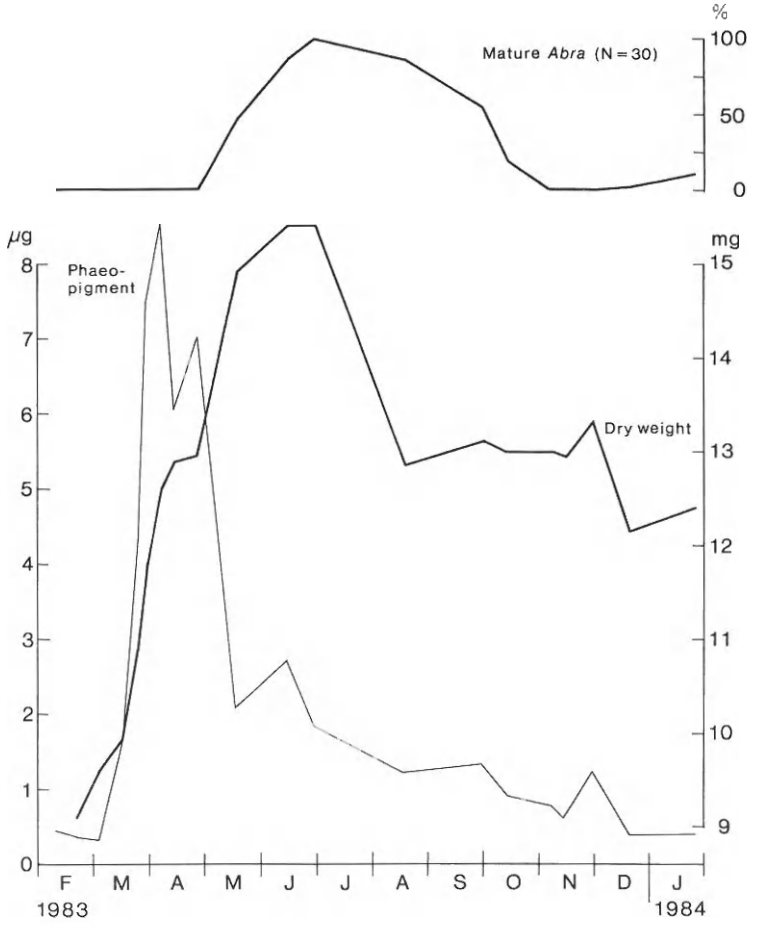

Fig. 3. Abra nitida. Seasonal changes in percentage of sexually mature individuals, in tissue dry weight and in phaeopigment content of a standard animal.

Spawning started slowly in July, and by the end of October most of the animals were spent. The shell growth also showed a seasonal pattern with maximum rate in October. The yearly increment in shell length was about 2.5 mm in a 12 mm long *A. nitida* (Fig. 7A), which is in agreement with Josefson's (1982) results.

Chlamys opercularis. A ten-fold increase, to a maximum of 22.5 μg, was observed in the phaeopigment content of the stomach between 14 and 23 March (Fig. 4, Table 3). This maximum was followed by a rapid decrease, creating a narrow spring peak. Compared to the regular decline during the summer and autumn in the pigment content of *N. tenuis* and *A. nitida*, that of *C. opercularis* varied irregularly, and particularly high values occurred in June, September and November. A winter minimum was common to all 3 bivalves.

