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Factors Affecting Macrobenthic Fauna in a Tropical Hypersaline Coastal Lagoon in Ghana, West Africa

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Abstract The macrobenthic fauna in the large, hypersaline, shallow Keta lagoon in Ghana was sampled at 20 stations in the wet (September 2002) and dry seasons (March 2003) to elucidate the effects of abiotic factors on community patterns. The macrobenthic fauna was low in density and species diversity and numerically dominated by bivalves and capitellid polychaetes. These organisms appear able to withstand physical disturbance (when lagoon water levels become extremely low) and osmotic stress (when salinities are extremely high) and tend to redistribute along environmental gradients. Parallel seasonal differences in several environmental variables and the macrobenthic fauna indicate a highly dynamic system. Species richness and diversity were higher in the wet season than the dry season. Salinity, percent clay, pH, and turbidity in that order were the major significant variables structuring the macrobenthic faunal assemblage in Keta lagoon. The strong effect of seasonal salinity changes on macrobenthic faunal assemblages may have trophic consequences for higher organisms of commercial importance, such as fishes and shorebirds, in the Keta lagoon.

Keywords Macrobenthic fauna · Seasonal variation · Multivariate analyses · Abiotic factors · Hypersaline coastal lagoon · Keta lagoon

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Introduction

As on many other coastlines of the world (Kjerfve 1994; Marcovecchio et al. 2005), the West African coast is dominated by a series of shallow coastal lagoons, most of which are oriented parallel to the shore. They are highly dynamic and unpredictable systems and considered distinct from other coastal systems such as estuaries (Kjerfve 1994). These lagoons are often characterized by strong spatial gradients in the physical and chemical characteristics of the water and the biological populations present (Guelorget and Perthuisot 1983). These characteristics reflect the mixing of fresh water and restricted sea inflows (Amanieu and Lasserre 1982), evaporation, and biogeochemical processes (Herrera-Silveire 1994).

Keta lagoon is the largest of more than 90 lagoons along the 550-km coastline of Ghana. It covers an area of approximately 340 km^2 and forms part of the wider wetland system of the Volta Delta. The lagoon is of high ecological and economic value (Armah 1993) and serves as an important overwintering site for Palearctic migratory shorebirds. A total of 37,519 Palearctic and other water birds belonging to 46 species have been reported in a single count at the lagoon (Piersma and Ntiamoa-Baidu 1995).

Over 20 settlements around the lagoon use its waters for the production of salt and are substantially dependent on its fisheries for their protein needs and sustenance. Studies on the fisheries have been carried out by Kwei (1977), Vodzogbe (1994), Shenker et al. (1998), Addo (2000), and Ababio (2001). The composition of higher trophic organisms of commercial importance such as fishes and shorebirds has been linked to the dynamics of sediment-dwelling macrofaunal assemblages (Colwell and Landrum 1993; Liang et al. 2002).

Sedimentary systems, in general, are of substantial socioeconomic importance throughout the tropics but, with the specific exceptions of mangroves and seagrass, they are largely overlooked in the scientific literature (Alongi 1989; Alongi and Sasekumar 1992).

Tropical sedimentary lagoon systems, in particular, are poorly understood (Alongi 1990) and those in Ghana are no exception (Gordon 2000). Although Keta lagoon has been studied by Finlayson et al. (2000), the community structure and processes that influence the macrobenthic fauna dynamics are still poorly known. In a dynamic and hypersaline ecosystem such as Keta lagoon, both long-term and short-term studies are necessary to achieve a better understanding of the processes, either natural or man-made, and to elucidate the spatial and seasonal abundance patterns. It has been shown that ranges of environmental variations are greater in tropical sedimentary systems than in higher latitude systems (Alongi 1989).

The macrobenthic fauna of tropical sedimentary systems experiences fluctuations in salinity and sediment erosion leading to wide variations in species diversity (Alongi 1989), but still little is known of the seasonal assemblage patterns in extremely fluctuating hypersaline tropical coastal systems in West Africa. Seasonal reduction in species diversity and irregular assemblage patterns of macrobenthic fauna have been reported in Keta lagoon (ESL/RPI/GLDD 2004). There is, however, a paucity of quantitative data on both macrobenthic fauna and abiotic factors in the lagoon. In the present study, we quantitatively describe the macrobenthic fauna and investigate the role of abiotic factors in the assemblage patterns.

Materials and Methods

Study Area

The study was conducted in the Keta lagoon of southeastern Ghana, West Africa, which falls within latitudes 0°49′ E and 1°02′ E and longitudes 5°47′ N and 6°03′ N. It covers an estimated area of 340 km^2 with water depths ranging from 0.47 to 0.94 m in the wet season and 0.14 to 0.56 m in the dry season. The lagoon has a maximum coastal length (east–west) and width (north–south) of 25 and 13.5 km, respectively (Fig. 1). The lagoon is separated from the sea by a narrow sand bar and, therefore, receives sea water only through overwash during periods of high tide.

The Keta basin was formed by coastal subsidence during the Precambrian (Akpati 1975). The upper geologic strata (about 24 m) are composed of coarse, unconsolidated beach sand and gravels both of fluviatile and shallow marine to estuarine origin (Akpati 1975). Most areas in the lagoon are typically muddy in the upper 10 cm. The sea grass *Ruppia maritima* occurs in the northeastern part of the lagoon and portions of the southern part. The macrophytic flora in the lagoon is dominated by *Typha domingensis* (used by the inhabitants to weave local mats) and *Paspalum vaginatum* in the northwestern and southwestern portions in the freshwater tributaries of the lagoon.

