Proceedings of the 1st Central European Diatom Meeting 2007
Kusber, W.-H. & Jahn, R. (ed.)
Botanic Garden and Botanical Museum Berlin-Dahlem, Freie Universität Berlin
ISBN 978-3-921800-63-8, © BGBM, Berlin 2007.
doi:10.3372/cediatom.135 (available via http://dx.doi.org/)

Gradient responses of epilithic diatom communities along the Swedish coast of the Baltic Sea

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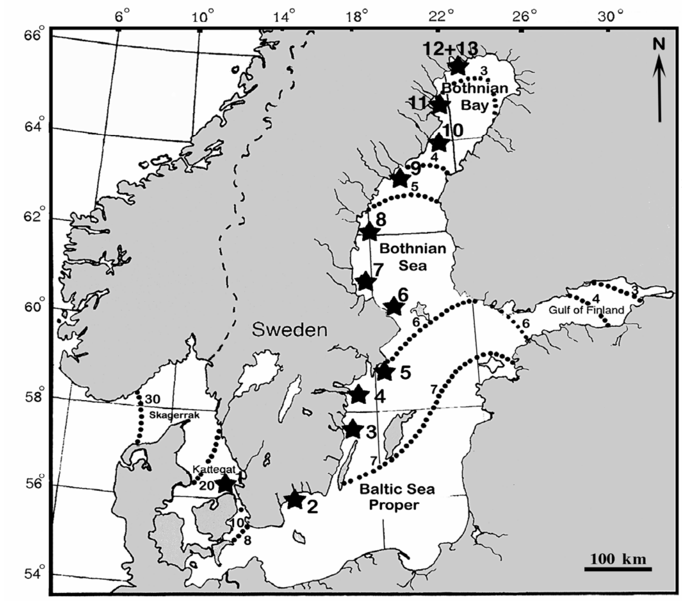

Fig 1. Figure, showing the locations of the thirteen sampling areas in the Baltic Sea area and isohalines for surface salinity.

524 quantitative samples of brackish-water epilithic diatoms were collected from submerged stones at 136 sites in thirteen areas along the Swedish coast line, between 56°00'N and 65°50'N and 12°26'E and 22°42'E (Fig. 1) in the spring and summer of 1990 and 1991.

Environmental factors and biomass were determined (Tables 1 and 2). Our previous studies of epilithic and epiphytic diatom communities (for the Bothian Bay, for the Bothian Sea and for the Baltic Sea proper) showed that there could be a large difference in the results of community analysis with multivariate statistics depending on the distribution of large (with biovolume's cell ≥ 1000 μm^3) and small (with < 1000 μm^3) diatoms. Therefore we count small and large diatoms separately.

The three data sets, S ("Small"), L ("Large") and SL ("Small and Large together"), were analysed with Detrended Canonical Correspondence Analysis (DCCA) with down-weighting of rare species to determine if the diatom taxa showed linear or unimodal responses to the environmental gradients. Environmental factors were fitted passively by multiple regression analysis on the ordination results.

RESULTS

Table 1. Ordinal scales used for exposure to wave action, beach type and soft bottom coverage.

Exposure to wave action	Beach type (the terrestrial part not covered by water)	Soft bottom coverage (between the stones below the waterline)
1 = Stagnant water	1 = > 90 % sand	1 = < 1 %
2 = Very little exposed	2 = > 25 % sand and > 25 % stones	2 = 1–10 %
3 = Little exposed	3 = > 90 % stones < 50 cm in size	3 = 11–25 %
4 = Medium exposed	4 = > 90 % stones > 50 cm in size	4 = 26–75 %
5 = Highly exposed	5 = > 25 % stones and > 25 % solid rock	5 = 76–90 %
	6 = > 90 % solid rock	6 = > 90 %

