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Influence of *Corophium volutator* and *Hydrobia ulvae* on intertidal benthic diatom assemblages under different nutrient and temperature regimes

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ABSTRACT: Epipelic diatoms dominate the microphytobenthos of estuarine sediments, where they play important roles in ecological processes such as primary production, secondary production and sediment stability. Grazing (top-down control) and nutrients (bottom-up control) regulate the biomass and species composition of intertidal benthic diatom assemblages. However, observations of grazing/predation effects on species richness differ under contrasting nutrient conditions. We investigated the interactive effects of grazing, nutrients and temperature and compared the impacts of *Corophium volutator* and *Hydrobia ulvae*—2 species that differ in their feeding strategies and bioturbation effects. Diatom assemblages were collected from 2 estuaries (Biezelingsche Ham, Westerschelde, high nutrient, and Zandkreek, Oosterschelde, low nutrient) in The Netherlands that differ in their dominant macrofaunal grazer species. Assemblages were grown in the laboratory without (control) and with grazing activity under different nutrient and temperature regimes. *C. volutator* exerted a strong regulatory influence on epipelic diatoms by reducing biomass, and preferentially consuming certain dominant taxa, thereby increasing species richness, evenness and diversity. The percentage of epipsammic species increased in the presence of *C. volutator*, at the expense of *Navicula* species. Biezelingsche Ham assemblages grazed by *C. volutator* were not influenced by nutrient or temperature regime, while control assemblages were influenced by temperature. In contrast, differences in the structure of diatom assemblages between the treatments were far less pronounced for *H. ulvae*-grazed and control Zandkreek assemblages. *H. ulvae* appeared to be a general consumer, grazing subdominant species. Species richness was greater at low temperature, regardless of nutrient level. Macrofaunal grazing did not predictably increase or decrease species diversity, but could potentially do both, and it may mask the effects of environmental and bottom-up control.

KEY WORDS: Benthic diatoms · Grazing · Nutrients · Temperature · *Corophium volutator* · *Hydrobia ulvae* · Estuaries · Intertidal mudflats

INTRODUCTION

Single-celled phototrophic diatoms often dominate the microphytobenthos of intertidal estuarine sediments (Paterson & Hagerthey 2001). Diatoms are of particular importance since they contribute significantly to estuarine primary production (MacIntyre et al. 1996), with estimates ranging from 29 to 314 g C m^{-2} yr^{-1} (Underwood & Kromkamp 1999). Microphytobenthos supports a large portion of estuarine secondary production (Miller et al. 1996, Page 1997) and minimizes sediment erosion through the production of extracellular polymeric substances (EPS) (Yallop et al. 1994, Paterson 1997, Austin et al. 1999). The factors that determine the abundance and distribution of diatom species in estuarine sediments are still poorly understood and the debate amongst ecologists contin-

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ues as to whether the primary control is by bottom-up (through available resources) or top-down factors (from predators) (Power 1992).

Tilman (1999) argues that ecosystem dynamics and functions are regulated by species composition, because species drive ecological processes and have individual traits. This implies that the regulatory and selective mechanisms such as competition, predation, and disturbance will affect microphytobenthic processes, including primary productivity, by regulating assemblage composition and biomass. While many studies have shown the effects of hydrodynamics (see Paterson & Hagerthey 2001), grazing (see Miller et al. 1996), and nutrient supply (Posey et al. 1999, Wulff et al. 2000) on microphytobenthic biomass, few have addressed species composition.

There is substantial evidence indicating that benthic diatoms are the primary food resource for many macrofauna and meiofauna taxa inhabiting estuarine sediments (Page 1997, Buffan-Dubau & Carman 2000). More importantly, some estuarine macrofauna regulate microphytobenthic biomass and production (Reise 1992, Underwood & Paterson 1993, Smith et al. 1996). Top-down control from grazers can be considered a major perturbation to diatom assemblages on an estuarine mudflat, with the amphipod *Corophium volutator* (Pallas) and the gastropod *Hydrobia ulvae* (Pennant) being among the most common and abundant grazers. *C. volutator* is generally considered to be an unselective deposit feeder, although suspension feeding and epipsammic browsing may occur (Gerdol & Hughes 1994a,b), while *H. ulvae* has been shown to rely on deposit feeding and browsing (Lopez & Kofoed 1980, Morrisey 1988a,b, Blanchard et al. 2000). *H. ulvae* and *C. volutator* are both capable of drastically reducing natural microalgal populations (Coles 1979). In addition to their feeding strategies, infauna may affect diatom assemblage structure through sediment bioturbation. *C. volutator* transports sediment vertically via burrow construction and irrigation, whereas *H. ulvae* horizontally mixes the surface sediment layer (Cadée 2001).

The few studies that have directly examined the effects of grazers on microphytobenthic species richness have shown that selective grazing by macrofauna can alter species composition, with the strength of the effect differing among macrofaunal species (Reise 1992, Smith et al. 1996). The selective effects may result from differences among diatoms as a viable resource, susceptibility and survival of grazing of individual diatom taxa, as well as the size and/or hunger level of the herbivore (Steinman 1991). It is important to recognise that observations of predation effects on species richness are neither clear nor universal, and grazing impacts on diversity tend to differ under different nutrient conditions (Proulx & Mazumder 1998). For example, Hillebrand et al. (2000) found that the diversity of a periphyton community grazed by crustaceans and gastropods was reduced when nutrient concentrations were low, but enhanced when concentrations were high.

Both the availability of nutrients and the ambient temperature are important in determining the species composition of estuarine intertidal benthic diatom assemblages. Species composition has been linked to ammonium concentration (Peletier 1996, Underwood et al. 1998), while other macronutrients (e.g. nitrate, orthophosphate, and silicate) do not appear to be limiting to benthic diatoms (Admiraal 1977, Pinckney et al. 1995, Underwood & Provot 2000). Seasonal succession patterns in species composition are well known (Admiraal et al. 1984, Oppenheim 1991, Underwood 1994, 1997, Saburova et al. 1995, Peletier 1996). However, many studies examine top-down and bottom-up effects as independent factors.

The objective of this laboratory study was to investigate the interactive effects of grazing, nutrients and temperature upon the biomass and composition of intertidal benthic diatom assemblages. Natural densities of *Corophium volutator* and *Hydrobia ulvae* were used in this experiment, and since these 2 macrofauna species differ in their feeding strategies and bioturbation effects, we hypothesised that their impacts on structuring diatom assemblages would differ. In addition, if intertidal diatoms have unique preferences for certain nutrient and environmental conditions, then we would expect to see structural segregation in diatom assemblages grown under different environmental conditions.