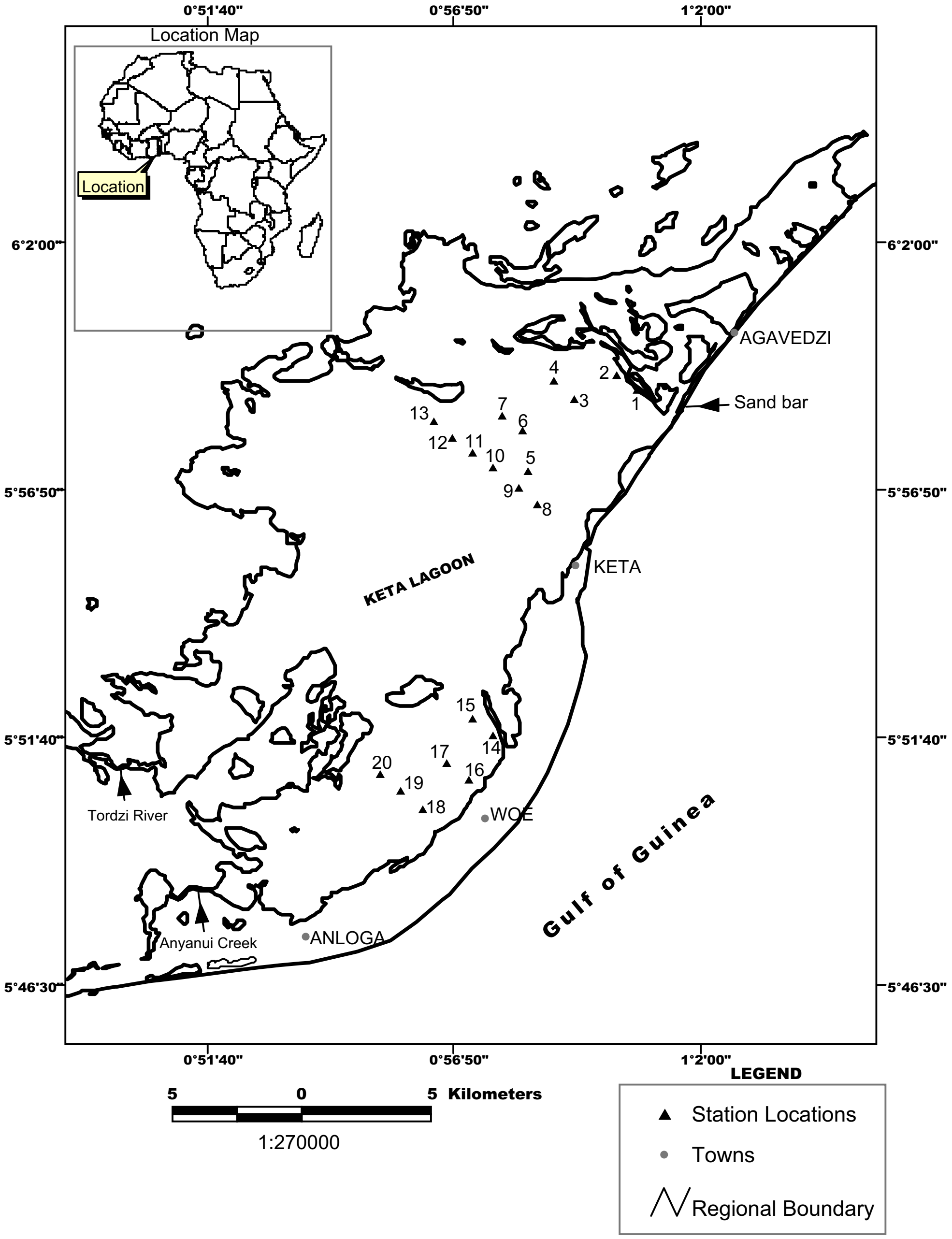
The Keta lagoon receives fresh water from large catchment areas including (1) runoff from the Tordzie river, which originates from the Akwapim–Togo ranges; (2) runoff from the Aka and Belikpa catchments, which enters the lagoon from the north; and (3) inflows from the Volta estuary through Anyanui creek (Entsua-Mensah and Dankwa 1997). The Tordzie river has a catchment area of 2,200 km^2 and a mean annual flow of 11 m^3 s^{-1}; Aka and Belikpa have catchment areas of 280 and 420 km^2, respectively; the total drainage area of the Volta estuary is 37,900 km^2 (Finlayson et al. 2000). Nevertheless, the volume of water (84,446 m^3) transferred to the lagoon during one flood period from the Volta estuary via Anyanui creek resulted in a tidal excursion of 5.4 km (Sørensen et al. 2003), indicating that the fresh water that flows from the Volta estuary into the lagoon is not substantial. The estimated static capacity of Keta lagoon is 360×10^6 m^3 when there is no flow of water into it (Finlayson et al. 2000).

The area lies within the dry equatorial region of Ghana, which has two wet seasons, one from May to July (major rainy season) and from September to November (minor rainy season). The mean annual rainfall is 750 mm (Dickson and Benneh 1988). The dry season begins in January and ends in March. Annual mean air temperatures range between 24°C and 32°C. Evaporation in the area far exceeds annual rainfall. It is only during the major wet season that monthly rainfall may exceed evapotranspiration and temporary streams flow (Biney 1986). The prevailing wind direction is from the southwest (the southwest monsoon), which is a feature of the entire coastal belt of the country (Finlayson et al. 2000). The mean monthly averages of daily wind speeds range from 5.86 to 8.06 m s^{-1} (Finlayson et al. 2000).

Field Sampling

Seasonal variations of abiotic factors in coastal lagoons are likely to affect the community assemblages of macrobenthic fauna. In quantifying the possible seasonal changes in macrobenthic faunal assemblages in the fluctuating hypersaline lagoon system, sampling was carried out in both wet and dry seasons. Wet season sampling was carried out in September 2002 and dry season sampling at the end of March 2003. The same 20 stations along the lagoon's southwestern–eastern axis were sampled in each season (Fig. 1). In the data analyses, the September 2002 samples are designated by A plus the station number (i.e., A1–A20)

Fig. 1 Map of Keta lagoon showing sampled stations and other features



and the March 2003 samples are designated B1–B20. Lack of access to the lagoon during the dry season as a result of low water levels informed the selection of stations.

The coordinates of the sampling stations were geo-referenced using a hand-held Garmin GPS 12. Four replicate samples (total volume of 0.0136 m^3) were taken at each station using a 0.076-m diameter PVC corer that was pushed 0.25 m deep into the sediment. Three cores were pooled (total surface area=0.0136 m^2) to constitute each replicate to ensure adequate sample representation at each station. The samples were put into a tray and screened over a sieve of 0.5-mm mesh and fixed with 10% borax prebuffered formaldehyde solution. Samples were sorted with the aid of a hand lens in the laboratory and preserved in 70% ethanol mixed with glycerol. Sorting of the species was carried out with the aid of a Leica 2000 microscope and the organisms were grouped into broad taxonomic units such as polychaetes, mollusks, crustaceans, and cnidarians. These broad taxa were identified to genus or species levels as possible and counted. Identifications were based on taxonomic guides and manuals (e.g., Day 1967a, b; Edmunds 1978) as well as voucher specimens in the Zoological Museum of the University of Ghana. Voucher specimens are available for examination. It is worth noting that *Tympanotonus fuscatus* and *Pachymelania* sp. (gastropods), which were seen in the lagoon on the sediment surface, were underrepresented in the counts. Live individuals withdrew far into their shells and closed their opercula so that we could not distinguish live from dead individuals. Nevertheless, they constitute an important part of the macrobenthic fauna in Keta lagoon.

Additional sediment was taken at each station from a 25-cm deep core. These samples were homogenized, air-dried, and used for granulometric analysis (i.e., sand, silt, and clay fractions) using Bouyoucos' (1934) method and also percent organic carbon and percent sulfur contents using the ELTRA 500 C-S determinator after pretreatment of the sediment with hydrochloric acid to remove inorganic carbon.

Environmental variables of the water (i.e., pH, dissolved oxygen, water depth, and water temperature) were measured in situ at middepth for all stations. Additional water samples were collected at the same depth for laboratory analyses of nitrate, phosphate, silicate, sulfate, conductivity, turbidity, total suspended solids, and total dissolved solids using the HACH DR/2010 spectrophotometer following the methods in A.P.H.A. et al. (1998).

Data Analysis

Analysis of the data was carried out using both univariate and multivariate techniques. The species abundance data for the four replicate samples taken in each station were combined before subjecting them to statistical analyses. An analysis of variance (ANOVA) tested for differences in the environmental variables between the two sampling dates. Graphical descriptors in the form of *K*-dominance curves were plotted for species abundance (Lambshead et al. 1983) to ascertain seasonal dominance.