Environmental variables

DCCA showed that salinity was the overriding environmental factor regulating diatom distributions while exposure to wave action and nutrient concentrations were of secondary importance. All environmental factors could be divided into three groups: (1) that varied mainly with salinity; (2) that varied mainly with exposure to wave action and (3) that varied stochastically with local discharges of DIN (total dissolved nitrogen) and/or DIP (total dissolved inorganic phosphorus). Salinity at the 135 sampling sites ranged between 0.4 and 11.4 and varied significantly between the thirteen sampling areas according to the north-south salinity gradient of the Baltic Sea (Fig. 1). Salinity was strongly negatively correlated with DSi (total dissolved silicate) and richness in all three size classes of diatoms. Salinity was negatively correlated to DSi, but not to DIN and DIP. However the relative ignition loss (ADW %), used in our study as an indirect measure of macro-algal cover, was positively correlated to salinity. Exposure to wave action was not associated with salinity, but both beach type and soft bottom coverage were correlated with exposure to wave action. DIN at the 135 sampling sites ranged between 0.2 and 34.6 μmol L^{-1} and varied significantly between the thirteen sampling areas. DIP at the 135 sampling sites ranged between 0.03 and 16.13 μmol L^{-1} and did not vary significantly between the thirteen sampling areas.

Biomass

The algal dry weight (DW) on the stones varied between 1 and 61 mg cm^{-2} among the 135 sampling sites and ash-free dry weight (ADW) between 0.4 and 8.7 mg cm^{-2}. DW and ADW varied significantly among the sampling areas. DW was weakly negatively correlated to exposure to wave action and ADW was weakly positively correlated to salinity. The indicator for the presence of macro algae, ADW %, varied between 7 and 69 % among the 135 sampling sites. ADW % varied significantly among the sampling areas. ADW % was weakly positively correlated to exposure to wave action and more strongly to salinity. The presence of macro algae thus tended to be higher at sites exposed to wave action and sites with higher salinity.

Diversity and species composition

Mean species richness per sampling site in the three data sets S, SL and L varied between 8 and 44, between 10 and 52 and between 2 and 31, respectively. The highest means of ratio between small and large specimens (S:L) were 38 and 36 (Area s3 and 11) and the lowest S:L was 2 in Area 1.

487 diatom taxa, 245 small and 242 large taxa belonging to 102 genera, were recorded in the 524 samples analysed. The most abundant five small species were *Diatoma tenuis* C.Agardh, *Navicula perminuta* Grunow, *Rhoicosphenia curvata* (Kütz.) Grunow, *Nitzschia inconspicua* Grunow and *Nitzschia frustulum* (Kütz.) Grunow. The most abundant five large species were *Tabularia fasciculata* (C.Agardh) D.M.Williams & Round, *Ctenophora pulchella* (Ralfs ex Kütz.) D.M.Williams & Round, *Gomphonema olivaceum* (Hornem.) Bréb., *Cymbella helvetica* Kütz. and *Epithemia sorex* Kütz.

Table 2. Area means for environmental and community variables (means for Areas 1 and 9 are not shown). Means are based on measurement per site or site means of 2-4 samples. Temp: water temperature; Salin: salinity; DIN: dissolved nitrogen (NO_2-N + NO_3-N); DIP: dissolved phosphorus (PO_4-P); DSi: dissolved silicate (SiO_2-Si); Si:P: ratio DSi:DIP; N:P: ratio DIN:DIP; Si:N: ratio DSi:DIN; Sand: weight of inorganic sediment grains in the samples; DW: dry weight; ADW: ash-free dry weight; ADW %: ADWx100 %/DW; RichS: richness of species with cell biovolume < 1000 μm^3 of 250 counted valves in Count 1a; RichSL: richness of species with cell biovolume < 1000 μm^3 and ≥ 1000 μm^3 together of 250 counted valves in Count 1b; RichL: richness of species with cell biovolume ≥ 1000 μm^3 of 125 counted valves in Count 2; S:L: ratio of number of specimens < 1000 μm^3 to specimens ≥ 1000 μm^3.