MATERIALS AND METHODS

Sediment cores were collected on 16 June 2000 from 2 intertidal mudflats whose estuaries differed in their dissolved nutrient concentrations (Table 1). The Biezelingsche Ham (B-Ham) mudflat is located on the north shore of the eutrophic Westerschelde Estuary in The Netherlands (51° 26′ N, 3° 55′ E). The Zandkreek mudflat is situated on the south shore of the oligotrophic Oosterschelde Estuary in The Netherlands (51° 32′ N, 3° 54′ E). Thirty-two cores (surface area 21 cm^2; length 7.6 cm) were collected from the upper intertidal shore of both mudflats, in regions of visibly high macrofaunal densities. *Corophium volutator* (68 ± 5 ind. $core^{-1}$; n = 3) was the dominant grazer at the B-Ham mudflat, whereas *Hydrobia ulvae* (158 ± 20 ind. $core^{-1}$; n = 3) dominated the Zandkreek mudflat. The experiment was terminated on 29 June 2000.

Four tidal tanks were established in a temperature-controlled room (15°C). Tides were synchronized with the ambient tidal cycle and corresponded to 4 h immersion and 8 h emersion periods. Tanks were illuminated for 16 h d^{-1} with an irradiance of 265 ± 1.9 µmol m^{-2} s^{-1} (mean ± SE). Two natural levels of nutrient treatment were used (high and low) to assess nutrient effects. For the high-nutrient treatment, 2 tidal tanks were filled with filtered (0.45 µm) water from the Westerschelde Estuary. For the low-nutrient treatment, 2 tanks were filled with filtered (0.45 µm) water from the Oosterschelde Estuary. Initial and final PO_4, NO_3, NO_2, and NH_4 concentrations were determined using standard automated colorimetric methods (Table 1). Temperature effects were assessed using 2 treatments, high (25°C) and low (18°C), for each nutrient treatment. Every 4 d, 50% of the water from each tank was removed and replaced to replenish nutrients and replace loss due to evaporation. This caused an increase in salinity.

Four treatments were used to assess the impact of macrofauna on microphytobenthos, and each treatment was replicated 4 times in each of the 4 tidal tanks; thus, there were 16 cores $tank^{-1}$. The treatments were (1) B-Ham cores with *Corophium volutator*; (2) B-Ham control cores (*C. volutator* removed); (3) Zandkreek cores with *Hydrobia ulvae*; and (4) Zandkreek control cores (*H. ulvae* removed).

Macrofauna were removed by hand from control cores and by placing a 63 µm mesh disc onto the sediment surface. The mesh facilitated the removal of grazers by driving them to the margins of the core and then onto the mesh, which allowed capture. Visual observations indicated that the majority of *Corophium volutator* and *Hydrobia ulvae* were removed within 48 h.

To ensure that microphytobenthic species composition and biomass were similar between macrofauna and control cores at the start of the experiment, a thin sediment slurry layer (between 4 and 6 mm and without macrofauna and most meiofauna) from the respective estuary was added to each core. The slurry consisted of algae, small sediment particles, and other organic material; it was obtained by sieving surface sediment through a 150 µm mesh. Thus, sieved B-Ham sediment was added to B-Ham cores and sieved Zandkreek sediment was added to Zandkreek cores. To prevent the immigration or emigration of macrofauna, a 200 µm mesh extending 5 cm above the top was wrapped around each core.

Microphytobenthic biomass was measured as chlorophyll *a* (chl *a*), minimum fluorescence (F_0^{15}; used as a biomass proxy after Honeywill et al. 2002) and cell density. Chl *a* was determined by HPLC (Wiltshire et al. 1998). A 5 mm deep sediment sub-sample was collected from each core using a syringe (1.8 cm diameter). Each sub-sample was frozen in liquid nitrogen and stored at –70°C until analysis. Chl *a* was extracted from ~0.1 g of freeze-dried sediment using 1 ml of dimethylformamide (90% DMF) for 24 h at 4°C. The solvent was then filtered (0.2 µm) and injected into an HPLC equipped with a Nucleosil C18 column and a photodiode array detector.

Minimum fluorescence measurements were made using a non-invasive pulse-amplitude-modulated (PAM) diving fluorometer (Walz). Dark-adapted measurements were made on surface biofilms after 15 min. This length of time is considered optimal for achieving a stable value for F_0^{15} (Barranguet & Kromkamp 2000, Perkins et al. 2001).

The composition and abundance of diatom cells from each treatment were characterised from diatoms collected using the lens tissue technique (Eaton & Moss 1966). Acid-cleaned samples were mounted in Naphrax, and taxa were observed and identified using a Zeiss Universal Light microscope (total magnification, 1250×). Three-hundred valves per slide were counted. Cell densities were expressed as the number of valves per unit area (cm^{-2}).

One-way ANOVA was used to determine whether measured parameters were significantly different

Table 1. Initial and final nutrient concentrations (µmol l^{-1} N or P) and molar N:P for each of the species assemblages. Low-nutrient water was collected from the Oosterschelde Estuary, whereas high-nutrient water was collected from the Westerschelde Estuary

	Oosterschelde (Zandkreek) Low nutrient				Westerschelde (Biezelingsche Ham) High nutrient			
	18°C (low)		25°C (high)		18°C (low)		25°C (high)	
	Start	End	Start	End	Start	End	Start	End
NH_4	6.2	0.2	15.3	6.8	15.2	2.0	22.5	7.4
NO_2	2.3	0.3	4.4	1.9	7.8	3.0	14.9	11.3
NO_3	57	8.0	70	9.4	204	40	213	108
PO_4	2.3	0.4	2.8	0.9	3.4	0.2	3.6	1.0
Molar N:P	28.5	21.3	32.0	20.1	66.8	225	69.6	126

among control and macrofaunal cores (Zar 1999). Data were log-transformed prior to analysis if this improved the homogeneity of variances. Student-Newman-Keuls (SNK) multiple range tests were used to test for significant ($p < 0.05$) differences between cell densities of grazed and control treatments. Canonical correspondence analysis (CCA) was used to assess the relationships between the relative abundances of diatom taxa and 12 environmental variables for each assemblage (i.e. B-Ham and Zandkreek). Correlations between relative abundances and environmental variables and the new canonical variable were used as the basis of interpretation. Environmental variables considered in the analysis were: macrofaunal presence or absence; chl *a*; F_0^{15}; temperature; salinity; sediment carbohydrate concentration (data not shown); final PO_4, NO_3,

