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Similarity in food source and timing of feeding in deposit- and suspension-feeding bivalves

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ABSTRACT: Although adapted to different methods of feeding, deposit- and suspension-feeding bivalves in the Wadden Sea (The Netherlands) appear to rely partly on the same limiting food sources. Two conditions for food competition, viz. use of the same food source and simultaneous feeding (in relation to season and tidal cycle), were studied in the field. The algal species composition in the stomachs of 3 suspension feeders (*Cerastoderma edule*, *Mya arenaria* and *Mytilus edulis*) and 2 deposit feeders (*Macoma balthica* and *Scrobicularia plana*) showed high correlations with the species composition of the water column, but lower correlations with the species composition of the sediment surface. During the phytoplankton spring-bloom periods in April and May, the stomachs of the suspension feeders *C. edule*, *M. arenaria* and *M. edulis*, and the deposit feeder *M. balthica* contained maximum amounts of algae. During the tidal cycle, the stomachs of the suspension feeders generally contained minimum amounts of algae when the tidal flat was drained and maximum amounts around times of high water. The stomachs of the deposit feeder *M. balthica*, however, contained relatively high amounts of algae during the entire tidal cycle. These results indicate that, although some difference in feeding behaviour was observed between deposit and suspension feeders, both groups rely on the same food source at the same time, irrespective of type of feeding.

KEY WORDS: Bivalves · Deposit feeder · Food competition · Suspension feeder · Wadden Sea

INTRODUCTION

Bivalve molluscs represent an important link in the food chain from primary producers, such as microalgae, to predators, such as fishes and birds. Shallow coastal seas, like the Wadden Sea (The Netherlands), are generally productive and support high stocks of bivalves. However, in the 1970s and 1980s a parallel increase in primary production and numbers and biomass of some bivalve species was observed in the western Wadden Sea (Beukema & Cadée 1986, Beukema 1991). This suggests that food can be a limiting factor for bivalve production in this area (Beukema & Cadée 1986). When this assumption is correct, competition for food may occur between bivalves.

In the Wadden Sea, several bivalve species live together on the tidal flats. The 5 most common species can be divided into 2 groups. The edible cockle *Cerastoderma edule* (L.), the blue mussel *Mytilus edulis* L. and the soft shelled clam *Mya arenaria* L. are obligate suspension feeders. They take their food out of the water column (Purchon 1968). The tellinid clams *Macoma balthica* (L.) and *Scrobicularia plana* (Da Costa) are facultative deposit feeders. They are able to take their food both from the surface of the sediment and out of the water column (Bradfield & Newell 1961, Hughes 1969, Bubnova 1972, Hummel 1985, 'Olafsson 1986, Thompson & Nichols 1988).

There is some evidence for intraspecific competition in *Cerastoderma edule* and *Mytilus edulis* in the Wadden Sea. Jensen (1992, 1993) observed low growth rates of *C. edule* within dense populations of the species. N. Dankers (pers. comm.) found lower growth rates in *M. edulis* inhabiting the center of mussel beds compared to individuals on the fringes. Indications of interspecific competition for food have also been found. Both stomach contents and growth rates of *C. edule* are negatively influenced by the nearby presence of *M. edulis* beds (Kamermans 1993). Kamermans

et al. (1992) showed that mixed populations of *C. edule* and *Macoma balthica* did not influence one another's growth in a small-scale basin experiment. This indicates that interspecific competition did not occur between a suspension and a deposit feeder on the small scale tested. However, field observations by Hummel (1985) showed that the algal species composition of the stomach contents of *M. balthica* resembled the composition of the water more closely than that of the sediment. Therefore, in the field, *M. balthica* appears to depend for its food primarily on material present in the water column. Thus, competition for food between deposit and suspension feeders should not be ruled out. Interspecific competition for food only occurs when 2 species simultaneously use the same food source.

This paper presents a direct approach for studying whether competition for food between intertidal deposit- and suspension-feeding bivalves can occur in the Wadden Sea. The species composition of microalgae in the stomachs of the bivalves was used as a tracer of food source and the variation in amount of algae in the stomachs was used as a tracer of timing of feeding.

MATERIALS AND METHODS

Study sites and sampling. The study was conducted at 7 intertidal stations located on a large tidal-flat area (Balgzand) in the westernmost part of the Dutch Wadden Sea (Fig. 1). The stations varied in tidal elevation, silt content of the sediment and abundance of the 5 species of bivalves studied (Table 1).