The faunal variability and seasonal difference was tested using a one-way analysis of similarity (ANOSIM). The null hypothesis was that there is no difference between the two studied seasons in terms of macrobenthic fauna abundance. Macrobenthic fauna similarity among the stations for each season was investigated applying cluster analysis (group average) based on the Bray–Curtis similarity index of species abundance after transformation (fourth root) (Clarke and Green 1988). The similarity matrix was used to produce a hierarchical agglomerative dendrogram for a graphical representation of community relationships (Clarke 1993) using pooled wet and dry season data sets. At the same time, a similarity profile test (SIMPROF; Clarke and Gorley 2006) was performed to test the null hypothesis that a specific subset of samples did not differ from each other in the multivariate structure.

The species that contributed the most to within-season similarity and species that discriminated one season from another were examined using the similarity percentage procedure (SIMPER) (Clark and Warwick 1994) to characterize the macrobenthic fauna. The results assisted in the interpretation of the faunal changes responsible for the observed patterns in the dendrogram (Clarke 1993).

Univariate analyses of diversity indices were calculated for the Margalef's species richness index (d'), which takes into account species present and number of individuals, and the Shannon–Weiner diversity index (H' using log to base e) (Shannon and Weaver 1963). Evenness was also estimated as defined by Pielou (1966), which shows how evenly the individuals are distributed among species.

A canonical correspondence analysis (CCA) was performed (Ter Braak 1986) for the pooled seasons' species abundance data [using the ten most abundant species which together contributed 80.6% and were selected based on the frequency of occurrence (F) (Guille 1970) >20% using the package CANOCO 4.5 (Ter Braak and Smilauer 2002)], which combines both ordination and regression to ascertain relationships between species and environmental variables (Ter Braak 1986). CCA was also applied separately for each season's species abundance (using the ten most abundant species) to determine the differences in species–environment interactions. Environmental variables with an inflation factor >20 (Ter Braak and Smilauer 2002) and variables that covaried were excluded from the CCA. Consequently, total dissolved solids, total suspended solids, conductivity, and sulfate were excluded from the pooled seasons' data while additional variables, depending on the season, were also excluded. All the environmental variables were transformed (Log $(x+1)$) to stabilize and normalize the variance.

In the CCA biplot, the first and second axes represent the most important environmental gradient along which the macrobenthic species are distributed. The direction of each environmental vector represents the maximum rate of change for that particular environmental variable and its length indicates the relative importance to the ordination. The significance of all primary CCA axes was determined by a Monte Carlo permutation test (199 permutations) of the eigenvalues (Ter Braak and Smilauer 2002). A forward selection procedure ordered the environmental variables according to the amount of variance they captured in the species data (Ter Braak and Verdonschot 1995). In the first step of this method, all environmental variables were ranked on the basis of the fit for each separate variable. Each variable was treated as the sole predictor variable and all other variables were ignored; hence, the variance explained represents marginal effects. At the end of the first step of the forward selection, the best variable was selected. Hereafter, all remaining environmental variables were ranked on the basis of the fit (amount of variance explained) that each separate variable gave in conjunction with the variable(s) (covariables) already selected (conditional or unique effects). At each step, the statistical significance of the variable added was tested using a Monte Carlo permutation test (199 unrestricted permutations) (Ter Braak and Smilauer 1998).

Results

Environmental Variables

The environmental variables showed large significant seasonal and spatial variations. The variables that exhibited marked significant differences were salinity, conductivity, water temperature, water depth, sulfate, phosphate, nitrate, and silicate (Table 1). Other factors which also showed seasonal and spatial changes included dissolved oxygen, pH, total dissolved solids, and total suspended solids. Spatial variability and the means for salinity, nitrate, and sulfate were higher in the dry season than the wet season. Conversely, the means for water depth and turbidity were substantially higher in the wet season than the dry season (Table 1). There were strong significant differences in water depth, water temperature, salinity, nitrates, sulfate, silicate (all $p<0.001$) and phosphate ($p<0.05$) between the wet and dry seasons (Table 1). Results of sediment analyses including percent sand (78.46±11.32), percent silt (11.21±8.64), percent clay (10.33±4.36), total organic carbon (0.77±0.54), and percent sulfur (0.09±0.07) in wet season did not show any significant difference ($p>0.05$) from dry season variables, namely, percent sand (78.49±10.25), percent silt (9.86±8.59), percent clay (11.65±4.64), total organic carbon (0.77±0.41), and percent sulfur (0.08±0.07).

Faunistic Composition

A total of 2,152 individuals (mean density=989 individuals per square meter) belonging to 35 macrobenthic faunal species were identified during the study. Of this number, polychaetes constituted 46.8%, mollusks 51%, and crustaceans 0.7%. Other taxa recorded included Hirudinea and Cnidaria, which together constituted 1.5%.

The wet season samples presented both a higher number of species and individuals than the dry season. The total number of species was 35 and 18 for the wet and dry seasons, respectively. The total densities for the seasons were 1,431 and 547 individuals per square meter for the wet and dry seasons, respectively. The number of individual mollusks for the wet season and the dry season were 794 (72.3%) and 304 (27.7%), respectively (Table 2). The number of individual polychaetes in the wet season was 717 (71.1%) while 291 individuals (28.9%) were recorded during the dry season (Table 2).

The seasonal and spatial distributions of the ten dominant species (Fig. 3) represent 80.6% of the pooled seasons' abundance. The pooled wet and dry season samples were numerically dominated by bivalves: *Tellina nymphalis* (19.8%), *Tivela tripla* (14.9%), and *Tivela bicolor* (7.4%) and polychaetes: *Nephtys* sp. (10.27%), *Notomastus latericeus* (7.4%), and other capitellids (7.9%) with numerical dominance in the wet season (Fig. 3). Significant seasonal differences in abundance were found for *N. latericeus* ($p<0.05$), *Nephtys* sp. ($p<0.001$), and *T. nymphalis* ($p<0.01$) (Fig. 2).

Spatially, stations located in the middle portions of the lagoon (i.e., A12, A13, and A7) and A14 presented the highest number of individual mollusks and polychaetes with dominance in the wet season (Fig. 3). Some of the animals recorded including *Capitella* spp., *Ancistrosyllis robusta*, *Marphysa sanguinea*, orbinid sp., *Ischyroceros* sp., *Neanthes* sp., and *Pseudopolydora* sp. are new records from the Keta lagoon.

The species *K*-dominance curves of abundance revealed slightly higher dominance in the wet season with fewer than ten species (Fig. 4). There was 75% saturation in cumulative dominance with the addition of the fifth species for the wet season curve (Fig. 4). The curves for the two seasons approached the asymptote after the tenth species by which 90% cumulative dominance was attained. Generally, species added beyond the limit of the asymptote are considered rare and seldom offer additional critical information. This suggests community dominance by ten species which could discriminate (see also Table 3) between the seasons.