Table 2. Correlations of the relative abundances of species and environmental data with canonical variables 1 (CA1) and 2 (CA2) for each diatom assemblage (Biezelingsche Ham and Zandkreek). Only species with a correlation coefficient that exceeded ±0.300 are shown

Biezelingsche Ham	CA1	CA2	Zandkreek	CA1	CA2
% variance explained	25.6	9.4	% variance explained	12.9	9.4
Cumulative % explained	25.6	35.0	Cumulative % explained	12.9	22.3
F_0^{15}	−0.824	−0.324	Salinity	−0.443	−0.230
Chl *a*	−0.440	−0.203	PO_4	−0.375	−0.228
Temperature	−0.120	−0.492	Temperature	−0.361	−0.148
PO_4	−0.119	−0.483	F_0^{15}	−0.352	0.385
Salinity	−0.118	−0.442	NH_3	−0.253	−0.094
NH_4	−0.114	−0.517	NO_2	0.208	−0.164
NO_2	−0.064	−0.496	NO_3	0.316	−0.139
NO_3	−0.044	−0.445	Chl *a*	0.446	0.004
Molar N:P	0.048	−0.044	Carbohydrates	0.472	0.037
Carbohydrates	0.059	−0.313	*Hydrobia ulvae*	0.495	−0.576
Corophium volutator	0.968	−0.302	Molar N:P	0.583	0.219
Navicula phyllepta	−0.746	−0.242	*Nitzschia frustulum*	−0.541	−0.170
Stauroneis sp. 1	−0.662	−0.598	*Stauroneis* sp. 1	−0.517	0.461
Navicula rostellata	−0.646	−0.125	*Navicula* sp. 5	−0.379	0.171
Nitzschia frustulum	−0.603	0.809	*Amphora* sp. 2	−0.348	0.378
Navicula digitoradiata	−0.522	−0.205	*Navicula* sp. 6	−0.328	0.130
Pleurosigma aestuarii	−0.448	−0.137	*Navicula* sp. 11	−0.321	0.128
Achnanthes sp. 2	−0.350	0.206	*Thalassiosira decipiens*	−0.318	0.203
Navicula sp. 11	−0.326	0.292	*Catenela adhaerans*	−0.315	0.064
Synedra ulna	−0.198	0.432	*Navicula cryptocephala*	−0.314	0.126
Navicula gregaria	0.303	−0.170	*Navicula flanatica*	−0.282	0.673
Plagiogramma vanheurckii	0.341	−0.142	*Pleurosigma aestuarii*	−0.025	0.562
Achnanthes sp. 1	0.343	−0.05	*Plagiotropis neovitrea*	0.205	0.528
Entomoneis paludosa	0.347	0.050	*Dimeregramma minor*	0.206	−0.207
Amphora sp. 1	0.363	−0.026	*Cocconeis scutellum*	0.215	−0.108
Cocconeis scutellum	0.381	−0.111	*Navicula vulpina*	0.218	0.541
Plagiotropis neovitrea	0.390	−0.165	*Gyrosigma macrum*	0.244	−0.135
Cyclotella atomus	0.399	−0.094	*Cyclotella meneghiniana*	0.259	−0.266
Actinoptychus senarius	0.426	−0.163	*Achnanthes exigua* var. *heterovalvata*	0.260	−0.072
Cylindrotheca closterium	0.428	−0.177	*Opephora guenter-grassii*	0.263	−0.190
Opephora guenter-grassii	0.435	0.065	*Eunotogramma dubium*	0.272	0.077
Pseudostaurosira perminuta	0.440	−0.152	*Amphora* sp. 1	0.273	−0.301
Navicula sp. 8	0.460	−0.222	*Tryblionella* sp. 1	0.277	−0.277
Cymatosira belgica	0.532	−0.117	*Navicula pygmaea*	0.288	−0.238
Rhaphoneis amphiceros	0.559	−0.166	*Cyclotella atomus*	0.299	−0.247
Cyclotella meneghiniana	0.609	−0.218	*Achnanthes* sp. 2	0.321	−0.054
Cocconeis peltoides	0.655	−0.238	*Opephora pacifica*	0.336	−0.231
Nitzschia recta	0.666	−0.214	*Cocconeis peltoides*	0.395	−0.131
Thalassiosira eccentrica	0.740	−0.256	*Amphora coffeaeformis* var. *acutiuscula*	0.460	−0.227
Achnanthes hauckiana	0.761	−0.161	*Plagiogramma staurophorum*	0.495	−0.304
Delphineis surirella	0.763	−0.194	*Nitzschia dissipata*	0.524	−0.075
Paralia sulcata	0.773	−0.241	*Achnanthes hauckiana*	0.556	−0.145
Nitzschia constricta	0.795	−0.232	*Nitzschia constricta*	0.596	−0.702
Amphora coffeaeformis var. *acutiuscula*	0.817	−0.168			

NO_2, NH_4; and molar N:P ratios. PC-ORD version 3.01 was used for CCA, species richness (S), species evenness (E), and diversity (Shannon Index, H') calculations. The SIMI similarity index (see Medlin 1983) was used to compare assemblages between treatments. SIMI produces an index between 0 (2 assemblages with no taxa in common) and 1 (2 assemblages identical in distribution and abundance), and it gives more weight to the abundant taxa.

RESULTS

Nutrients

Initial and final nutrient concentrations for each tank are shown in Table 1. The high nutrient treatment had NO_3 and molar N:P ratios approximately 4 and 5 times higher than the low nutrient treatment. Concentrations of nutrients declined throughout the course of the experiment.

Biezelingsche Ham assemblage

A total of 93 diatom species were identified in the B-Ham assemblages. The 2 canonical axes accounted for 25.6 and 9.4% of the total variance, respectively (Table 2). The first canonical axis contrasts assemblages strongly influenced by *Corophium volutator* (indicated by a high positive correlation; r = 0.968) (Fig. 1, Table 2). In addition, F_0^{15} and chl *a* were negatively correlated with the first axis, indicating that these variables tended to be higher in the absence of *C. volutator*. The second canonical axis contrasts the environmental treatments (Fig. 1, Table 2). With respect to the diatom taxa, *Navicula phyllepta*, *Stauroneis* sp. 1, *Navicula rostellata*, *Nitzschia frustulum*, and *Navicula digitoradiata* were negatively correlated with the first canonical axis, indicating that these taxa were not associated with *C. volutator*. In contrast, *Amphora coffeaeformis* var. *acutiuscula*, *Nitzschia constricta*, *Paralia sulcata*, *Achnanthes hauckiana*, *Delphineis surirella*, and *Thalassiosira eccentrica* had strong positive correlations with the first canonical axis, and thus they were associated with *C. volutator*. Only 2 taxa were correlated with the second canonical variable: *Stauroneis* sp. 1 was negatively associated, and *N. frustulum* was positively associated, indicating a preference for high nutrient-high temperature and low nutrient-low temperature conditions, respectively.