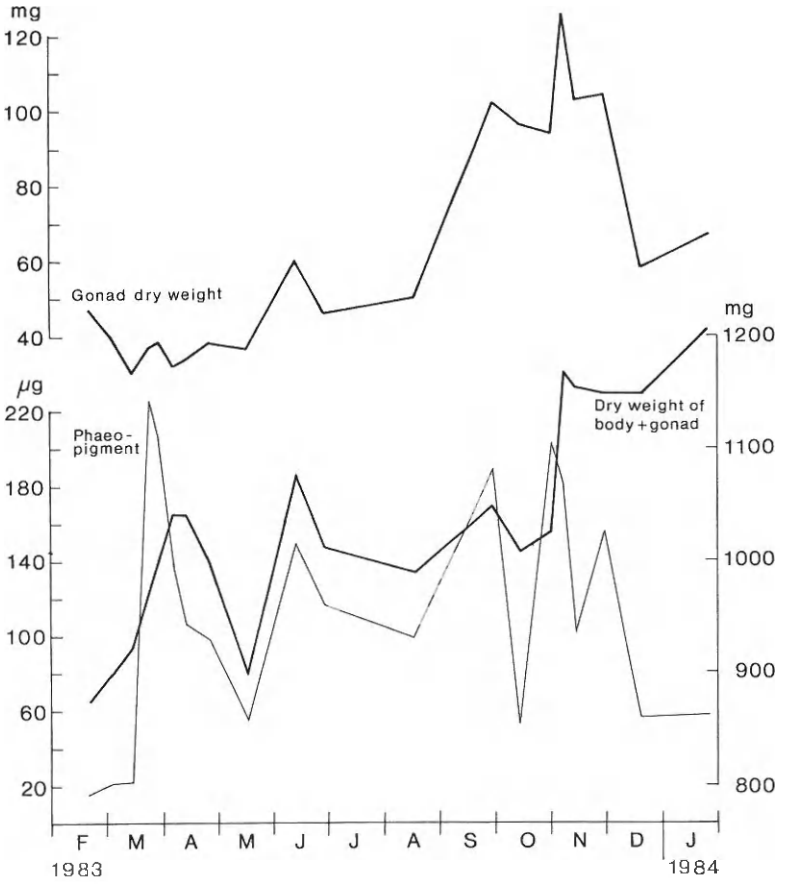

Fig. 4. Chlamys opercularis. Seasonal changes in dry weight of the gonad, dry weight of body plus gonad, and in phaeopigment content of the stomach of a standard animal.

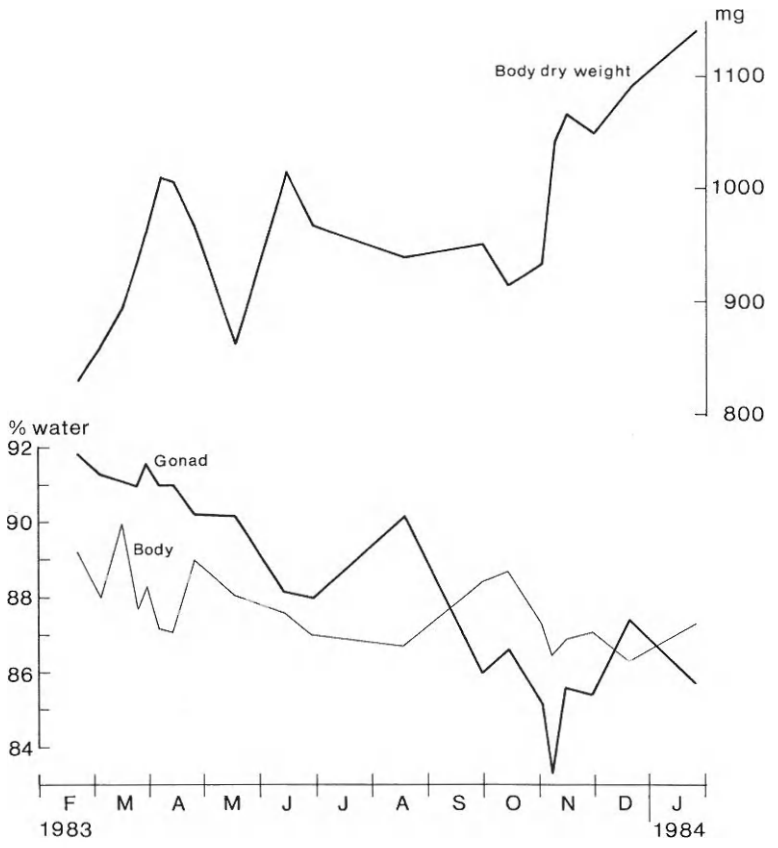

Fig. 5. Chlamys opercularis. Seasonal changes in body dry weight and water content of the gonad and body of a standard animal.