Variable	Baltic Sea proper (from Ulanova & Snoeijs 2006)				Bothnian Sea (from Busse & Snoeijs 2003)			Bothnian Bay (from Busse & Snoeijs 2002)			
	Area 2	Area 3	Area 4	Area 5	Area 6	Area 7	Area 8	Area 10	Area 11	Area 12	Area 13
Temp (°C)	13.1	12.8	14.5	14.9	13.3	7.1	6.8	8.1	8.5	8.3	10.3
Salin (psu)	7.8	6.8	6.7	5.7	5.1	4.8	4.9	3.1	2.4	2.2	0.7
DIN ($\mu mol\ l^{-1}$)	0.47	1.84	0.35	0.66	0.85	0.65	0.40	0.69	4.10	6.08	3.14
DIP ($\mu mol\ l^{-1}$)	2.20	0.92	0.46	0.13	0.04	0.17	0.15	0.28	0.09	0.20	0.18
DSi ($\mu mol\ l^{-1}$)	2.50	5.58	5.45	4.27	6.54	11.18	15.32	19.23	27.81	45.15	47.68
Si:P (by moles)	6.1	6.8	27.6	78.3	188.0	209.0	179.0	252.0	522.0	418.0	667.0
N:P (by moles)	0.9	2.4	2.0	15.5	25.0	8.0	5.0	36.0	75.0	61.0	41.0
Si:N (by moles)	6.3	7.2	15.9	9.8	8.0	25.0	43.0	10.0	7.0	8.0	17.0
Sand ($mg\ cm^{-2}$)	491.0	27.0	292.0	1516.0	399.7	95.8	1087.8	193.6	117.0	72.2	100.7
DW ($mg\ cm^{-2}$)	15.8	10.6	9.3	21.5	15.3	7.9	19.2	9.2	10.1	14.8	17.4
ADW ($mg\ cm^{-2}$)	3.8	5.6	3.5	4.9	3.0	2.4	4.0	2.2	1.6	2.2	1.7
ADW %	35.5	53.3	42.0	24.9	26.4	34.5	32.5	28.3	20.2	20.1	10.8
RichS	15.5	18.1	20.7	22.4	26.5	22.2	21.8	24.3	21.6	29.8	37.8
RichSL	20.3	21.7	25.1	26.8	35.0	29.2	29.4	32.3	26.7	39.1	52.1
RichL	7.0	12.0	9.6	8.0	20.5	20.6	28.5	18.4	16.3	23.3	23.8
S:L	4.3	37.7	6.9	5.4	10.7	16.0	12.6	24.3	37.6	14.9	8.8

Small and large diatoms

Recently the idea has been put forward (Snoeijs et al. 2002) that small species in a diatom community may respond differently to environmental variation than large species in the same community. For the Bothnian Bay, salinity was found to be a major environmental factor affecting large diatoms (with cell biovolume ≥ 1000 μm^3), while exposure to wave action was the major factor affecting small diatoms (with cell biovolume < 1000 μm^3). Opposite to findings in the Bothnian Bay, for the Baltic Sea proper, it was found that the small diatoms responded more to salinity and less to exposure to wave action than the large diatoms, but the hypothesis that small and large diatoms respond differently to environmental variables was confirmed (Busse & Snoeijs 2002, Ulanova & Snoeijs 2006). In the present study, when we used the merged data sets for Bothian Bay, Bothian Sea and Baltic Sea proper, which were used separately before, this hypothesis was not confirmed. Separate analyses for small and large taxa yielded similar results. We are thus concluding that small and large diatoms may respond to environmental variables in similar ways when the gradients of environmental factors are widespread, like in our case, along the whole Swedish coast of the Baltic Sea, but they respond differently when the gradients of environmental factors are narrow. The present results show that it is still necessary to count both large and small diatoms.

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