Chl *a* and total cell densities did not differ significantly between *Corophium volutator* and control assemblages, except for the high nutrient-high temperature treatment, where chl *a* was 3 times greater in the control than *C. volutator* assemblage (Table 3). F_0^{15} was significantly greater in control than *C. volutator* assemblages for each nutrient-temperature treatment (Table 3).

Corophium volutator effects on diatom assemblage

There was very little similarity in assemblage structure between control and *Corophium volutator* assemblages (Fig. 2, Table 4). Species richness was greater for the *C. volutator* treatments than controls, except under low nutrient-high temperature conditions. Similar higher values were observed for evenness and diversity. The percentages of *Navicula* species were lower, whereas the percentages of epipsammic species were greater for the *C. volutator* treatments than the controls (Table 4). F_0^{15} of control assemblages increased under all environmental treatments, with this difference corresponding to higher proportions of motile *Navicula* taxa and lower proportions of epipsammic species (Tables 3 & 4). This suggests that *C. volutator* negatively affected epipelic diatom biomass and assemblage composition. The following patterns in relative abundances and cell densities were observed for each treatment combination (Table 5).

Low nutrient-low temperature—The control assemblages were dominated by *Nitzschia frustulum*, while the *Corophium volutator* assemblages lacked a dominant species. Cell densities of *Achnanthes hauckiana*, *Delphineis surirella*, *Navicula gregaria* and *Nitzschia constricta* were significantly greater in the grazed assemblage.

High nutrient-low temperature—The control assemblage were comprised primarily of *Nitzschia frustulum*

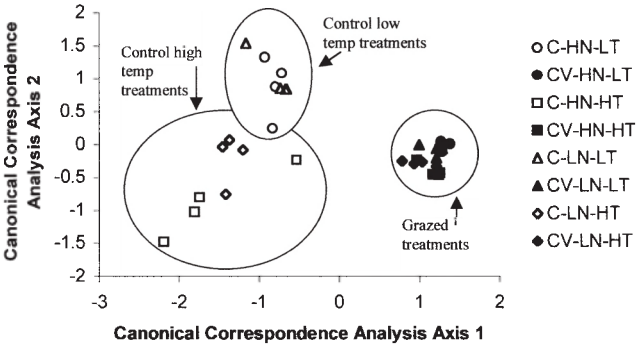

Fig. 1. Canonical correlation analysis (CCA) plot of Biezelingsche Ham diatom assemblages in the presence or absence of *Corophium volutator* and under different environmental conditions. Canonical variables are derived for the relative abundance of diatom taxa. C: control (no macrofauna); CV: with *C. volutator*; HN: high nutrient; LN: low nutrient; LT: 18°C; HT: 25°C

Table 3. Mean ± SE chl *a*, cell density, and minimum fluorescence (F_0^{15}) for control and macrofauna treatments (*Corophium volutator* or *Hydrobia ulvae*) for each environmental treatment. One-way ANOVA was used to compare between control and animal treatments within environmental treatment. SNK tests were used to identify significant differences ($p < 0.05$) between control and *C. volutator*, or control and *H. ulvae* treatments. Significant differences are indicated in **bold**. n = 4

	$F_{3,12,0.05}$ p-value	Low nutrient-low temperature				$F_{3,12,0.05}$ p-value	High nutrient-low temperature			
		Biezelingsche Ham		Zandkreek			Biezelingsche Ham		Zandkreek	
		Control	*C. volutator*	Control	*H. ulvae*		Control	*C. volutator*	Control	*H. ulvae*
Chl *a* (mg m^{-2})	2.96 0.075	16.1 ± 3.2	13.0 ± 1.8	9.7 ± 2.9	19.9 ± 1.9	1.77 0.207	36.2 ± 6.6	24.3 ± 5.6	25.0 ± 3.4	36.8 ± 4.4
Cell density (×10^3 cm^{-2})	3.14 0.065	76.7 ± 18.5	87.0 ± 11.3	52.0 ± 18.6	98.9 ± 23.3	2.33 0.126	77.4 ± 28.3	135.6 ± 11.7	27.9 ± 10.6	62.2 ± 22.3
F_0^{15}	18.05 <0.001	**315 ± 41**	**62 ± 4**	182 ± 25	161 ± 9	8.63 0.003	**371 ± 70**	**63 ± 1**	252 ± 26	216 ± 44
	$F_{3,12,0.05}$ p-value	Low nutrient-high temperature				$F_{3,12,0.05}$ p-value	High nutrient-high temperature			
		Biezelingsche Ham		Zandkreek			Biezelingsche Ham		Zandkreek	
		Control	*C. volutator*	Control	*H. ulvae*		Control	*C. volutator*	Control	*H. ulvae*
Chl *a* (mg m^{-2})	2.92 0.078	19.3 ± 5.5	12.2 ± 2.5	6.0 ± 2.1	16.0 ± 2.0	3.75 0.041	**42.4 ± 4.9**	**13.2 ± 2.9**	19.6 ± 9.6	26.7 ± 6.7
Cell density (×10^3 cm^{-2})	1.83 0.195	82.7 ± 18.0	119.0 ± 17.5	63.1 ± 13.4	52.3 ± 8.7	2.22 0.138	129.3 ± 39.8	180.2 ± 36.4	124.0 ± 40.8	132.4 ± 15.1
F_0^{15}	18.08 <0.001	**588 ± 65**	**131 ± 20**	288 ± 56	377 ± 16	29.98 <0.001	**1038 ± 112**	**108 ± 5**	**617 ± 98**	**275 ± 32**

and *Navicula phyllepta*, although cell densities of these 2 taxa were not significantly greater than the grazed assemblages. *Achnanthes hauckiana*, *Nitzschia constricta*, and *Thalassiosira eccentrica* were significantly higher in the grazed assemblages.

Low nutrient-high temperature—Cell densities and relative abundances of *Stauroneis* sp. 1, *Nitzschia frustulum*, and *Navicula phyllepta* were significantly greater for the control assemblages. *Nitzschia constricta*, *Navicula gregaria* and *Amphora coffeaeformis* var. *acutiuscula* dominated the *Corophium volutator* assemblages in terms of relative abundances. However, only *N. constricta* and *A. coffeaeformis* var. *acutiscula* had significantly higher cell densities.