The dry weight of the body plus gonad increased from 900 mg in March to 1200 mg in December-January (Fig. 4), and during that period weight variations paralleled variations in the levels of pigment content. The gonad dry weight increased very slowly from March to August, but more than doubled, from 50 to 120 mg, from September to November. A decrease followed immediately in November-December. The ripe gonads were brilliantly red and white, and had a water content of 84-85 % (Fig. 5), compared to the almost colourless gonads in March-August with more than 90 % of water. The body water content (Fig. 5) varied between 87 and 89 %, with the lowest values in November-January, when the dry weight was highest.

Anobothrus gracilis. The weight-specific phaeopigment content is summarized in Fig. 6. A winter level of 10 μg per g dry weight was found in December-February. From 14 to 23 March the phaeopigment content increased from 18 to 58 μg/g, and

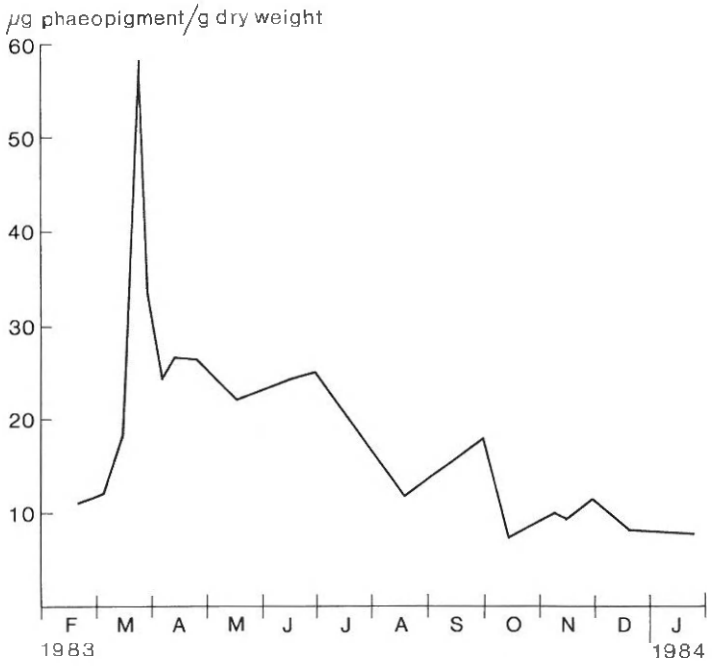

Fig. 6. Anobothrus gracilis. Seasonal changes in the weight-specific phaeopigment content.

was followed by an abrupt decrease, to 24 µg/g on 6 April, in a pattern like the one seen in *Chlamys opercularis*. From April the pigment content decreased slowly to the winter level.

The ratio of chlorophyll-*a* phaeopigment in the animals fluctuated irregularly between 0.05 and 0.12, with the highest values in *Anobothrus gracilis* and *Abra nitida*.

DISCUSSION

Pigment content

The pigments extracted from the animals derived from their food, and were present in the stomach of *Chlamys opercularis*, and probably in all of the digestive system of the other species. The concentration of pigment thus reflects the amount of phytogenous food taken in by the animals.

The phaeopigment content of the invertebrates increased in March-April to 5-20 times the winter values. Such large increases cannot be explained by increased feeding activity due to temperature changes, as the increase in temperature at the sampling station was only 1°C (Fig. 9). Instead, they result from increased concentrations of pigment in the sediment and in the bottom-near water. The maxi-

mum depth of the compensation light intensity at the sampling station is 18-20 m, so primary production at the bottom (30 m) must be negligible, and the large amounts of plant pigments in the spring was the result of sedimentation from the water.