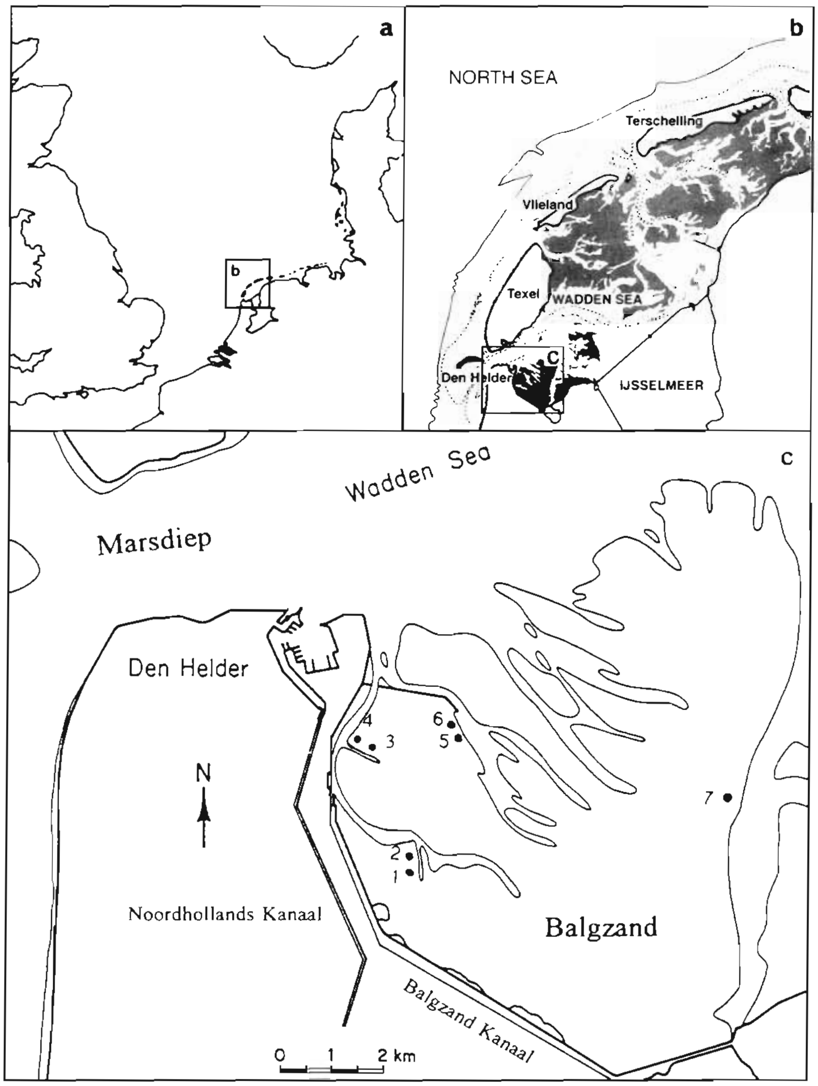


Fig. 1. Sampling stations in the Wadden Sea

In the periods March to September 1988 and March to October 1989, samples of the upper layer of the sediment, the overlying water and the stomachs of the bivalves were collected simultaneously at each station. Winter samples were not taken, because during these months both food supply and feeding activity of the bivalves are low (e.g. Thompson & Bayne 1972, Bayne & Widdows 1978, Hummel 1985).

Water samples: Possible stratification in the distibution of food particles in the water column was studied by sampling at 3 heights above the bottom. A water sampling device was placed on the tidal flat at low tide. Three tubes (opening diameter 1.5 mm) were placed above each other perpendicular to the prevailing flow direction. Two tubes were placed at 1 and 10 cm above the bottom. The third tube was kept at 9 cm below the surface of the water starting at a minimum water depth of 40 cm. The 3 tubes were connected to 3 jars that could be filled by vacuum pumping (maximum 10 cm Hg pressure) with a hand vacuum pump. To avoid contamination by resuspension, the person taking the samples was always situated downstream of the water sampling device. Water depths and temperatures of the surface water were monitored on each sampling occasion. Current speed of surface water was occa-

Table 1. Tidal elevation, silt content (fraction <50 µm expressed as percentage of total) of upper 10 cm of sediment and density (ind. m^{-2}) and biomass (g AFDW m^{-2}) of bivalves at Stns 1 to 7 in August. MTL: mean tidal level; nd: no data available; –: not present

Station:	1	2	3	4	5	5	6	7
Year:	1989	1989	1989	1989	1988	1989	1989	1988
Tidal height (cm from MTL)	-2	+18	-30	-6	-33	-48	-41	-60
Silt content (%)	4.9	1.1	34.0	5.6	10.9	11.8	0.8	7.5
Cerastoderma edule								
Density	5	33	876	152	567	370	22	272
Biomass	0.2	9.5	nd	97.2	51.5	58.6	6.0	35.2
Macoma balthica								
Density	995	658	179	1077	233	179	141	194
Biomass	2.7	7.2	nd	6.8	8.9	3.2	2.6	9.7
Mya arenaria								
Density	16	–	5	–	28	22	–	44
Biomass	1.9		nd		31.3	10.8		44.3
Mytilus edulis								
Density	–	–	16	5	144	22	–	5
Biomass			nd	1.8	15.0	6.9		0.7
Scrobicularia plana								
Density	–	–	5	5	5	–	–	–
Biomass			nd	0.2	3.2			

sionally measured at the time of sample collection by timing the movement of a small plastic container, which floated just beneath the surface, along a rope over a distance of 1 m.

Sediment samples: Sediment samples (1 to 10 each time) were collected with corers (diameters 24 and 26 mm). When the tidal flat was drained, the corer was used with a stopper. When the tidal flat was covered by water, the corer was connected to a stick and the stopper was fitted with a valve at the top. In this way sediment was sampled without a water layer on top. The top 3 mm of the sediment core was sliced off for analysis. Sediment surface temperature was measured when the tidal flat was drained.

Stomach samples: Bivalves were collected at the same time as the water and sediment samples by means of a big corer and a sieve. After collection, the bivalves were immediately placed on ice to halt digestion, and transported to the research vessel. There they were stored at 0 °C until they were taken out of their shells. The shell length was measured along the longest axis to the nearest 0.05 mm. The stomach was removed with a syringe and stored with a fixative or on a filter in the freezer. The time between collection and conservation of the samples never exceeded 90 min.

Algal species composition. The algal species composition in the water, sediment and stomach samples was used to trace the origin of the food in the stomachs following Hummel (1985). The stomach content of the 5 species of bivalves (per individual), water samples (100 cm^3 per sample) and sediment samples (top 3 mm of cores) were fixed with a modified Lugol solution (potassium iodide, iodine, acetic acid, glutaraldehyde and ethanol; D. Thomas, University of Tasmania) for identification and counting of the algae.

To facilitate detection of the algae in the sediment-surface samples, sand grains and algae were separated using a modification of a method described by de Jonge & Bouwman (1977) and de Jonge (1979). Part of the sediment sample was mixed with 20 % Ludox (a colloidal silica polymer) and 80 % demineralized water. The sample was shaken for 30 s in a Braun-Melsungen CO_2-cooled homogeniser to release the algae from the sand grains without damaging the algae. The sediment-Ludox solution was then placed on top of an 80 % Ludox and 20 % demi-water solution in a beaker through a needle with a conical head (described by de Jonge & Bouwman 1977). The sample was covered with demi water with the same needle and left to settle. After 16 h most sand grains and some heavy algae had settled on the bottom of the beaker and most algae and some light sand grains had settled on the inter-face between 20 and 80 % Ludox. The top fraction, including the interface, was removed with a sucking-apparatus (described by de Jonge & Bouwman 1977) connected to a vacuum pump. Both top and bottom fraction were diluted with demi water and centrifuged at 1500 rpm (2134 × *g*) for 10 min. The pellet was collected and fixed again with the modified Lugol solution.

Microalgal species in the water samples, stomach samples and both fractions of the sediment-surface samples were identified according to Drebes (1974), van Essen (1974), Belcher & Swale (1976), Pankow et al. (1976) and van der Werff (1984). A minimum of 100

cells were counted in 5 cm^3 counting chambers with an inverted microscope (magnification 500×) after 24 h of settling.