Table 1 The mean and standard deviation (in parenthesis) for environmental variables in the wet and dry seasons

Environmental variable	Wet season	Dry season	*p* value
Water depth (m)	0.73 (0.13)	0.30 (0.13)	<0.001
Water temperature (°C)	27.72 (1.68)	30.94 (1.85)	<0.001
Salinity (‰)	27.90 (2.38)	61.80 (25.13)	<0.001
Nitrate (mg L^{-1})	0.33 (0.13)	1.08 (0.27)	<0.001
Conductivity (mS/cm)	35.86 (1.29)	67.88 (24.56)	<0.001
Phosphate (mg L^{-1})	0.27 (0.12)	0.20 (0.10)	<0.05
Sulfate (mg L^{-1})	2887.50 (284.18)	6708.75(3162.22)	<0.001
Silicate (mg L^{-1})	9.48 (4.07)	5.84 (1.76)	<0.001
Turbidity (NTU)	110.00 (78.34)	69.20 (68.14)	>0.05

Significance levels are based on ANOVA between the wet season and dry season. Only variables indicating significant differences are reported except for turbidity

Table 2 Seasonal abundance (number of individuals) and densities of major macrobenthic faunal groups in the Keta lagoon

Taxa	Wet season		Dry season	
	Abundance (no. of individuals)	Density (individuals per square meter)	Abundance (no. of individuals)	Density (individuals per square meter)
Polychaetes	717	659	291	268
Mollusks	794	730	304	279
Crustaceans	14	13	0	0
Others	32	29	0	0
Total	1,557	1,431	595	547

Densities were determined using a total surface area of 1.088 m^2 [i.e., 3 cores (surface area=0.0136 m^2)×4 replicates (i.e., 0.0136 m^2 ×4= 0.0544 m^2)×20 stations (0.0136 m^2 ×4×20=1.088 m^2)]

Community Structure

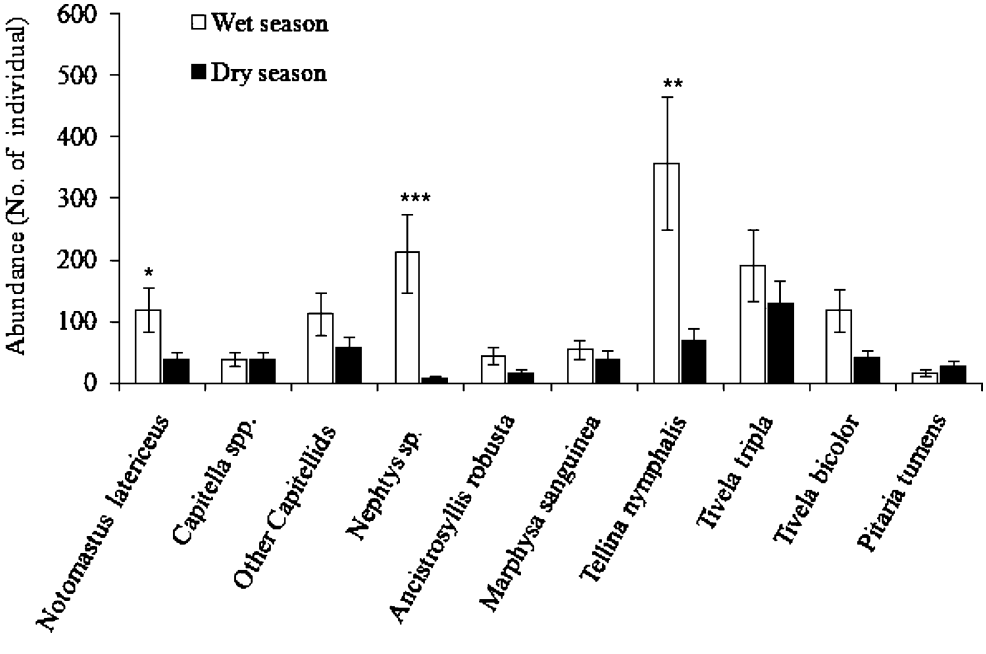
Possible macrobenthic fauna differences between the wet and the dry seasons were tested using one-way ANOSIM and revealed a significant difference ($r=0.156$, $p<0.05$).

An agglomerative dendrogram of the pooled seasons' species abundance revealed six significant station groups distinguished at a Bray–Curtis similarity level of 40% (Fig. 5). Five of the station groups showed >50% Bray–Curtis similarity. However, station group 1F, a group of four stations sampled in the dry season that lacked any macrofauna clustered at the 100% similarity level. Station group 1A represented a mixture of the same stations (A14, B14, A15, B15, A19, B19, A20, and B20) sampled in both seasons. These stations clustered at a similarity level of 55% indicating low interseasonal variability in macrobenthic faunal abundance and composition. The dominant species in station group 1A were *Pitaria tumens*, *Capitella* spp., *N. latericeus*, and other capitellids. Station group 1C, which was a cluster of stations mainly from the dry season, was dominated by *Nephtys* sp., *T. nymphalis*, *T. tripla*, *T. bicolor*, *Capitella* spp., and *N. latericeus*.

Station groups 1B and 1E consisted of mixtures of stations dominated by the wet and dry season stations, respectively, revealing some seasonal specificity in the macrobenthic faunal assemblages. The species that contributed appreciably to station group 1B were *A. robusta* and *M. sanguinea* whereas station group 1E comprised *M. sanguinea* and *T. nymphalis*. Station group 1D was dominated by *Nephtys* sp., *N. latericeus*, *T. nymphalis*, and *T. bicolor*. Essentially, the clustering distinguished stations with pronounced interseasonal variability in macrobenthic faunal assemblage from those that showed fewer changes (Fig. 5). Although there were spatial and seasonal differences in macrobenthic faunal composition, overall, the groups were significantly similar at >40% using the Bray–Curtis index.

Ten species, namely, *T. nymphalis*, *Nephtys* sp., *T. tripla*, other capitellids, *N. latericeus*, *T. bicolor*, *M. sanguinea*, *A. robusta*, *Capitella* spp., and *P. tumens* were responsible for the dissimilarity between the wet and dry season and discriminated between them (Table 3). These species together contributed 68.14% to an average dissimilarity of 70.12% between the wet and dry season. Four species, namely, *T. nymphalis*, *Nephtys* sp., *T. tripla*, and *N. latericeus*, contributed slightly >50% to the average similarity of 45.21% in the wet season. Over 50% of the average similarity of 27.53% realized in the dry season was contributed by *T. tripla*, *P. tumens*, other capitellids, and *T. nymphalis*.