The spring phytoplankton bloom in the Øresund typically shows 2 peaks, one in March and another in April (Nicolaisen & Christensen, unpublished), in a pattern very similar to the one observed in the sediment (Fig. 1). During this period the concentration of chlorophyll-*a* in the water increases to 10-50 times the winter level, while the herbivore biomass remains low until May (Nicolaisen & Christensen, op. cit.). So in March and April, sedimentation of phytoplankton from the spring bloom has a major effect on the pigment content of the sediment and on the food of the bottom invertebrates at a depth of 30 m in the Øresund.

The four species of bottom invertebrates examined obtain their food from vertically different levels, above and below the sediment surface: *C. opercularis* is a suspension feeder, capable of pumping large amounts of water (Vahl 1972) from just above the surface of the sediment. *A. gracilis* inhabits a mucus-lined tube which projects obliquely some 5-10 mm above the substrate. Little is known about the biology of this species, but Fauchald & Jumars (1979) include it in a general description of the feeding biology of ampharetid polychaetes. They stretch the feeding tentacles over the substrate, and presumably take their food from the sediment surface. Considering the delicate structure of the tentacles, these are not likely to penetrate into the sediment in search for food, and we never observed any feeding traces around the tubes, nor did we see the tentacles in contact with the sediment. *Abra nitida* takes up particles from the sediment surface by means of the inhalent siphon (Hughes 1975, Wikander 1980). This species is capable of penetrating a few mm into the sediment with the muscular siphon, producing clear feeding traces (Wikander 1980). The Nuculidae normally lie beneath the surface of the substrate and use the extensible palp proboscides to collect deposits from below the sediment surface (Younge 1939, Young 1971, Owen 1956). This description also applies to *Nuculoma tenuis*.

The peaks in pigment content of the animals and the sediment did not appear at the same time (Fig. 7). Maximum pigment content first appeared in *Chlamys opercularis* and *Anobothrus gracilis* on 23 March, then in the sediment surface on 28 March, (85 μg chlorophyll-*a* plus phaeopigment *a*) in *Abra nitida* on 6 April, and in *Nuculoma tenuis* on 13 April. These observations clearly demonstrate the effects of feeding microhabitats among the macrofauna species: The suspension feeding *C. opercularis* exploits a sedimenting food source before it appears on the sediment surface. When this happens, the surface deposit feeding *A. nitida* experiences increased availability of food. It took 3 weeks of incorporation into the sediment, probably by way of bioturbation, before the subsurface deposit feeder *N. tenuis* obtained a maximum in food intake. The pigment variations in *A. gracilis* closely followed those of *C. opercularis* during the spring, but not in June and in the autumn months. The reason for this is not clear. But the similarity of the