Chlorophyll concentration. Water, stomach and sediment samples were collected during a tidal cycle at a frequency of once every 1 to 3.5 h. Following Hummel (1985), the concentration of chlorophyll *a* (chl *a*) and its derivates was used as a measure of the amount of food present in the water, on the sediment surface and in the stomachs of the bivalves. Because of limited numbers of *Scrobicularia plana*, 4 species of bivalves were sampled in 1988 (the suspension feeders *Cerastoderma edule*, *Mytilus edulis* and *Mya arenaria* and the deposit feeder *Macoma balthica*). To increase the sampling frequency per species only *C. edule* and *M. balthica* were sampled in 1989.

Water samples (100 or 200 cm^3) and stomach contents (1 to 4 individuals) were filtered on a Whatman GF/C filter. The filters and the top 3 mm of the sediment cores were stored at −20 °C until analysis. Chl *a* was released in 20 cm^3 90 % acetone by sonification (30 s) with an ultrasonic disintegrator Soniprep MSE and centrifuged. Concentrations were measured with a Turner fluorometer following the method of Strickland & Parsons (1968). This method ensures rapid determination of the low amounts of chl *a* present in the stomachs. Concentrations of phaeopigments (the degradation products of chl *a*) were also measured. Chl *a* and phaeopigment concentrations were calculated according to Strickland & Parsons (1968). The ratio of chl *a* and phaeopigment concentrations was used as an indication of 'freshness' of the food.

Statistical analysis. The significance of differences between means of samples were tested with Student's *t*-tests (Sokal & Rohlf 1981). Linear correlation coefficients were used to evaluate the significance of correlations between 2 factors (Sokal & Rohlf 1981). Chl *a* concentrations at the different levels in the water were compared using a sign test under the null hypothesis of the same chl *a* concentration at all levels (Sokal & Rohlf 1981).

RESULTS

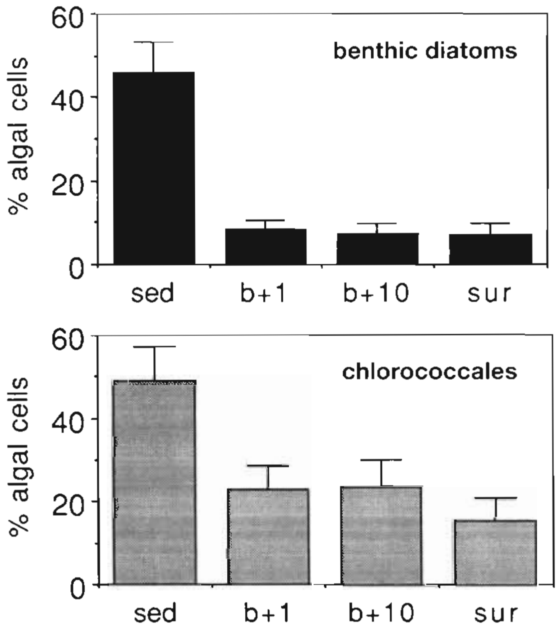
Food sources

Algal composition in water and sediment

Five different groups of algal species could be distinguished: flagellates, blue-green algae, pelagic (mainly centric) diatoms, chlorococcales and benthic (mainly pennate) diatoms (Fig. 2). In the case of blue-green algae, colonies rather than single cells were counted to avoid high percentages unrepresentative of the percentage of biovolume contributed by these very small (diameter 3 to 10 µm) algal cells. The diatoms were grouped as either pelagic or benthic according to their classification in the literature (see references above). For species classified as both pelagic and benthic the most frequent occurrence in either sediment or water samples determined in which group the species was included. The chlorococcales were freshwater green algae species that had entered the Wadden Sea via the nearby lake (IJsselmeer) and canals (Balgzandkanaal and Noordhollands Kanaal) (Fig. 1) (Cadée 1980). All the distinguished groups were present in water samples, but only 3 groups (viz. pelagic diatoms, benthic diatoms and chlorococcales) were found in sediment samples (Fig. 2). Pelagic diatoms were present in significantly higher percentages in water samples than in sediment samples (*t*-tests, $p < 0.05$), whereas benthic diatoms were present in significantly higher percentages in sediment samples (*t*-tests, $p < 0.001$). The presence of pelagic diatoms in sediment samples indicates that sedimentation of these algae had occurred, and the presence of benthic diatoms in water samples indicates that resuspension of benthic diatoms had taken place (Fig. 2). The chlorococcales were found in significantly higher percentages in sediment samples (*t*-tests, $p <$ 0.05 to 0.01). This indicates considerable sedimentation of this group. The distributions of the algae at different levels in the water column were not significantly different (*t*-tests, $p > 0.05$), although there was a slight decrease in benthic diatom cells with increasing height above the bottom (Fig. 2). Data on the chlorococcales were not included in further analysis because this group was not counted in all samples. Cells of the flagellate *Phaeocystis* sp. and 3 unidentified flagellate species were highly abundant in the water in 1988, but unfortunately were not clearly visible in the stomachs of the bivalves. Therefore, these species could not be used as tracer algae and were not included in further analysis. The remaining cells were allocated to 2 groups, viz. pelagic algae (flagellates, blue-green algae and pelagic diatoms together) and benthic algae (benthic diatoms only) (Fig. 3). This grouping had the advantage that it could be used in all months, whether the separate groups of pelagic diatoms, flagellates and blue-green algae were abundant or scarce. Benthic diatoms were plentiful in all months.

Algal composition in stomach contents

A total of 46 species or groups of algae were identified in the samples. As many as 24 species were found in the stomachs of both deposit and suspension feeders. The 8 most common species, occurring in more than 50 % of the samples and with abundances up