Fig. 2 Mean abundance of dominant macrobenthic taxa in wet and dry seasons. *Vertical bars* indicate 95% confidence interval of abundance. Significance levels are based on ANOVA for differences between the wet and dry seasons' species: *$p<0.05$, **$p<0.01$, ***$p<0.001$



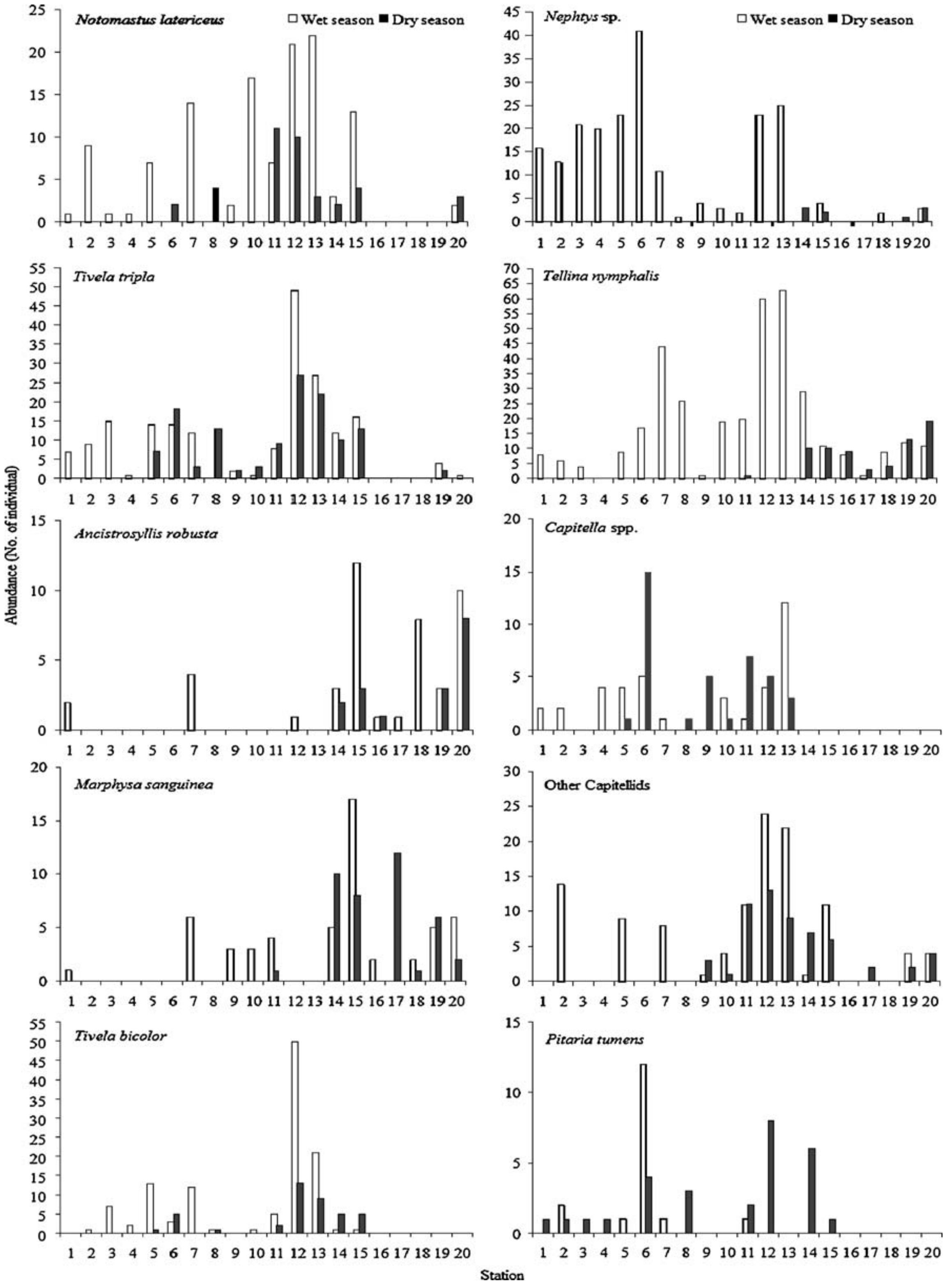


Fig. 3 Distribution and abundance of dominant macrobenthic taxa in Keta lagoon in wet and dry seasons

Community Structure Analysis

Species richness (d'), species diversity (H'), and species evenness (J') calculated for the two seasons in the lagoon showed a seasonal pattern in the distribution of the macrobenthic fauna. Spatially, the highest values of H' and d' were obtained at stations A1, A2, A7, A9, A15, and A20 for the wet season and B11, B14, B15, and B20 for the

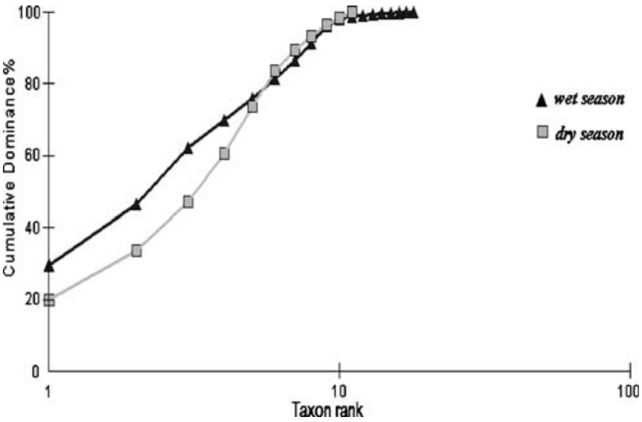


Fig. 4 Cumulative dominance curves for macrobenthic taxon abundances for wet and dry seasons. Higher dominance in wet season for the first five species and slightly higher dominance for dry season samples after the addition of the tenth species

dry season. The lower values of H' and d' in the wet season were obtained at stations A4, A8, and A17 while the dry season stations were B18, B16, and B9.

Species–Environment Interactions

In the CCA, the environmental variables are shown as arrows, the lengths of which indicate the relative importance and the directions of which are obtained from the correlation of the variable to the axes. The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along that particular environmental gradient. In the CCA analysis, the first four ordination axes accounted for 51.5% of explained total variance in the species (dominant) abundance by the measured environmental variables (using the pooled seasons' abundance data). The first canonical axis accounted for 25.0% and, together with the second axis, 39.6% of the variance in the species abundance was explained by the environmental variables. The CCA resulted in a significant model as depicted by the Monte Carlo test ($p \leq 0.005$). The first ordination axis reflected samples with a gradient largely related to percent clay, percent organic carbon, phosphate, and percent sulfur in that order of importance at the positive end of the axis and salinity and percent sand at the negative end (Fig. 6). The second axis was associated with water temperature at the positive end of the axis while the negative end was related to nitrate, pH, turbidity, dissolved oxygen, and silt content (Fig. 6). It is apparent that the first axis largely reflected sediment-related variables while the second axis represented water column variables. As such, it is possible to discriminate between species whose abundances were influenced by sediment-related variables (e.g., *A. robusta*, *M. sanguinea*, *T. nymphalis*, *Capitella* spp., *T. tripla*, *T. bicolor*, and *N. latericeus*) and those influenced by water column variables (*Nephtys* sp., *P. tumens*, and other capitellids). The percentage of variance explained by each environmental variable as the sole predictor variable (marginal effects) was significantly largest for salinity (19%), percent clay (15%), pH (11%), and turbidity (6%).

Applying the species abundance for the two seasons separately to the CCA resulted in the first two axes accounting for 45.4% and 53.6% of explained total variance in the species abundance for the wet and dry seasons, respectively. The CCA model was not significant ($p > 0.05$) for the wet season. However, the ordination diagrams (Fig. 7) revealed some correlations which are consistent with the observations in the combined analysis (Fig. 6). These correlations were between *T. nymphalis* and percent sulfur, *A. robusta* and *M. sanguinea* with percent clay and percent organic carbon, as well as *Nephtys* sp. with dissolved oxygen and turbidity. In the wet season, temperature (16%) and pH (13%) were the significant sole predictors, while silicate (47%) and nitrate (15%) were the significant sole predictors of the variance in species abundance for the dry season.