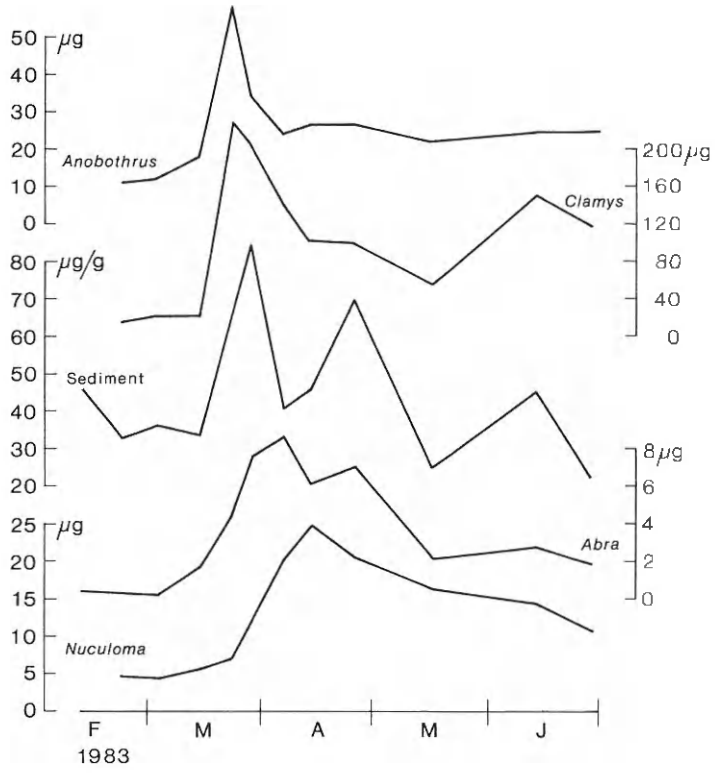

Fig. 7. Pigment content in standard animals of *Abra nitida*, *Nuculoma tenuis*, *Chlamys opercularis*, *Anobothrus gracilis*, and in the sediment surface, to show time lags in the increases of pigment content during spring. Vertical axis, animals: μg phaeopigment per standard animal, sediment: μg total pigment per g dry weight.

patterns and the timing of the pigment variations in the 2 species during the spring, and the position of the tube of *A. gracilis* above the substrate, suggest that it may be possible for this species to feed from sedimenting phytoplankton, suspended in the water.

The pigment maxima in the sediment in June and September-October, were clearly reflected only in the pigment content of *C. opercularis*. Obviously, the material sedimenting on these occasions was much less available to the other macrofauna species. It may relate to the quality of the sedimenting material, which was different from the quality of the sedimenting phytoplankton in the spring (Fig. 1C). Already Hunt (1925) showed that the composition of stomach content of *C. opercularis* directly reflected the seasonal variations in the types of particulate material present in the water. Our results (Fig. 4B) imply that this may be true on a quantitative basis also, and a more intensive sampling programme may have shown several pigment peaks in *C. opercularis* between March and December.

The narrow character of the March pigment peaks in *C. opercularis* and *A. gracilis* indicates, that for suspension feeders, only a short period of time is available for exploiting a sedimenting food source. Once at the bottom, the material is no longer available for the suspension feeders. In contrast, the broad pigment maxima found in the deposit feeders (Figs 2 & 3) show that they experience extended periods of increased food intake following the sedimentation.

Growth

The seasonal variations in dry weight of the soft tissues of the standard animals reflect variations in the amount of organic material stored in the soft body, and is thus a measure of the general condition of the species.

The increased pigment content of the bivalves resulted in rapid increments of their body weights. Whether this applies to the polychaete also, is not known. The correlation between increased pigment content in the spring and the weight increments, is very clear in *Abra nitida* and *Nuculoma tenuis*. In both of these, the maximum weight was already attained when the pigment content dropped to much lower summer levels, for *A. nitida* in May, and for *N. tenuis* in June. Further changes in the weights of these two species did not take place, until spawning reduced their weights abruptly, and all of the yearly increment in dry weight was directly connected with the increased intake of sedimenting phytoplankton.