High nutrient-high temperature—Cell densities and relative abundances of *Stauroneis* sp. 1 and *Navicula phyllepta* were significantly higher for the control assemblages. In contrast, relative abundances of *Nitzschia constricta*, *Achnanthes hauckiana*, *Amphora coffeaeformis* var. *acutiuscula*, and *Navicula gregaria* were greater for the grazed assemblages, although only cell densities of *N. constricta* and *A. coffeaeformis* var. *acutiuscula* were significantly higher.

Differences among environmental treatments

Diatom species composition of control assemblages was strongly influenced by temperature, but not by nutrients (Fig. 1). Higher cell densities of *Stauroneis* sp. 1 and *Navicula phyllepta*, and lower densities of *Nitzschia frustulum* represented the major difference between the 25 and 18°C tanks of the control assemblages (Table 5). Salinity co-varied with temperature; thus, differences among assemblages may also be a result of salinity differences. The pooled species richness for control assemblages was greater for low-nutrient conditions, regardless of temperature, and greater for low-temperature conditions, regardless of nutrient treatment. Species evenness and diversity of control assemblages were not affected by the environmental treatments (Table 4). Taxa associated with final nitrate concentrations >40 µmol l^{-1} (18°C) were *Entomoneis paludosa*, *Navicula gregaria*, and *Nitzschia dissipata*, and taxa associated with nitrate

concentrations >100 µmol l^{-1} (25°C) were *E. paludosa*, *N. gregaria*, *Navicula flanatica*, *N. phyllepta*, *Navicula rostellata*, *Pleurosigma aestuarii*, and *Stauroneis* sp. 1.

Among the nutrient and temperature treatments, *Corophium volutator* assemblages had a high degree of similarity, species richness, evenness and diversity (Table 4, Figs. 1 & 2). Cell densities of *Amphora coffeaeformis* var. *acutiscula* and *Nitzschia constricta* were greater for the high-temperature treatment, while cell densities of *Achnanthes hauckiana* and *N. constricta* were greater when nutrients were high (Table 5).

Table 4. Species richness, evenness, and diversity values for control and macrofauna treatments (*Corophium volutator* or *Hydrobia ulvae*) for each environmental treatment. Values are pooled among the 4 replicates per treatment. The relative abundances (%) of naviculoid and epipsammic taxa are also given

	Low nutrient-low temperature				High nutrient-low temperature			
	Biezelingsche Ham		Zandkreek		Biezelingsche Ham		Zandkreek	
	Control	*C. volutator*	Control	*H. ulvae*	Control	*C. volutator*	Control	*H. ulvae*
Richness (*S*)	54	57	53	52	47	51	56	52
Evenness (*E*)	0.61	0.79	0.58	0.70	0.61	0.76	0.76	0.74
Diversity (*H'*)	2.45	3.14	2.29	2.75	2.4	3.0	3.04	2.94
Navicula (%)	25.4	20.2	23.1	29.4	29.7	12.4	41.1	27.1
Epipsammic (%)	16.6	28.2	14.0	24.1	9.7	36.1	15.5	32.2
	Low nutrient-high temperature				High nutrient-high temperature			
	Biezelingsche Ham		Zandkreek		Biezelingsche Ham		Zandkreek	
	Control	*C. volutator*	Control	*H. ulvae*	Control	*C. volutator*	Control	*H. ulvae*
Richness (*S*)	48	43	46	54	38	55	47	49
Evenness (*E*)	0.61	0.76	0.64	0.60	0.57	0.72	0.68	0.58
Diversity (*H'*)	2.34	2.85	2.44	2.40	2.07	2.88	2.63	2.24
Navicula (%)	36.5	23.2	40.2	26.8	44.5	29.4	33.4	33.4
Epipsammic (%)	9.9	32.5	9.4	12.6	4.2	34.4	12.4	12.4

Table 5. Mean ± SE cell densities (×10^3 cm^{-2}) and relative abundances (%) for selected diatom species for control and *Corophium volutator* assemblages, under each environmental treatment. np: not present

	Low nutrient-low temperature		Low nutrient-high temperature		High nutrient-low temperature		High nutrient-high temperature	
	Control	*C. volutator*	Control	*C. volutator*	Control	*C. volutator*	Control	*C. volutator*
Achnanthes hauckiana	3.4 ± 0.8 5%	10.3 ± 0.8 12%	2.4 ± 0.6 3%	7.4 ± 1.6 6%	2.1 ± 0.7 3%	22.2 ± 2.4 17%	1.0 ± 0.3 1%	14.9 ±1.4 9%
Amphora coffeaeformis var. *acutiscula*	1.0 ± 0.6 1%	5.2 ± 0.3 6%	0.06 ± 0.06 <1%	11.2 ± 2.5 9%	0.6 ± 0.4 <1%	7.3 ± 0.5 6%	0.05 ± 0.05 <1%	17.5 ± 6.1 10%
Delpheneis surirella	0.3 ± 0.2 <1%	5.1 ± 1.6 6%	0.2 ± 0.2 <1%	4.1 ± 0.8 4%	0.7 ± 0.6 1%	8.9 ± 2.2 6%	0.2 ± 0.2 <1%	4.7 ± 0.7 3%
Navicula gregaria	2.7 ± 1.1 4%	7.4 ± 1.1 9%	4.6 ± 2.0 5%	13.8 ± 3.5 13%	3.5 ± 1.6 6%	7.7 ± 2.4 6%	9.9 ± 3.9 11%	16.2 ± 2.0 10%
Navicula phyllepta	6.2 ± 2.3 9%	2.2 ± 0.6 3%	18.6 ± 4.9 21%	3.2 ± 0.7 3%	6.4 ± 3.0 11%	1.8 ± 0.5 1%	34.8 ± 14.4 23%	3.0 ± 0.9 2%
Nitzschia constricta	0.3 ± 0.2 <1%	11.1 ± 1.5 13%	0.6 ± 0.2 <1%	28.0 ± 7.6 23%	1.0 ± 0.7 1%	15.2 ± 1.8 11%	1.2 ± 0.2 1%	51.9 ±18.1 26%
Nitzschia frustulum	39.5 ± 18.1 45%	0.6 ± 0.2 <1%	17.2 ± 6.5 23%	2.8 ± 0.6 2%	41.8 ± 23.6 45%	1.3 ± 0.5 <1%	11.5 ± 5.5 8%	1.9 ±0.7 <1%
Stauroneis sp. 1	0.2 ± 0.01 1%	np	20.0 ± 6.5 24%	np	0.3 ± 0.1 <1%	np	49.7 ± 16.6 37%	0.2 ± 0.2 <1%
Thalassiosira eccentrica	0.3 ± 0.1 <1%	7.4 ± 1.5 9%	np	4.1 ± 2.6 3%	0.2 ± 0.1 <1%	13.3 ± 1.0 10%	np	5.3 ± 2.7 3%