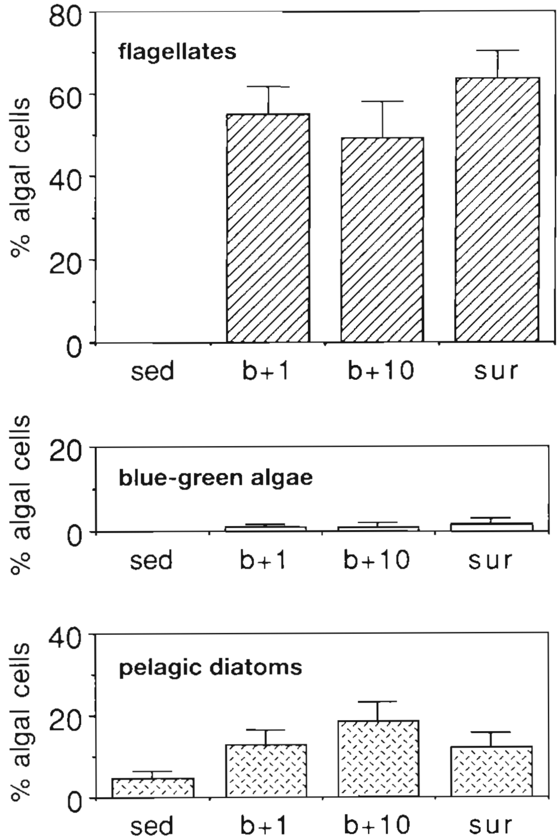


Fig. 2. Algal-group composition of simultaneously collected sediment samples (upper 3 mm; sed) and water samples (3 heights; b+1: 1 cm above bottom, b+10: 10 cm above bottom; sur: surface). Means (+ SE) of 7 sampling occasions, Stns 5 & 7, May to September 1988. For each group, the proportion (mean %) of the total numbers of cells in each sample counted is given

to 89%, were all found in this category. Two species were found in stomachs of deposit feeders only, and 10 species in stomachs of suspension feeders only. These species were not very common. The remaining 10 species were not observed in the stomachs and were not common in the water and sediment samples. They were observed only in 1 to 3% of the samples, and their maximum abundance never exceeded 30%.

The concentrations of chl *a* in stomach samples were invariably higher than phaeopigment concentrations (Table 2). This indicates that, at the time of sampling, advanced digestion had not taken place in the stomachs. The chl *a* to phaeopigment ratios of stomach contents were between the values observed for water and sediment (Table 2).

Table 2. Mean (± SE) chl *a* to phaeopigment ratio (chl *a*/Phaeo) in water, sediment and stomach samples of 5 species collected at Stns 5 & 7 in March to September 1988

Sample	Chl *a*/Phaeo	n
Water	27.06 ± 11.67	11
Sediment	1.57 ± 0.17	12
Cerastoderma edule	1.70 ± 0.31	11
Mya arenaria	2.23 ± 0.70	9
Mytilus edulis	16.70 ± 9.84	6
Malcoma balthica	2.71 ± 1.41	11

To trace the origin of the stomach contents, the species compositions of simultaneously collected sets of water, sediment and stomach samples were compared. The algae were divided into 2 groups (benthic algae and pelagic algae) and the proportions of the 2 groups were calculated for each type of sample. As the height above the bottom at which the water was collected did not significantly influence the algal-group composition of the water samples, only those collected at 1 cm above the bottom were used in this comparison. The percentage of benthic algae was used in the following analysis. Replicate stomachs sampled for each species showed variability among individuals, and linear correlation coefficients were not significant ($p > 0.05$) (Fig. 4).

If stomach contents originate mainly from 1 of the 2 sources (water or sediment), the percentage of benthic algae in the stomachs would be expected to show a positive relation with the percentage of benthic algae in this source. Significant positive correlations were observed between benthic algae in the water and in the stomachs of both suspension feeders ($p < 0.01$) and deposit feeders ($p < 0.01$) (Fig. 5a). The data sets for the

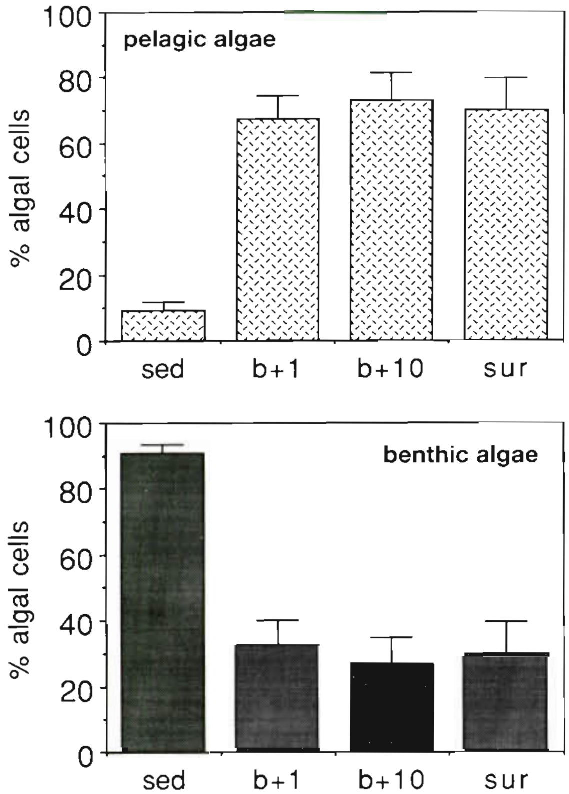


Fig. 3. Modified (see text) algal-group composition of simultaneously collected sediment samples (upper 3 mm; sed) and water samples (3 heights; b+1: 1 cm above bottom; b+10: 10 cm above bottom; sur: surface). Means (+ SE) of 7 sampling occasions, Stns 5 & 7, May to September 1988. For each group, the proportion (mean %) of the total number of cells in each sample counted is given

individual species all showed positive correlations with the water samples, which were significant for *Macoma balthica* ($p < 0.01$), *Mytilus edulis* ($p < 0.05$) and *Mya arenaria* ($p < 0.01$) (Fig. 5a).

The benthic algae present on the sediment surface are not expected to be the primary food source, because correlations between stomach contents and sediment samples were not significant ($p > 0.05$) (Fig. 5b). The benthic algae in the stomachs of both deposit and suspension feeders were generally present in lower percentages than would be expected if only sediment was taken in. Moreover, the proportion of benthic algae in the stomach samples varied strongly: from nearly 0 to >80% of all algal cells. This variability did not reflect the low variability of the algae on the sediment surface: from >60 to nearly 100%. It is more likely a reflection of the variability in the water column: from nearly 0 to >60%. The relative concentration of benthic algae in the water and on the sediment surface did not show a significant correlation ($p > 0.05$).