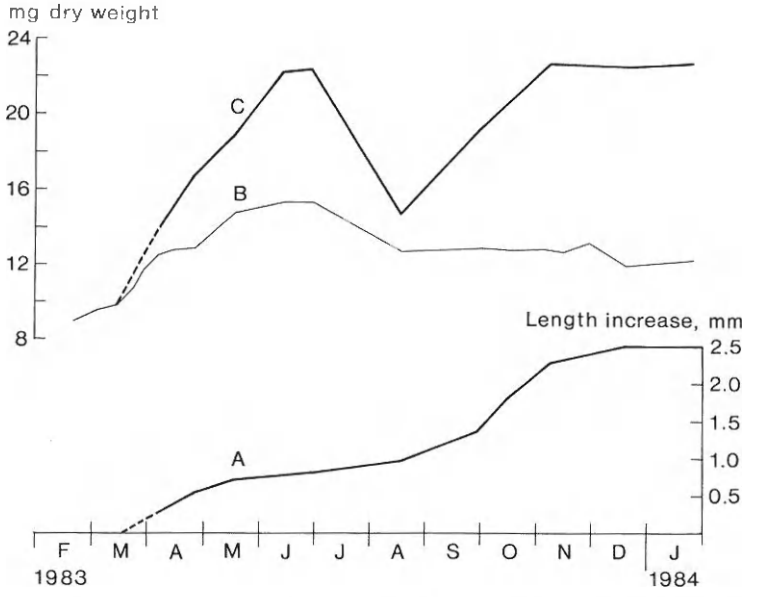

Fig. 8. Abra nitida. Seasonal changes in: A, mean increase in shell length. B, tissue dry weight of a standard animal, and C, calculated tissue dry weight of an animal growing from 12 mm (March) to 14.5 mm (December) in length. (See text.)

These results apply to standard animals, and do not include weight increments due to growth in length. In *A. nitida*, this somatic weight increment may be estimated from the shell growth rate, and the length to dry weight regressions obtained from each sampling. The result of this calculation is shown in Fig. 8: Shell growth started in March (Fig. 8A). A 12 mm long *A. nitida* (10.1 mg dry weight) would by 6 April have a length of 12.25 mm, and a dry weight of 13.8 mg (Fig. 8C), as calculated from the length to dry weight regression from 6 April. By the end of the year the length was 14.5 mm, and the dry weight was 23 mg. In June-October the dry weight decreased due to spawning, and increased due to somatic growth. However, Fig. 8C shows that about $^2/_3$ of the total (somatic plus reproductive) growth in dry weight during the year was connected with feeding from the settlement of phytoplankton in the spring.

From May-June to October the pigment content of *Nuculoma tenuis, Abra nitida* and *Anobothrus gracilis* was lower than in the spring, but it remained above the winter level. The food intake during these months probably constitutes the basis for the somatic growth, which in *A. nitida* mainly took place at high temperatures in September-October. In both *N. tenuis* and *A. nitida* there are strong indications of weight losses in February-early March (Figs 2 & 3).

Ansell described the seasonal changes in phaeopigment content and body weight of *Chlamys septemradiata* (1974b), *Nucula sulcata* (1974c) and *Abra alba* (1974a) from the Clyde Sea area. It is of interest to compare his results for animals from 80-100 m depth with those of the closely related Øresund species (30 m depth) because the general seasonal cycle in phytoplankton abundance in the 2 areas is similar, with spring and autumn blooms and minor peaks during the summer (Nicolaisen & Christensen, unpublished, Marshall & Orr 1927). Ansell stated that the coupling between the increments in pigment content and body weight found in *Abra alba* was much less clear in *Nucula sulcata*. However it is obvious from his figures that in both species the increase in tissue dry weight was initiated by the spring increment in phaeopigment content, and that the increases in dry weight stopped when the pigment concentrations dropped to lower summer levels.

In *Chlamys opercularis* too, a close connexion exists between increased pigment content and weight increments (Fig. 4). But in this species several periods of increased pigment content and accumulation of reserves, alternated with periods of low pigment content and utilization of the reserves. Ansell (1974b) found a similar pattern in *Chlamys septemradiata*. Also working in the Clyde Sea, Taylor & Venn (1979) followed the dry weight of *C. opercularis* during 3 consecutive years. Their fig. 6 shows, that in 1976 all the seasonal weight increment took place from July to September, in 1977 from March to October, and in 1978 from March to June.

The above results show, that the sedimentation of phytoplankton is the major factor regulating the growth of both suspension feeding species of *Chlamys*, and of deposit feeding species of *Nucula* and *Abra*. The high sedimentation which takes

place in the spring, can only be exploited by suspension feeders during the short period it remains suspended in the water. This makes the suspension feeders less dependent on the spring sedimentation than the deposit feeding species.