Zandkreek assemblage

A total of 85 benthic diatom species were identified in the Zandkreek assemblages. SIMI index values ranged between 0.63 and 0.96, indicating a high degree of similarity between diatom assemblages for control and *Hydrobia ulvae* treatments (Fig. 2). This similarity was mirrored in the CCA, in which the first 2 canonical axes accounted for 12.9 and 9.4 % of the total variance, respectively (Table 2). The first canonical axis was negatively correlated with salinity and positively correlated with molar N:P, suggesting a nutrient and temperature effect. *H. ulvae* was negatively and F_0^{15} was positively correlated with the second canonical axis. *Nitzschia frustulum* and *Stauroneis* sp. 1 were negatively correlated with the first canonical axis, while *Nitzschia constricta*, *Achnanthes hauckiana*, and *Nitzschia dissipata* were positively correlated with the first canonical axis, suggesting preferential differences in salinity tolerances and nutrient requirements. *N. constricta* was negatively correlated, whereas *Navicula flanatica*, *Pleurosigma aestuarii*, and *Plagiotropis neovitrea* were positively correlated with the second canonical axis, indicating a weak grazing effect.

Benthic algal biomass measured as chl *a*, F_0^{15}, and cell densities did not differ significantly between *Hydrobia ulvae* and control treatments, except for the high nutrient-high temperature treatment, where F_0^{15} was approximately 2.3 times greater in the control than *H. ulvae* treatment (Table 3). Compared to B-Ham control assemblages, the surface biofilm (F_0^{15}) in Zandkreek control assemblages was not as substantial (Table 3), with the exception again being the high nutrient-high temperature tank, where high densities of *Navicula phyllepta* and *Stauroneis* sp. 1 maintained a surface biofilm.

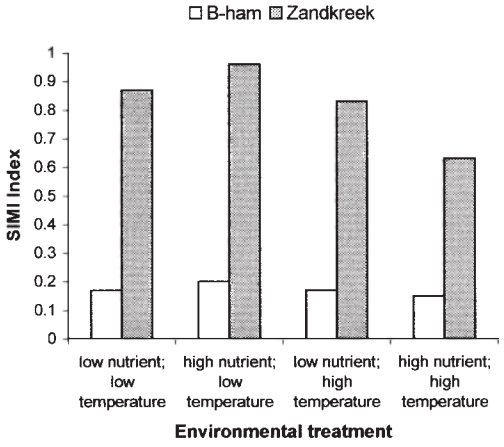

Fig. 2. SIMI similarity indices comparing control and grazed assemblages under the 4 environmental treatments. An index of 0 means the samples have no taxa in common, and an index of 1 means the samples have the same taxa and relative abundance

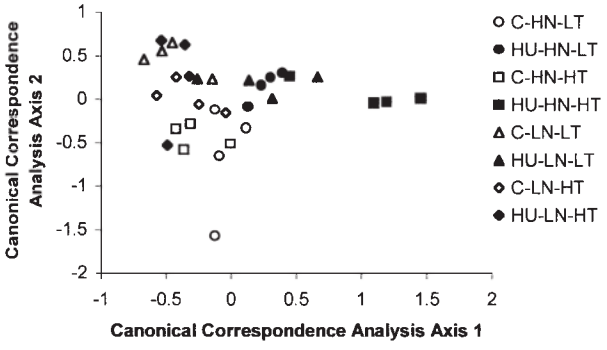

Fig. 3. CCA plot of Zandkreek diatom assemblages in the presence or absence of *Hydrobia ulvae* and under different environmental conditions. Canonical variables are derived for the relative abundance of diatom taxa. HU: with *H. ulvae*; other abbreviations as in Fig. 1

Hydrobia ulvae effects on diatom assemblage

There was a high degree of similarity between diatom assemblages grown in the presence and absence of *Hydrobia ulvae*, in both the type and proportion of diatom species present, regardless of environmental treatment (Figs. 2 & 3). Within each environmental treatment, the presence of *H. ulvae* did not have a significant effect on species richness, diversity, evenness, the percentage of *Navicula* species, or percentage of epipsammic species present (Table 4). The following patterns in the relative abundances and cell densities were observed for each treatment combination (Table 6):

Low nutrient-low temperature—Nitzschia frustulum cell densities were similar between treatments, but the relative abundance of *N. frustulum* in the control assemblages was double that in the *H. ulvae* assemblages. *Achnanthes hauckiana*, *Navicula gregaria*, *Nitzschia dissipata*, *Navicula phyllepta* and *Nitzschia constricta* were dominant species in the *H. ulvae* assemblages, but only cell densities of only *A. hauckiana*, *N. gregaria*, and *N. dissipata* were significantly greater.

High nutrient-low temperature—Achnanthes hauckiana, *Navicula gregaria*, *Navicula phyllepta*, *Nitzschia constricta*, and *Nitzschia frustulum* were the dominant species in both assemblages, having relative abundances greater than 10 %. Cell densities of these taxa did not differ significantly between treatments, with the exception of *A. hauckiana*. Cell densities of *Cocconeis peltoides* and *Opephora guenter-grassii* were significantly greater, and cell densities of *Rhaphoneis amphiceros* and *Stauroneis* sp. 1 were significantly less for the *Hydrobia*

ulvae treatment, although in general, these taxa comprised less than 2% of the total relative abundance.

Low nutrient-high temperature—Nitzschia frustulum was the dominant species of the control and *Hydrobia ulvae* assemblages. *Navicula gregaria*, *Navicula phyllepta*, and *Stauroneis* sp. 1 also made up a significant proportion of the relative abundances (>10%) of both assemblages, and they had similar cell densities. The proportion of *Stauroneis* sp. 1 was greater in the presence of *H. ulvae*.

High nutrient-high temperature—Nitzschia constricta dominated the *Hydrobia ulvae* assemblage, where cell densities were 20 times greater than controls. Cell densities of *Stauroneis* sp. 1 were 2 orders of magnitude greater for the control than *H. ulvae* assemblage. *Achnanthes hauckiana*, *Navicula gregaria*, *Navicula phyllepta*, and *Nitzschia frustulum* had high relative abundances (>10%) in both assemblages, but the cell densities of these taxa did not differ significantly between the control and *H. ulvae* assemblages.