Discussion

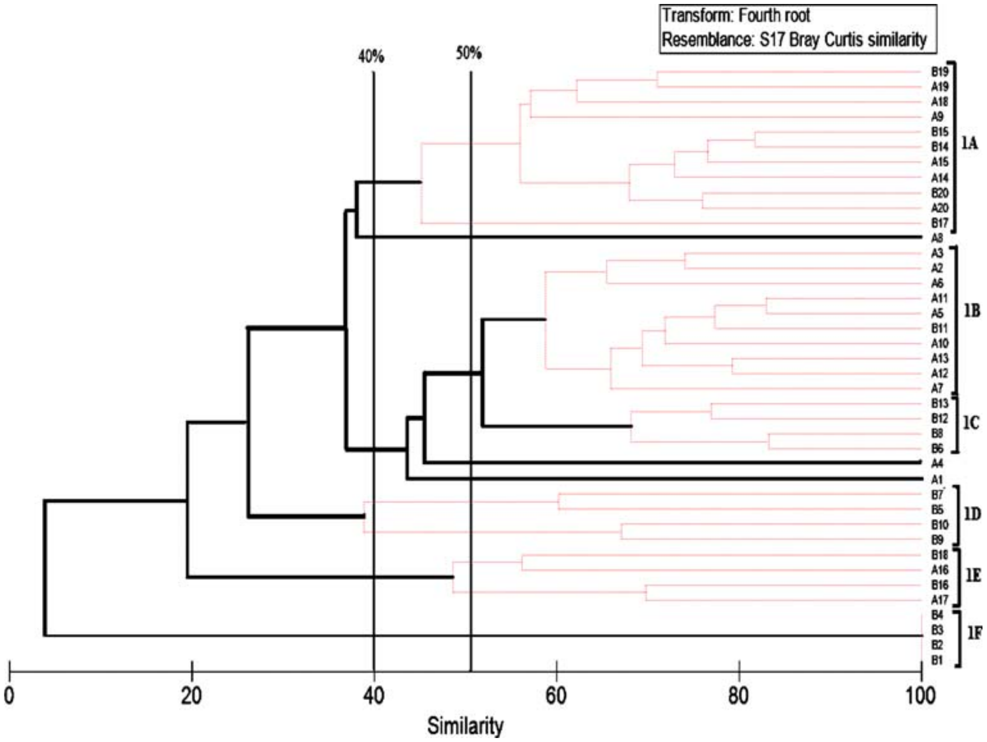
There were significant spatial and seasonal differences in the environmental variables (one-way ANOSIM, $r = 0.552$, $p = 0.001$) and the macrobenthic faunal communities of Keta lagoon (one-way ANOSIM, $r = 0.156$, $p = 0.003$). Spatial differences observed in the environmental variables were mainly the result of seasonal characteristics due to the

Table 3 SIMPER analysis results: species contributing to the average Bray–Curtis dissimilarity for the wet and dry seasons resulting from the simultaneous analysis of abundance data for the two seasons

Species	Contrib. %	Cum. %
Tellina nymphalis (B)	10.50	10.50
Nephtys sp. (P)	8.83	19.33
Tivela tripla (B)	7.38	26.71
Other capitellids (P)	6.84	33.54
Notomastus latericeus (P)	6.49	40.04
Tivela bicolor (B)	6.16	46.19
Marphysa sanguinea (P)	5.97	52.16
Ancistrosyllis robusta (P)	5.74	57.90
Capitella spp. (B)	5.19	63.10
Pitaria tumens (B)	5.04	68.14

Faunistic contribution to the average Bray–Curtis dissimilarity between the wet season and the dry season, also expressed as a cumulative percentage (Cum %). For brevity, only species that contributed >5% are listed. The codes in the parenthesis after the species name indicate: *B* bivalve, *P* polychaete. Average dissimilarity between wet and dry seasons=70.12

Fig. 5 Group average agglomerative dendrogram of Bray–Curtis similarity of macrobenthic faunal abundance data for the wet and dry seasons' stations. The prefix letters *A* and *B* indicate stations for the wet and dry seasons, respectively. *Thin lines* indicate significant evidence of structure (SIMPROF test, $p<0.05$) and *thick lines* indicate no evidence of structure



relative magnitude of fresh water inflow, evaporation, biogeochemical processes, and reduced sea water exchange (Herrera-Silveire 1994; Mistri et al. 2000). Variables such as dissolved oxygen, pH, percent clay, percent silt, and percent sand, although they varied spatially, did not show any significant seasonal differences. Seasonally, the most significantly changed variables were salinity, conductivity, water depth, water temperature, silicate, nitrate, phosphate, and sulfate (Table 1). The spatial and seasonal variability resulted in habitat heterogeneity among the stations. This effect was manifested in the station clusters (Fig. 6). Distinct station clustering was based on sets of environmental variables. For instance, salinity, pH, and nitrate resulted in one grouping of stations; percent clay and percent organic carbon in another grouping; dissolved oxygen, turbidity, and percent silt constituted another station group; percent sand gave rise to another group, while phosphate, percent sulfur, and silicate accounted for another (Fig. 6). This heterogeneity among the stations as a result of the environmental variables possibly created conditions that influenced the abundance patterns of the macrobenthic fauna.

Macrobenthic faunal dynamics follow seasonal patterns (Mistri et al. 2001) and are characterized by high variability in abundance and dominance patterns within years (Posey 1986). As expected, the macrobenthic fauna in Keta lagoon showed distinct spatial and seasonal differences (Figs. 3 and 5) with species dominance (Fig. 4) and diversity higher in the wet season. The observed spatial and seasonal variability coupled with greater station group similarities (i.e., >50%) (Fig. 5) indicate that (1) a few dominant macrobenthic species controlled the community structure (Fig. 4 and Table 3), (2) the dominant species were distributed throughout the study area (Fig. 3), and (3) these species redistributed themselves in response to variations in environmental variables (Fig. 6). This further suggests that the dominant species are selected from a limited species pool in Keta lagoon. The significant seasonal variability in the macrobenthic community was due to the differences in the relative contributions of individual discriminating species (Table 3). Notable among these species are the bivalves (e.g., *T. nymphalis*, *T. tripla*, *T. bicolor*, *P. tumens*) and polychaetes of the families Capitellidae (*N. latericeus*, *Capitella* spp., and other capitellids), Nepthyidae (*Nephtys* sp.), Pilargidae (*A. robusta*), and Eunicidae (*M. sanguinea*). The relative abundances and contributions of the species (total contribution of 68.14%) led to the 70.12% average dissimilarity between the two seasons (Table 3). The spatial similarities within each season were also contributed largely by these species confirming their importance in controlling the community structure in the lagoon. There was lower average spatial similarity in the dry season than the wet season, indicating intense ecological stress which possibly created limitations in the observed species distribution and abundance (Fig. 3).