Levinton (1972) developed a hypothesis of trophically unspecialized, infaunal suspension feeders, as opposed to deposit feeders which were trophically specialized, due to competition for food. Reviewing the literature he found, that suspension feeders live with unpredictable and fluctuating food supplies, relying largely on sedimenting phytoplankton for food. *C. opercularis* fits well into this general description, despite the muddy and often resuspended substrate, which is untypical for a suspension feeder. Levinton further argued, that deposit feeders utilize bacteria as their main food source, and large seasonal changes may occur in the plankton or in deposition rate, with little change in the amount of food available to deposit feeders. He suggested that the rate-controlling process for the production of food for these species is the bacterial conversion of sediment organic matter, which would offer constant food levels for the deposit feeders. In contrast to this we found large seasonal changes in the food intake and the growth rate of the deposit feeding species of *Nuculoma* and *Abra*, and essentially all of the tissue growth in these, was connected with feeding from sedimenting phytoplankton.

Levinton's view of deposit feeders as consumers of bacteria are in agreement with the historical association of the nutritional value of detritus with microbes. Since Newell's (1965) work on *Hydrobia* many studies have confirmed that detritus particles, or fecal pellets are stripped of microbes in the gut of deposit feeders and the detritus particles are egested essentially unchanged (see e.g. Fenchel 1970, Mann 1972, and Gerlach 1978).

Many of these observations are based on laboratory experiments involving chemical treatment and sterilization of detritus, which may provide substrates unlike those present in natural sediments. Even more important, all the observations are based on detrital material derived from macrophytes, either vascular plants like *Spartina* or *Zostera*, or seaweeds. In these, particularly in the vascular plants, and in detritus derived from them, carbohydrates predominate other chemical constituents, in contrast to phytoplankton, which show a general predominance of protein. And it is the protein enrichment of macrophyte detritus by microbial fixation of nitrogen, that increases the nutritional value of the detritus for the deposit feeders.

Our results, and those of Ansell (1974), show that this protein enrichment may be less important outside laboratories, because deposit feeders obtain the bulk of their nourishment from sedimenting phytoplankton material, rich in protein. Jensen & Siegismund (1980) compared the amount of microbial biomass ingested by species of *Hydrobia* with the amount of organic matter required by the animals and found, that on natural sediments bacteria played only a minor role in the diet of *Hydrobia*. Similar results were obtained by Cammen (1980) for the deposit feeding polychaete *Nereis succinea*, and Tenore (1981) has shown, that higher

biomasses of the polychaete *Capitella capitata* could be supported by detritus derived from seaweeds that were relatively rich in nitrogen content than by the more nitrogen-poor detritus from vascular plants.

Evidently, microbial activity adds to the nutritional value of nitrogen-poor detritus. But too much emphasis on this may obscure the fact, that most of the primary produced material in the sea is phytoplankton, and this represents a high-protein food source which also becomes available to the benthic deposit feeders through sedimentation. In neritic environments, even with comparatively high loads of terrigenous material like the Øresund, macrobenthic deposit feeders do not rely on microbes for nourishment. Rather, like many suspension feeders they take advantage of the favourable chemical composition of the phytoplankton.

Reproduction

Seasonal weight variations of invertebrates often reflect reproductive cycles. This was also the case with the weight changes which we observed in *Nuculoma tenuis* (Fig. 2) and in *Abra nitida* (Fig. 3).

Spawning of *N. tenuis* took place in October-January, simultaneously with a weight decrease. The larvae of this species are probably lecitotrophic and fairly independent of food availability in the plankton.

The weight loss of *A. nitida* connected with spawning (Fig. 3) amounted to only half of the weight increase, which took place in the spring. However, our method of detecting gonadal development was much less detailed than that of Brown (1982), who made serial sectioning of the foot. A considerable amount of developed gametes may have been present in those specimens that we characterized as being without ripe gonads. Larvae of *A. nitida* are common in the plankton of the Øresund in October-November, and they appear in small numbers in May-August (Fosshagen 1965). Muus (1973) observed that settlement took place in October and again in January. We found the main spawning period to be July-October, but individuals with ripe gonads appeared again in January (Fig. 3). These observations all agree with the results of Brown (1982), who found an extended, or even continuous reproduction of *A. nitida* in the Skagerrak, with spawning taking place mainly in the autumn.