Differences among environmental treatments

Zandkreek diatom assemblages were weakly influenced by nutrients (Fig. 3). In general, high *Nitzschia frustulum* densities were associated with low-nutrient conditions. Species richness of control assemblages was greater at the lower temperature than at the higher one, regardless of nutrient treatment (Table 4). However, the species evenness and diversity of control assemblages did not follow a temperature or nutrient pattern (Table 4). Species evenness and diversity of *Hydrobia ulvae* assemblages was lowest for the high-temperature treatments, and species richness was similar between nutrient treatments (Table 4).

DISCUSSION

Three interacting factors regulate the structure of intertidal microphytobenthic communities (i.e. the species present and their abundance). These are bottom-up, top-down, and disturbance events. Here we examined the interactions between bottom-up and top-down factors and their effects on the structure of intertidal diatoms assemblages. The results imply that top-down effects (i.e. direct consumption of microalgae or bioturbation) are predator (grazer) specific and differ in the degree to which they change the biotic and abiotic characteristics of the ecosystem. Additionally, bottom-up effects vary depending on the strength of top-down factors.

It has been suggested that most of the grazing pressure on diatom is directed towards the larger epipelon, while the small-sized epipsammon are less affected

Table 6. Mean ± SE cell densities ($\times 10^3$ cm^{-2}) and relative abundances (%) for selected diatom species for control and *Hydrobia ulvae* assemblages, under each environmental treatment. np: not present

	Low nutrient-low temperature		Low nutrient-high temperature		High nutrient-low temperature		High nutrient-high temperature	
	Control	*H. ulvae*	Control	*H. ulvae*	Control	*H. ulvae*	Control	*H. ulvae*
Achnanthes hauckiana	1.3 ± 0.3 3%	9.4 ± 2.0 10%	1.1 ± 0.8 4%	1.7 ± 0.5 2%	1.6 ± 0.9 6%	7.4 ± 2.2 14%	12.5 ± 1093 6%	9.5 ± 4.6 7%
Cocconeis peltoides	0.4 ± 0.3 <1%	0.6 ± 0.2 <1%	0.3 ± 0.1 <1%	0.3 ± 0.2 <1%	0.5 ± 0.3 2%	1.6 ± 0.6 3%	0.04 ± 0.04 <1%	0.4 ± 0.1 <1%
Navicula gregaria	1.9 ± 0.4 5%	13.0 ± 4.0 13%	8.0 ± 1.7 14%	4.5 ± 1.9 9%	3.2 ± 1.0 12%	3.8 ± 1.6 6%	12.0 ± 4.6 15%	21.9 ± 2.3 18%
Navicula phyllepta	4.0 ± 1.1 9%	11.2 ± 3.8 10%	9.9 ± 3.7 14%	5.5 ± 1.7 11%	3.8 ± 1.5 14%	8.8 ± 3.7 14%	31.5 ± 15.6 21%	16.0 ± 4.6 12%
Nitzschia constricta	0.7 ± 0.4 1%	7.4 ± 3.8 7%	1.7 ± 1.0 3%	0.9 ± 0.3 2%	1.0 ± 0.3 4%	3.1 ± 1.8 4%	2.3 ± 0.9 2%	40.3 ± 5.4 31%
Nitzschia dissipata	0.09 ± 0.09 <1%	2.3 ± 1.1 4%	0.03 ± 0.03 <1%	0.3 ± 0.1 <1%	0.1 ± 0.1 <1%	4.9 ± 1.6 6%	1.0 ± 0.9 <1%	0.6 ± 0.3 <1%
Nitzchia frustulum	28.9 ± 12.2 50%	26.7 ± 11.1 26%	20.6 ± 7.1 34%	22.7 ± 10.3 41%	5.2 ± 3.4 16%	10.5 ± 4.0 17%	16.9 ± 7.0 14%	23.0 ± 8.8 17%
Opephora guenter-grassii	1.6 ± 1.2 2%	2.5 ± 1.6 4%	1.0 ± 0.4 2%	1.3 ± 0.7 3%	0.03 ± 0.03 <1%	4.6 ± 3.2 6%	0.9 ± 0.6 <1%	1.2 ± 1.0 <1%
Rhaphoneis amphiceros	0.05 ± 0.05 <1%	0.8 ± 0.5 <1%	0.04 ± 0.04 <1%	0.06 ± 0.06 <1%	0.3 ± 0.1 1%	0.1 ± 0.1 <1%	0.3 ± 0.2 <1%	0.4 ± 0.2 <1%
Stauroneis sp. 1	0.1 ± 0.04 <1%	0.1 ± 0.1 <1%	2.5 ± 0.7 4%	4.8 ± 3.5 10%	0.4 ± 0.2 2%	np	17.0 ± 8.1 12%	0.2 ± 0.1 <1%

(Reise 1992). Grazing pressure should, therefore, increase the percentage composition of epipsammic species. Our results support this hypothesis, with the epipsammic fraction either increasing or occasionally remaining the same in the presence of grazers.

In the absence of grazing, competition for nutrients between species generally reduces diversity (Begon et al. 1990). For example, McClatchie et al. (1982) found that grazer exclusion decreased the number of species in a mudflat diatom assemblage. Grazer removal from B-Ham sediments decreased diversity and species richness under all environmental conditions, except for the increased species richness of the control assemblage under low nutrient-high temperature conditions. In contrast, species richness and diversity illustrated a variety of responses upon grazer removal from Zandkreek sediments.

Proulx & Mazumder (1998) suggested that grazer effects are confounded by the trophic state, and they found that under oligotrophic conditions grazers reduced plant species richness, but under eutrophic conditions grazers increased, decreased, or did not affect species richness, depending on the study. For high nutrient treatments, species richness and diversity of B-Ham assemblages grazed by *Corophium volutator* were greater than the corresponding control assemblage. *C. volutator* grazing increased diversity under low-nutrient conditions, while species richness increased at low temperature and decreased at high temperature. Zandkreek assemblages grazed by *Hydrobia ulvae* did not follow a nutrient-related pattern.

Corophium volutator effects

Field and laboratory studies have shown that benthic diatoms are an important component of *Corophium volutator*'s diet, and *C. volutator* feeding can significantly reduce biomass (Gerdol & Hughes 1994b) and influence diatom species composition (Smith et al. 1996). For example, Gerdol & Hughes (1994b) recorded significant reductions in chl *a* and cell numbers at *C. volutator* densities as low as 9000 ind. m^{-2}. In this study, amphipod density was equivalent to approximately 32 000 ind. m^{-2}. Significant differences in chl *a* and total cell densities between control and *C. volutator* assemblages were not found, with the exception of chl *a* concentrations for the high nutrient-high temperature treatment. However, F_0^{15} values were significantly greater for control assemblages, indicating a higher surface biomass in the absence of *C. volutator* grazing. The similarity in overall chl *a* concentrations between control and *C. volutator* assemblages may have occurred due to variation in the depth distribution of chl *a*. The bioturbatory activity of *C. volutator* may prevent a stable biofilm forming at the surface by regularly redistributing chl *a*. This will influence any measure of surface biomass, such as F_0^{15}, but be much less apparent in measurements of total chl *a* unless the depth of sampling is at an extremely high resolution (Wiltshire et al. 1997, Wiltshire 2000, Kelly et al. 2001). To date, there are no studies comparing distributions of chl *a* between sediments with low and high densities of infauna.