Variability in the abundances of macrobenthic organisms has been attributed to temporal variability in environmental conditions that may affect recruitment, survival, and reproduction (Posey et al. 1998). As observed, the distribution patterns of the macrobenthic fauna over the season indicated periodic changes ranging from a rich community

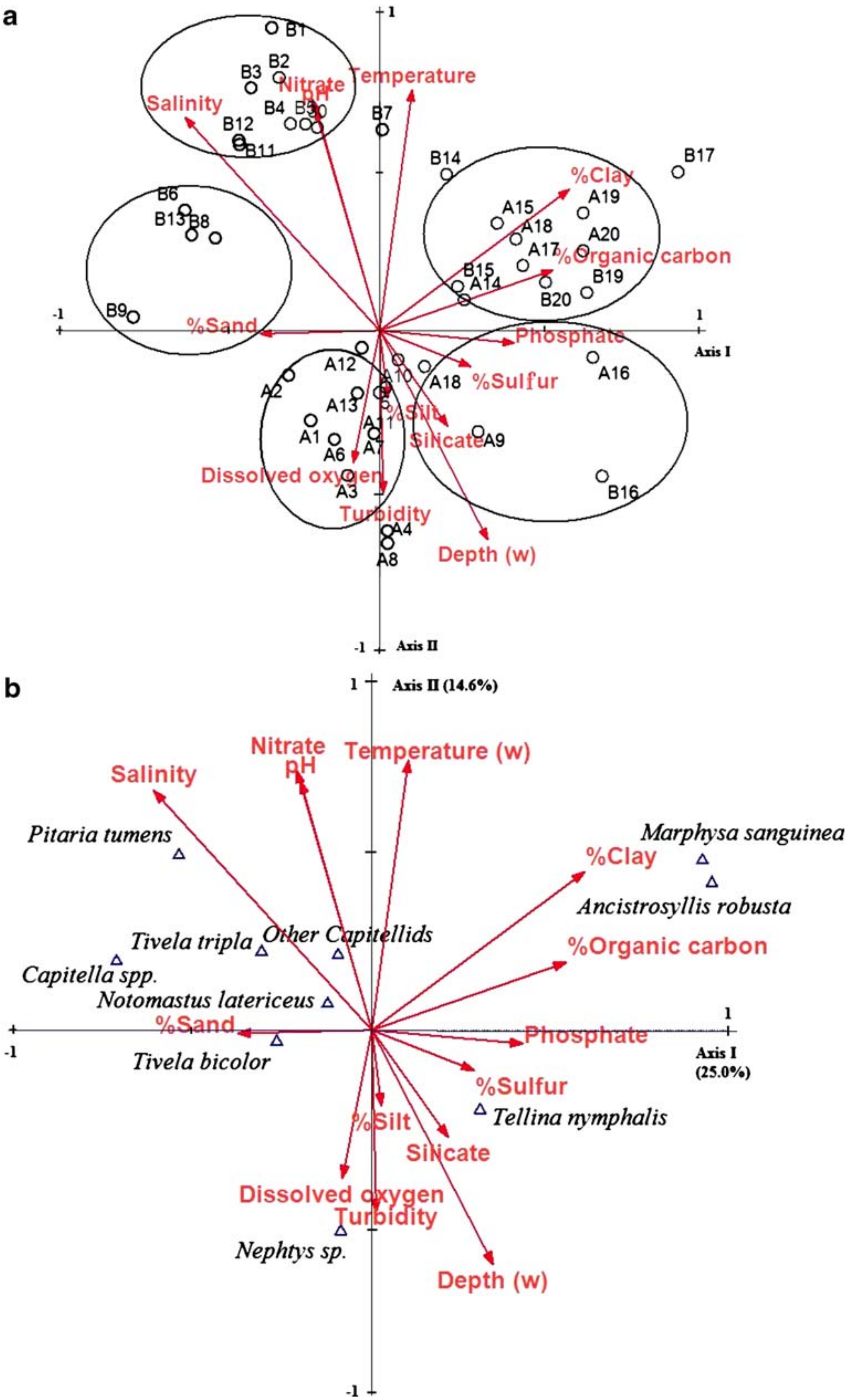
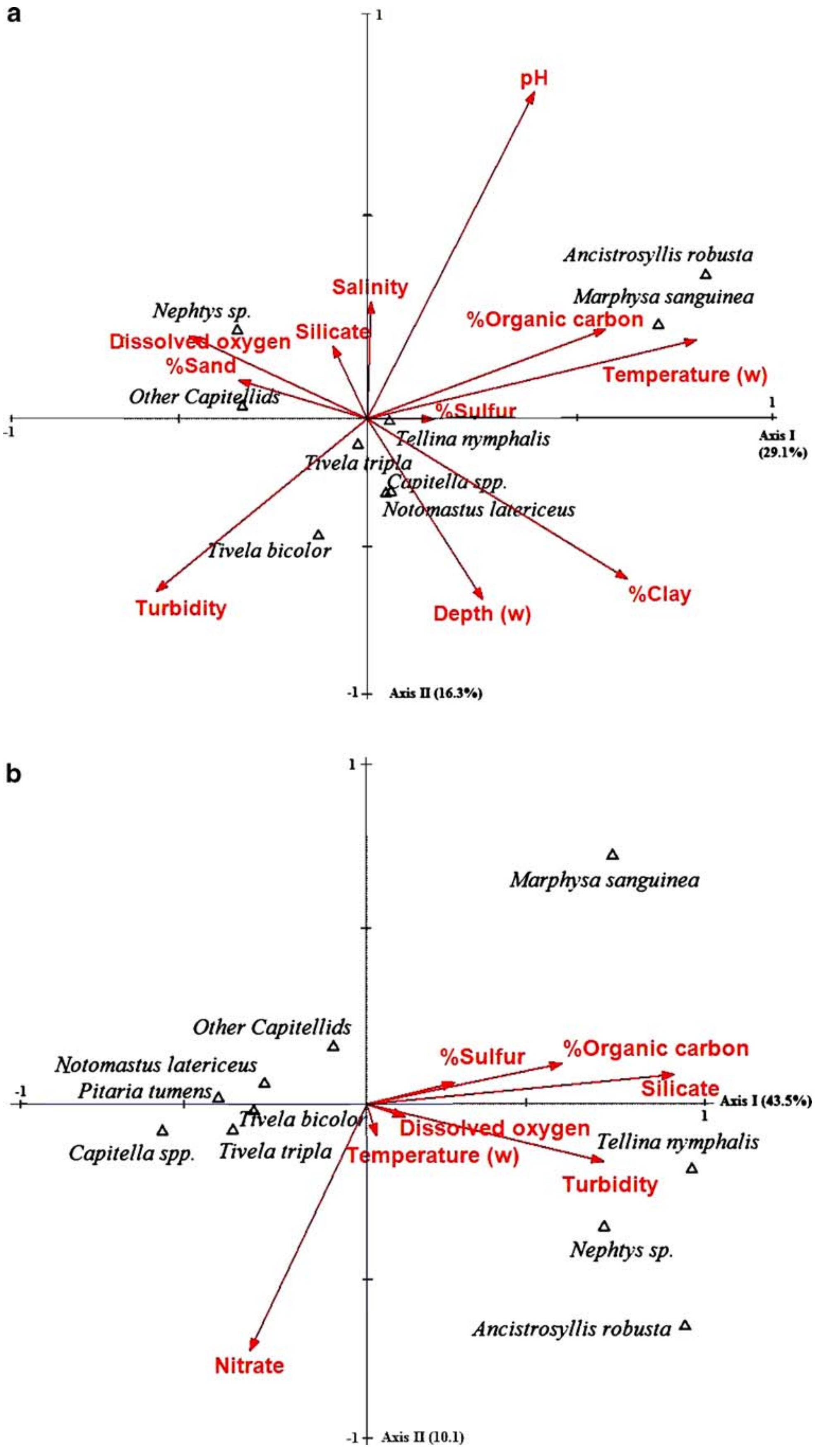