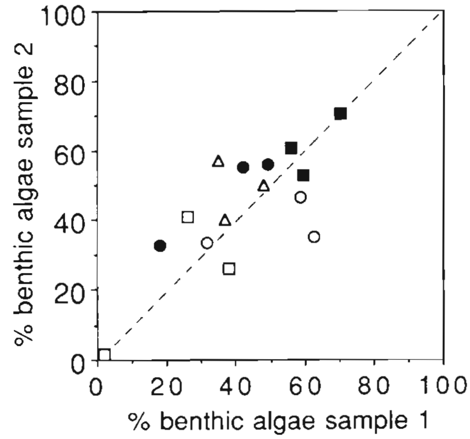


Fig. 4. Percentages of benthic algae in simultaneously collected replicate individual stomachs (samples 1 & 2) from Stns 5 & 7, March to September 1988. Broken line indicates equal proportions. (□) *Cerastoderma edule*; (●) *Macoma balthica*; (○) *Mya arenaria*; (△) *Mytilus edulis*; (■) *Scrobicularia plana*

If stomach content was a perfect reflection of the available algae in the water column, the percentages of benthic algae would have been the same in the water and in the stomachs, i.e. the data points would have been evenly scattered along the line of equal percentages (broken line in Fig. 5a). However, most points were located above this line, indicating that a higher percentage of benthic algae was found in the stomachs than would be expected if only water was taken in. The stomach contents of both deposit and suspension feeders thus appear to be a combination of material collected mostly from the water column and a small amount from the sediment surface.

Timing of feeding

Seasonal fluctuations

To exclude possible influences of tidal cycle, the results of samples collected around high water were used to study seasonal changes in potential food for the bivalves. In 1988, monthly mean chl *a* concentrations in the water sampled at 1 cm were only slightly higher than at 10 cm (Fig. 6a). Both levels showed the same seasonal pattern. A maximum chl *a* concentration was observed in April and a second, but lower, peak in July (Fig. 6a). Chl *a* concentrations in the nearby Marsdiep tidal inlet (Fig 1) during high tide closely resembled values from the same days at the tidal flat (Fig. 6a). In 1989, chl *a* concentrations in the water were again similar at the 2 sampling levels (Fig. 6b). High chl *a* concentrations were observed in

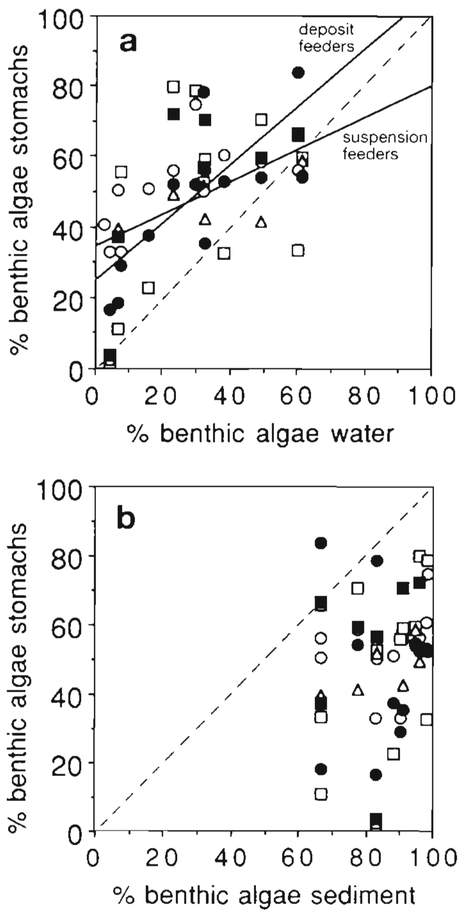


Fig. 5. Relationships between percentages of benthic algal cells observed in stomachs and in (a) water (1 cm above bottom) and (b) sediment (upper 3 mm) samples collected at Stns 5 & 7, March to September 1988. Broken line indicates equal proportions. (□) *Cerastoderma edule*; (●) *Macoma balthica*; (○) *Mya arenaria*; (△) *Mytilus edulis*; (■) *Scrobicularia plana*

May, July, August and September (Fig. 6b). The spring maximum in the water was lower than the values found in July and September. However, the variability between stations was high. Chl *a* concentrations in the Marsdiep inlet were similar to the tidal-flat concentrations, except that the July value was much lower than on the tidal flat (Fig. 6b). The seasonal fluctuation in the chl *a* concentration on the sediment surface showed a maximum in June 1988 (Fig. 6c) and August 1989 (Fig. 6d). Variability was again high between stations.

Because differences in size between individual bivalves of the same species could account for differences in chl *a* contents in the stomachs, the chl *a* amounts per individual were divided by their body weights. Weights were calculated from relations between shell length and ash-free dry weight as established monthly in 1988 and 1989 by J. J. Beukema (pers. comm.). In 1988, the most complete series of observations on chl *a* contents of the stomachs was available for *Mya arenaria* and *Macoma balthica*. Both species showed high amounts of chl *a* in their stomachs already in March and reached maximum values in April, after which a gradual decline was observed during the remainder of spring and the summer (Fig. 6e). For *Cerastoderma edule* and *Mytilus edulis* stomach samples are missing in March and April, but a similar decline from May to September as in the other 2 species was found (Fig. 6e). The amount of chl *a* in *C. edule* increased slightly in September. In 1989, a March to October data set is available for *M. balthica* and *C. edule*. Amounts of chl *a* in their stomachs increased from March to a maximum in May (Fig. 6f). A second, but lower, peak was observed in July for *M. balthica* and in September for *C. edule* (Fig. 6f). The amounts of chl *a* in the stomachs were variable between individuals collected at the same time and the same station; linear correlation coeffients were significant only for *M. balthica* ($p < 0.01$) (Fig. 7).

The maxima in chl *a* contents observed in the stomachs (April 1988 and May 1989) corresponded with the spring maxima that were present in the water column (April 1988 and May 1989). The maximum chl *a* concentrations observed in the water column in July and September 1989 could also be detected in the stomachs of *Macoma balthica* (July) and *Cerastoderma edule* (September). The summer maxima found in the upper 3 mm of the sediment (June 1988 and August 1989) did not correspond with any of the maxima in the stomachs. This indicates that the amounts of chl *a* in the stomachs were related more closely to the seasonal fluctuations in chl *a* concentration in the water column than at the sediment surface. Deposit and suspension feeders both contained highest amounts of chl *a* in the stomachs during the same season, the phytoplankton spring-bloom period.

Tidal fluctuations

Water samples, collected simultaneously at 3 heights above the tidal flat (1 cm, 10 cm and surface), could be compared 176 times (in 38 submersion periods). Differences in chl *a* concentration between sampling levels were generally small (<35 % difference in 62 % of the cases). Highest chl *a* concentrations were observed more often (in 65 % of the cases) at the 1 cm level than at the other levels, but this was not significant (sign test, $p > 0.05$).