Assemblages grazed by *Corophium volutator* had higher species evenness compared with control assemblages under the same environmental conditions, indicating that the dominant species were preferentially selected (Lubchenco 1978). As a generalisation, selective predation may be expected to induce higher community diversity if the preferred prey is competitively dominant (Begon et al. 1990). We infer that *Nitzschia frustulum*, *Stauroneis* sp. 1, and *Navicula phyllepta* were the chosen prey of *C. volutator*, since all were competitively dominant species in control assemblages, but represented only minor components of the diatom assemblages in which *C. volutator* was present. Among the environmental treatments, the structures of diatom assemblages exposed to the effects of *C. volutator* were remarkably similar. In all 4 *C. volutator* assemblages, *Achnanthes hauckiana* and *Nitzschia constricta* were common, which may indicate that these 2 taxa are less susceptible to grazing. Algae such as diatoms may resist herbivory by having a large size (Lubchenco & Gaines 1981) or conversely by being small and prostrate on the sediment surface and avoiding predation due to the morphological constraints of grazer mouthparts (Steinman et al. 1987). These results show that, at sufficiently high densities, *C. volutator* can regulate the assemblage composition of intertidal benthic diatoms and supersede the potential effects of the environmental conditions established in this experiment.

Hydrobia ulvae effects

Hydrobia ulvae has been shown to consume sediment microalgae (Morrisey 1988a,b, Blanchard et al. 2000, Herman et al. 2000). However, the effects of *H. ulvae* on the sediment-dwelling algae are unclear and complicated by grazing intensity and bioturbation (Levinton & Bianchi 1981). In our study, densities of *H. ulvae* were high (equivalent to 75 000 ind. m^{-2}) but did not appear to impart a strong regulatory function on the structure of Zandkreek diatom assemblages. We suspect that this is due to negative density-dependent effects, whereby the growth rate (and therefore grazing rate) of *H. ulvae* is reduced as snail density

increases (Morrisey 1987). Blanchard et al. (2000) reported that above a density of 25 000 snails m^{-2} ingestion rates for individual snails declined from 26.6 ± 1.1 to 22.4 ± 1.0 ng chl *a* $snail^{-1}$ h^{-1}. A greater proportion of biomass was consumed at high temperatures, which agrees with the results of Hylleberg (1975), who found *H. ulvae* had maximal ingestion at the combination of high salinity (30) and high temperature (30°C). Morrisey (1988a) suggested that a substantial fraction of microalgae grazed by *H. ulvae* was not assimilated, and in this experiment *H. ulvae* did not significantly reduce the abundance or cell density of any diatom taxa. We suspect *H. ulvae* preferred grazing subdominant species, since diversity was generally lower for grazed assemblages compared to non-grazed assemblages under the same conditions (see Swamikannu & Hoagland 1989).

Hydrobia ulvae assemblages were weakly affected by the nutrient conditions (Fig. 3), and particularly under high nutrient conditions, the density of several taxa, including *Achnanthes hauckiana*, *Amphora coffeaeformis var. acutiscula*, *Navicula gregaria* and *Nitzschia constricta*, increased relative to control assemblages. Gastropod excreta may also have had a role to play by enriching and fertilising the diatom populations and the sediments (López-Figueroa & Niell 1987).

Environmental effects

The composition of diatom assemblages in the absence of grazers varied in response to the environmental conditions. Species composition of control B-Ham assemblages were more strongly influenced by temperature (Fig. 1), while control Zandkreek assemblages were more strongly influenced by nutrients (Fig. 3). This indicates that adaptations of diatom taxa to the different interspecific competitive environments are potentially important when grazing pressure is minimal. High nutrient concentrations within the B-Ham sediment may have buffered the diatoms against the treatments of reduced nutrient concentrations.

Benthic algal growth is stimulated by increased temperature (see mini-review by Davison 1991) and nutrients (Posey et al. 1999), and more importantly, nutrients are hypothesized to impart a strong regulatory influence on algal dynamics (competition) and hence species composition. A major tenant of this hypothesis is that species differ in their resource requirements (taxonomic tradeoffs). Underwood & Provot (2000) demonstrated that the form of nitrogen and salinity affected the growth rates of 4 common intertidal diatoms. *Navicula phyllepta* was the only taxon studied by Underwood & Provot (2000) that was also present in our study. The highest densities of *N. phyllepta* observed corresponded to the environmental optima proposed by Underwood & Provot (2000) and therefore support their conclusion (*N. phyllepta* optimal growth rates are between 25 and 150 µM NH_4, 25 and 250 µM NO_3, and salinity 10 and 20). In our study, few taxa from either the B-Ham or Zandkreek assemblages showed strong responses to either nutrients or temperature (Table 2).

Conclusion

Macrofaunal species that graze on estuarine sediment populations do not simply increase or decrease species diversity of the diatoms, but can potentially do both. The precise effect depends on the relationships between food preferences, diatom competitive abilities, relative resistance to grazing, and the intensity of the grazing pressure. Within this context the dietary spectrum of the individual grazers has an important role to play and was obviously different between the grazers. *Corophium volutator* preferentially consumed certain dominant diatom species, while *Hydrobia ulvae* appeared to be a more general consumer. This is in contrast to results obtained by Morrisey (1988a), who concluded that the similar amphipod *C. arenarium* had a broader dietary range than *H. ulvae*. *C. volutator* exerted a strong regulatory influence on the species composition of benthic diatom biofilms, and it masked the potential regulatory effects of environmental conditions. This contrasted with *H. ulvae*, for which grazing effects were far less pronounced and assemblages were weakly influenced by nutrients.

Both species bioturbate the sediment, and therefore intensity of bioturbation cannot be excluded as a potentially important mechanism regulating biofilm species composition.

The estuarine milieu is by definition a harsh environment, where environmental and chemical gradients can vary steeply on both spatial and temporal scales. The lack of a nutrient and temperature response for the majority of taxa in the absence of grazers indicates that these estuarine diatom species are well adapted for a broad range of nitrogen concentrations, salinity, and temperatures.

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