Fig. 6 CCA ordination diagrams for **a** station–environment biplot and **b** taxon–environment biplot. Taxon scores along the first and second axes in relation to environmental variables. Prefix *A* indicates stations sampled in wet season and prefix *B* for stations sampled in dry season

in the wet season to a relatively impoverished one in the dry season (Fig. 3). The situation in the dry season was apparently related to intense environmental stress, such as hypersalinity, leading to a reduction in the number of species. Such environmental conditions probably affected the physiological responses of the macrobenthic organisms

Fig. 7 CCA ordination diagrams for the abundance of macrobenthic dominant taxon. Taxon scores along the first and second axes in relation to environmental variables for **a** wet season biplot and **b** dry season biplot



resulting in the observed distribution patterns (Fig. 3). Grassle and Grassle (1976) indicated that the adaptation of certain species to unpredictable environments can be related in part to their life history characteristics. Newell (1970) pointed out that where the tolerance limits for a particular environmental variable have been determined for an organism, the organism's realized distribution is much more restricted than its potential distribution. It is reasonable, therefore, to presume that the relatively large significant seasonal fluctuations in environmental variables (Table 1) probably ensured that only species that are tolerant to broad changes in such variables survive and are distributed widely in such hypersaline ecosystems as Keta lagoon. The extreme hypersaline conditions possibly accounted for the low faunistic densities recorded (Table 2). The density of the polychaetes for instance (Table 2) in the lagoon was extremely low compared to 1.17×10^4 individuals per square meter recorded in other hypersaline lagoons (García de Lomas et al. 2005). Gordon (2000) has also reported low numbers of benthic macroinvertebrates in the hypersaline Muni lagoon in Ghana.

A number of environmental variables including sediment structure, organic matter content, temperature, salinity, dissolved oxygen, nutrient concentrations, pH, turbidity, water transparency, and depth have been correlated with the abundance, density, and diversity of macrobenthic organisms in lagoon systems (Barnes 1980; Nicolaidou et al. 1988; Arvanitidis et al. 1999; Hagberg and Tunberg 2000; Mistri et al. 2000). Additionally, variables involved with food supply, e.g., nutrients and organic matter, have also been documented (Gray 1981; Nixon 1982). This is consistent with our result that a substantial part of the total variation in species assemblages, both in space and time, was explained by the observed environmental variables (see Fig. 7). The species assemblage and the abundance of the individual species were correlated with the environmental variables (mostly) at the station level (Fig. 6). Alongi (1990) showed that benthic organisms in Indian estuaries for instance were more abundant in areas where salinities remained <40‰. Salinity-mediated patterns of abundance of macrobenthic species were very obvious in Keta lagoon. Appreciable numbers of macrobenthic species (e.g., *T. nymphalis*) were recorded at stations where the salinity range was <33‰ ($r=-0.48$). Other macrobenthic organisms, notably polychaetes, e.g., *Nephtys* sp. ($r=-0.39$), *A. robusta* ($r=-0.33$), and *M. sanguinea* ($r=-0.38$), also appeared to redistribute themselves such that high abundance occurred in areas where salinities were relatively lower, i.e., below 33‰, corroborating the observation by Alongi (1990). A broader range of salinity tolerance was exhibited by other taxa (i.e., bivalves and capitellid polychaetes) resulting in higher numbers in salinities below 40‰ and above 60‰. Such species may well represent specialized lagoon species with the requisite traits to tolerate large fluctuations in physical and chemical variables (Guelorget and Perthuisot 1992; Gray et al. 2002; Sconfietti et al. 2003). Salinity has been reported to control the distribution and the reproduction of certain macrobenthic fauna. It was identified as a key regulatory factor in the breeding cycle of the bivalve *Anadara* sp. (Macintosh 1994). Yankson (1982) reported that *Anadara senilis* occurring in Fosu lagoon in Ghana could tolerate salinity up to 50‰ in the dry season. It is reasonable to assume that the slightly lower salinities in the wet season ensured the recruitment of certain macrobenthic organisms such as bivalves as illustrated by the high species richness and diversity. It has been reported that a decrease in salinity appears to be responsible for an increase in reproductive output of species with a planktonic larval stage (Alongi 1990).

The CCA model also indicated that environmental variables correlated with significant part of the variations in the individual species abundance. Important significant correlations were found between individual species (dominant) and key environmental variables, notably, salinity, percent clay, percent sand, dissolved oxygen, and percent sulfur (Fig. 6). The specific correlations of individual species with certain environmental variables included: *Nephtys* sp. correlated with dissolved oxygen and turbidity in cooler water temperature; *N. latericeus* and *T. bicolor* correlated with percent sand containing low organic carbon; *T. nymphalis* correlated with percent sulfur; *A. robusta* and *M. sanguinea* correlated with percent clay and percent organic carbon. These illustrate that changes in community structure and distribution of macrobenthic organisms are influenced, to a large extent, by a suite of environmental variables to which each species in the community may respond differently (Warwick and Clarke 1991). Importantly, sediment variables played crucial roles in determining macrobenthic community structure (Gray 1974; Flint 1981) and such correlations with infauna (Dayton 1984) have often been related to functional groups (Rhoads 1974; Fauchald and Jumars 1979). The capacity for sediment to adsorb organic matter is related to its clay content, which influences the feeding habitats of the benthic fauna. Depending on its lifestyle, an organism may require a given size range of sediment for tube building, burrowing, or feeding (Wieser 1959). The occurrence of *M. sanguinea* and *A. robusta*, carnivorous or omnivorous polychaetes (Fauchald and Jumars 1979), in organically rich, clayey sediment is probably linked to functional adaptations such as tube building, burrowing, or motility rather than feeding. It was obvious that most of the variables found to explain the species assemblage suggested indirect effects. For instance, forward selection identified temperature and pH and silicate and nitrate for the wet and dry season, respectively, as significant sole predictors of species dynamics. This not only reflects specific seasonal differences in species dominance and key environmental variables, but also shows that aquatic primary productivity could play a role in macrobenthic species assemblage. Water temperature and pH have been found to correlate with the abundance of bacterioplankton (i.e., primary producer) in lagoons (Carvalho et al. 2003). Agyekumhene (2004) demonstrated that nitrate, turbidity, phosphate, silicate, and to a limited extent, water temperature largely influenced seasonal and spatial patterns in water column chlorophyll concentrations (essential component in primary productivity) in the Keta lagoon. Furthermore, there is a coupling between primary productivity and the abundance of macrobenthic organisms in lagoons (Alongi 1990; Mistri et al. 2001). This may suggest ecological relationships between environmental variables, phytoplankton primary productivity, and abundance of macrobenthic fauna in Keta lagoon.

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