All stations were covered with water between 3 to 6 h before and 3 to 6 h after high water (Fig. 8a). The maximum water height depended on the tidal eleva-

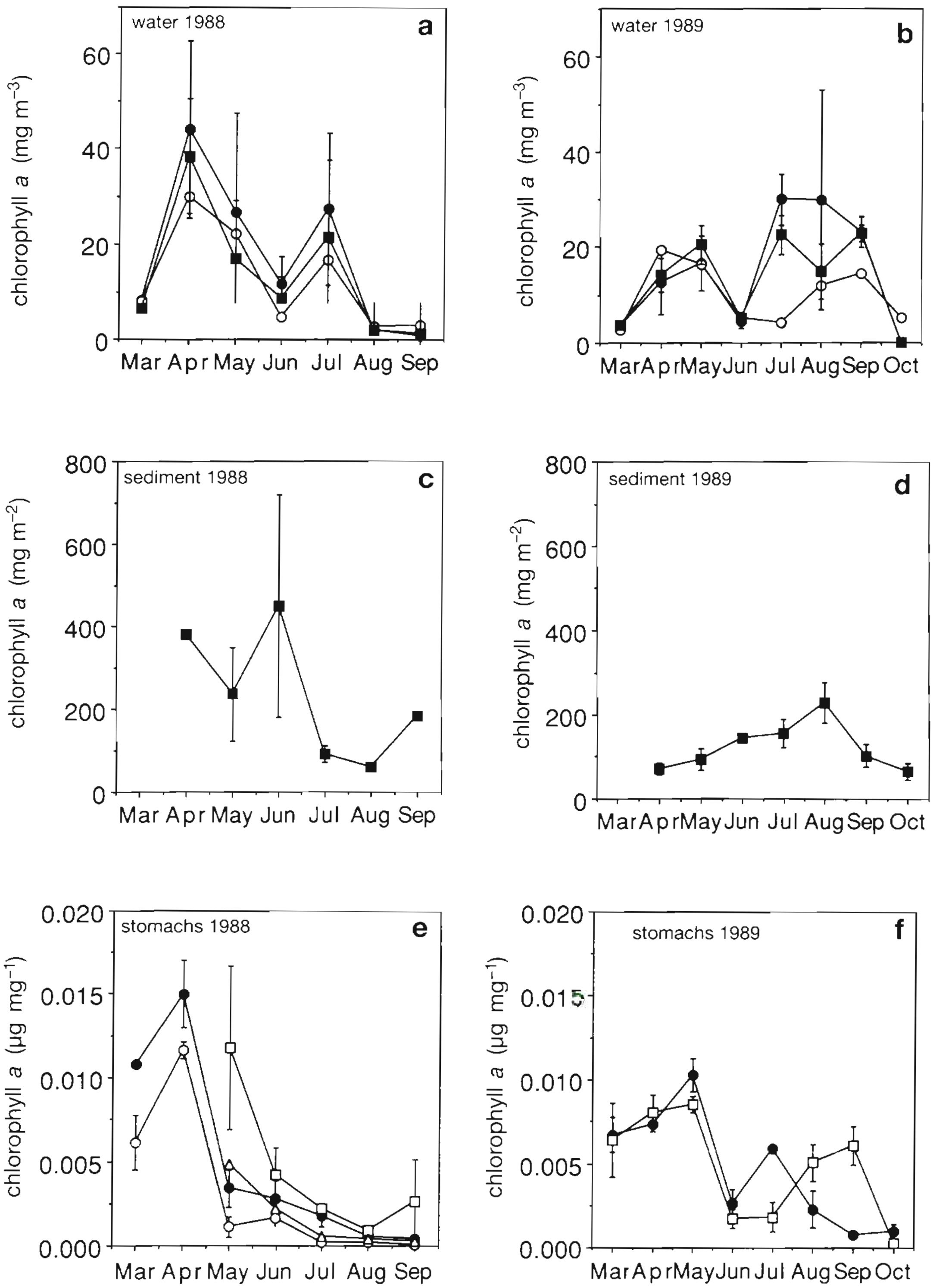


Fig. 6. Seasonal fluctuations in chl *a* concentration. (a, b) Mean monthly chl *a* concentrations in water at 1 cm (●) and 10 cm (■) above Balgzand tidal flats and in the Marsdiep tidal inlet (O) (G. C. Cadée pers. comm.): (a) 1988, Balgzand tidal-flat Stns 5 & 7, and (b) 1989, Balgzand tidal-flat Stns 1 to 6. (c, d) Mean monthly chl *a* concentrations on the sediment surface (upper 3 mm) of Balgzand tidal flats: (c) 1988, Balgzand tidal-flat Stns 5 & 7, and (d) 1989, Balgzand tidal-flat Stns 1 to 6. (e, f) Mean monthly amounts of chl *a* in the stomachs of *Macoma balthica* (●), *Mya arenaria* (O), *Cerastoderma edule* (□) and *Mytilus edulis* (Δ): (e) 1988, Balgzand tidal-flat Stns 5 & 7, and (f) 1989, Balgzand tidal-flat Stns 1 to 6. Values closest to high water (for stomachs and water) and low water (for sediment) were used. Standard error bars are presented

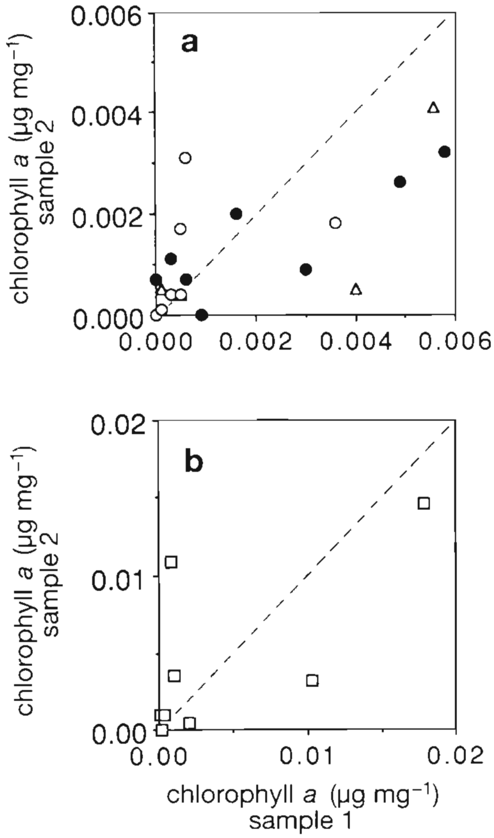


Fig. 7. Amounts of chl *a* in simultaneously collected replicate individual stomachs (samples 1 & 2) from Stns 5 & 7, May to September 1988. Broken lines indicate equal amounts. (●) *Macoma balthica*; (△) *Mytilus edulis*; (○) *Mya arenaria*; (□) *Cerastoderma edule*