Also in *C. opercularis* the main weight changes, in September-December, were connected with the development of reproductive tissue (Fig. 4), but from March to August the weight and water content (Fig. 5) of the gonad changed only little, despite large variations in the stomach pigment content. Further, Taylor & Venn (1979) found a completely different cycle of gonadal weight changes in *C. opercularis* from the Clyde Sea. In these, the weight increased during winter, and reached a maximum in February-June. In pectinids, however, glycogen reserves in the adductor muscle are used during gametogenesis (Ansell 1974b, Taylor & Venn 1979). This metabolic transfer of energy from the adductor to the gonads must be

temperature dependent, and differences in temperature may explain the different reproductive cycles in the Clyde Sea and the Øresund.

The temperature range to which *C. opercularis* is exposed at the northern boundary of its distribution is 5-9°C in northern Norway, and 5-10°C in Faroese waters (Ursin 1956). Broom & Mason (1978) found a temperature of 5-6°C to be the lower limit of shell growth in the Plymouth area. On this basis we assume that below a temperature of about 6°C proliferation of gonads does not take place.

The seasonal temperature ranges in the Øresund and the Clyde Sea are compared in Fig. 9. In the Clyde Sea, *C. opercularis* is never exposed to temperatures below 6°C. Gametogenesis is controlled mainly by the amount of reserves in the adductor, and can take place during the winter and spring. In the Øresund proliferation does not start until the temperature increases to above 6°C in July.

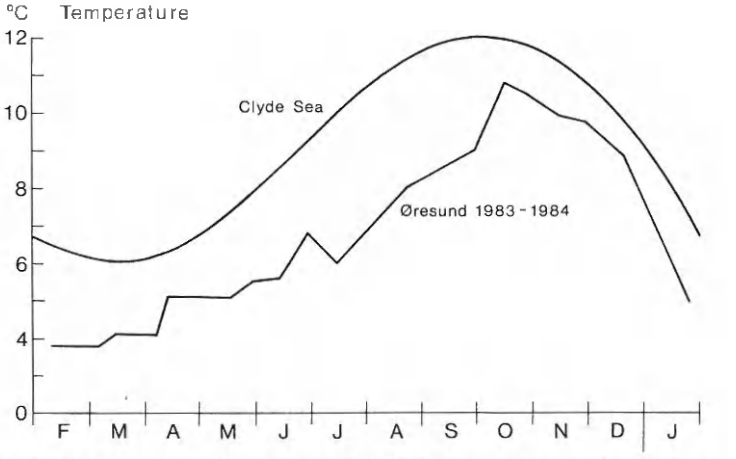

Fig. 9. Annual cycles of temperature of the bottom water in the Clyde Sea (from Taylor & Venn 1979, fig. 10) and of the sediment surface in the Øresund.

Spawning took place in the Clyde Sea at about 9°C and in Plymouth waters at 8-18°C, in both places following 5 months with maximum gonad dry weight. In the Øresund the gonad dry weight decreased in November-December, after only 2 months with high gonad weight, and when the temperature dropped to below 9°C. This decrease occurred simultaneously with, and corresponded in size to, an increase in body dry weight (Fig. 5), at a time when food intake was minimal (Fig. 4) and probably too low to allow for any weight increases. These observations are explained by assuming, that in the Øresund *C. opercularis* does not spawn, but instead it reabsorbs what is built up of gonadal tissue. The assumption is in agreement with observations on the occurrence of the larvae: If the decrease in gonad weight was caused by spawning, larvae would be expected to occur in December-February. In several investigations (Jørgensen 1946, Schramm 1962, Fosshagen 1965) larvae have been observed only in May and in July-November, with the

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