tion of each station (Fig. 8a, Table 1). Current velocity was highest at early flood and late ebb tide (Fig. 8b). The chl *a* concentration in the water was generally higher during flood than during ebb (Fig. 8c). Highest chl *a* concentration in the top layer of the sediment was observed when the tidal flat was drained (Fig. 8d). Both the suspension feeders and the deposit feeder contained high amounts of chl *a* in the stomachs when the tidal flat was covered with water (Fig. 8e, f, g). The stomach contents of the suspension feeders contained the least chl *a* when the tidal flat was drained, increased chl *a* after the tidal flat was covered with water and decreased chl *a* during the remaining part of the covered period (Fig. 8e, f, g). In 1989, this pattern was very distinct for *Cerastoderma edule*. In 1988, lower values were observed 1 to 2 h before high water. The deposit feeder *Macoma balthica* exhibited no tidal pattern (Fig. 8f, g). These results indicate that the patterns of chl *a* in the stomachs of the deposit-feeding and the suspension-feeding bivalve species during the tidal cycle are different.

DISCUSSION

Food sources

The algal-group composition (benthic and pelagic algae) in the stomachs of deposit feeders and suspension feeders was similar to that in the water column. Moreover, the seasonal fluctuations in chl *a* concentrations in the water column were reflected in the stomachs of both feeding groups. Therefore, the first condition for food competition, use of the same food source by the different bivalve species, was present in the field. One would expect deposit feeders to be capable of avoiding competition for food with suspension feeders by using a different food source. Indeed, experiments in a basin showed intraspecific competition between *Macoma balthica* individuals, but interspecific competition between *M. balthica* and *Cerastoderma edule* was not evident (Kamermans et al. 1992). It is, therefore, surprising to find similarity in the stomach contents of deposit and suspension feeders in the field.

Although the algal-group composition in the stomachs showed high correlations with algae present in the water column, the stomachs contained higher proportions of benthic algae than would be expected if the water column had been the only food source. Furthermore, the chl *a* to phaeopigment ratio of the stomach contents showed values between those for water and for sediment. One explanation can be that the samples taken at 1 cm above the bottom do not represent the height at which the bivalves collect their food. Because the water column is well mixed, a better similarity of the stomachs with water samples collected at locations lower than 1 cm above the bottom does, however, not seem likely.

Another possible explanation for the over-representation of benthic diatoms in the stomachs of both suspension- and deposit-feeding bivalves is that both groups of bivalves may have collected particles from the surrounding sediment layer. The deposit feeder may have taken up these particles with its inhalant siphon from the surface of the sediment, while currents produced by the inhalant siphons of the suspension feeders may have transported the particles towards their inhalant siphons. Rasmussen (1973) observed this phenomenon for *Mya arenaria*. Similarly, deposit-feeding bivalves may suck in particles from the water column. Yonge & Thompson (1976) and Hummel (1985) suggested that *Macoma balthica* inhales large amounts of water while collecting material from the top layer of the sediment. The same may hold for *Scrobicularia plana* (Hughes 1969).

An alternative explanation for the similarity of the stomach contents of deposit feeders with water samples may be a switch from deposit to suspension feed-

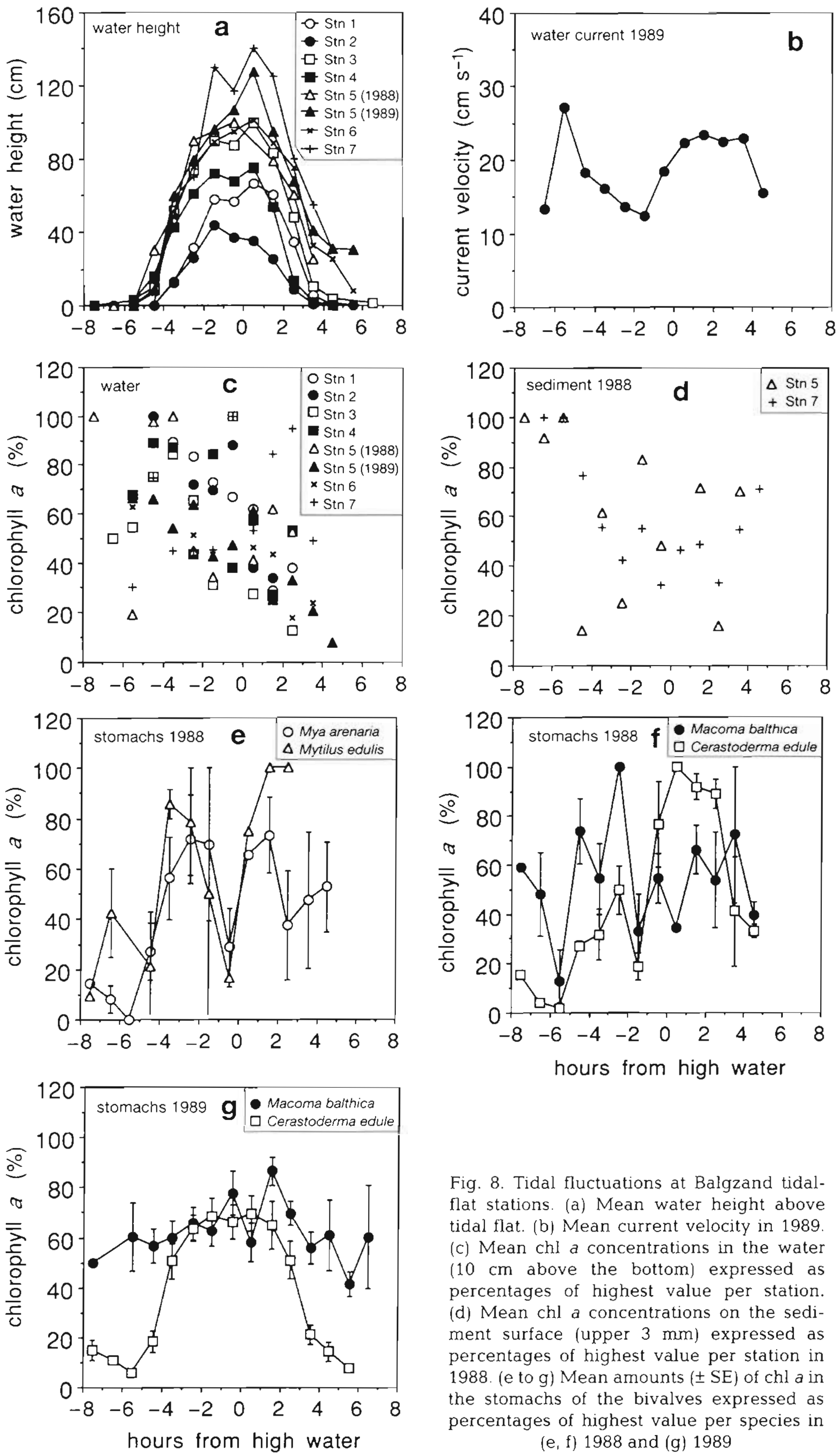


Fig. 8. Tidal fluctuations at Balgzand tidal-flat stations. (a) Mean water height above tidal flat. (b) Mean current velocity in 1989. (c) Mean chl *a* concentrations in the water (10 cm above the bottom) expressed as percentages of highest value per station. (d) Mean chl *a* concentrations on the sediment surface (upper 3 mm) expressed as percentages of highest value per station in 1988. (e to g) Mean amounts (± SE) of chl *a* in the stomachs of the bivalves expressed as percentages of highest value per species in (e, f) 1988 and (g) 1989

ing under the influence of siphon predation as proposed by Zwarts & Wanink (1989). Flatfish, gobies, shrimps and small shore crabs feed on siphon tips of *Malcoma balthica* that are protruding above the sediment (de Vlas 1985). By shifting from deposit to suspension feeding, *M. balthica* could keep its inhalant siphon near the sediment surface and avoid siphon predation (Zwarts & Wanink 1989). Predators upon siphon tips were not present in the basin experiment where *M. balthica* and *Cerastoderma edule* did not compete (Kamermans et al. 1992). Therefore, a shift in *M. balthica* from deposit to suspension feeding was not expected.

When different species use the same food source, differences in particle selection could reduce competition. Several studies indicate that the suspension feeders *Mytilus edulis*, *Mya arenaria* and *Cerastoderma edule* can select algae preferentially from a mixture of algae and silt particles (Kiørboe et al. 1980, Kiørboe & Møhlenberg 1981, Prins et al. 1991). Selection of food particles on the basis of size has not been observed for the 5 bivalve species studied (Hughes 1969, Bayne et al. 1977, Gilbert 1977, Møhlenberg & Riisgård 1978). Food-particle selection by means of characteristics other than particle size does not seem likely either (Cucci et al. 1985). Indeed, stomach contents analysis of the 5 species of bivalves in these field populations showed high similarity in algal species composition. This supports the lack of food particle selection.

Timing of feeding

Season

In each of the 4 bivalve species in which the amounts of chl *a* in the stomachs was determined, maximum values were observed during the same period, in April and May. These months represent a major part of the growing season of the bivalves in the Wadden Sea (*Malcoma balthica* March to July: Beukema et al. 1985; *Cerastoderma edule* April to August: Beukema 1974; *Mytilus edulis* April to August: Dankers et al. 1989; *Mya arenaria* April to August: Zwarts 1991). The months of maximum chl *a* contents of the stomachs corresponded with months of maximum chl *a* concentrations in the water. Surprisingly, the chl *a* maxima in summer were not detected in the stomachs as clearly as the maxima in spring. Temperatures of both water and sediment were much higher in summer (16 to 20 °C) than in spring (5 to 15 °C) and this may have influenced feeding of the bivalves. Growth of *M. balthica* seems to be influenced by temperature. De Wilde (1975) showed growth of this species in the laboratory at temperatures between 0 and 15 °C. Beukema et al. (1985) observed that growth of *M. balthica* in the field was restricted to water temperatures between 4 and 16 °C.

Tide

Highest chl *a* concentrations were observed in the water column above the tidal flat during flood at several stations and in several months. Other studies in the Balgzand area on fluctuations in chl *a* concentrations in the water overlying the tidal flats (Hummel 1985) or present in a tidal channel (Cadée 1982) showed similar patterns. Both wind- and tide-induced resuspension have been suggested to increase concentrations of chl *a* in the water (Roman & Tenore 1978, Baille & Welsh 1980, de Jonge & van Beusekom 1992, de Jonge 1994). Indeed, in this study, the presence of benthic diatoms in the water column, a slightly higher chl *a* concentration close to the sediment surface than higher in the water column, and lower chl *a* concentrations at the sediment surface during submersion than during emersion all suggest resuspension of algae. Carlson et al. (1984) observed lower chl *a* concentrations in ebb waters than in flood waters at the entrance of an intertidal cove and concluded that *Mytilus edulis* and *Mya arenaria* had filtered phytoplankton out of incoming waters. Such depletion of chl *a* by tidal-flat suspension feeders may have caused lower chl *a* concentrations during ebb at the Balgzand.

The feeding pattern of the bivalves during a tidal cycle showed differences between the suspension feeders and the deposit-feeder *Macoma balthica*. The amount of food present in the stomachs of suspension feeders was low at high current velocities during early flood and late ebb tide. This suggests a negative effect of these high current velocities on the food intake of suspension feeders. At flow velocities >25 cm s^{-1} in a flume, filtration rates of *Mytilus edulis* were strongly reduced (Wildish & Miyares 1990). Cole et al. (1992) also showed that filtration rate of a suspension feeding bivalve was influenced by flow velocity.

In contrast to the suspension feeders, *Macoma balthica* showed no tidal pattern in feeding. This suggests more equal feeding times for the deposit feeder. The results indicate a partly different feeding behaviour for *M. balthica*. However, high amounts of chl *a*, present in the stomachs of both deposit and suspension feeders, indicate maximal food intake during submersion.

In summary, 2 conditions for food competition, viz. similarity in food source and (seasonal and tidal) timing of feeding, are present in intertidal suspension- and deposit-feeding bivalves in the western Wadden Sea. This indicates that competition for food between these 2 groups is possible.

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