Transitional Waters Bulletin
TWB, Transit. Waters Bull. 1(2008), 13-30
ISSN 1825-229X, DOI 10.1285/i1825229Xv2n1p13
http://siba2.unile.it/ese/twb

RESEARCH ARTICLE

Abiotic and biotic patterns across Mediterranean coastal wetland systems, North East Aegean, Greece

Dikou A*, Dinapoya V, Evaggelatou K, Lambrianidis E, Troumbis A

Dept. of Environment, University of the Aegean, Mytilene 81100, Greece
*Corresponding author: Dikou A., tel: +30 24210 93259, fax: +30 24210 93157, e-mail: angeladikou@hotmail.com

Abstract

1 - Coastal wetlands are regarded as transitional ecosystems regulating fluxes of materials and energy between the land and the sea and are protected habitats under the NATURA 2000 European network of protected areas. Description of spatial heterogeneity in abiotic and biotic constituents of coastal wetland systems is a prerequisite for the establishment of long-term monitoring programs and a first step in elucidating their functional role in the landscape; both of particular significance to management. Spatial variability of water and substratum physicochemical variables and of substratum macroinvertebrate fauna composition and abundance across five sea-coastal wetland-land systems, Kalloni bay, Lesvos Island, Greece, were quantified during the growing season of 2005.

2 - The studied coastal wetlands develop on an alluvial flat plain of mineral soils as indicated by low values of percent organic matter, circumneutral pH, and high values of bulk density. Trends in physicochemical variables of substratum varied among the five coastal wetland systems studied even when the same variable was examined. Canonical discriminant analysis indicated that the most important substratum physicochemical variable in differentiating among the sea-wetland-land units of the studied gradients was electrical conductivity (salt influence) in four out of the five coastal wetland systems. Total nitrogen concentration of substratum was the only variable among the ones studied which was related positively either with total phosphorus concentration or/and percent organic matter of substratum in all wetland systems studied; the highest values occurred where vegetation was present.

3 - Distribution and abundance of substratum macroinvertebrate taxa across the sea-wetland-land gradients studied reflected the interaction between the marine and terrestrial environment. Gasteropoda, bivalvia and schaphopoda were found in higher abundances at sea and sea-influenced stations, which gradually decreased towards the land. On the other hand, insecta appeared at stations further away from the shore and their abundance progressively increased towards land. Gasteropoda and insecta were the taxa responsible for the identification of at least three clusters of stations across all five coastal systems studied. Two clusters contained clearly "terrestrially-influenced" or "sea-influenced" stations while intermediate clusters contained stations with varying degree of salt influence.

4 - Distribution and abundance of gasteropoda and insecta, however, were found to be directly related to nutrient status and not to electrical conductivity of substratum.

Keywords: transitional coastal wetlands, Mediterranean, physical and chemical gradients, macroinvertebrate gradients.

Introduction

Coastal wetlands (estuaries, saltmarshes, and coastal lagoons) are regarded as transitional ecosystems (Mitch and Gosselink, 2000) and as critical transitional zones (Levin *et al.*, 2001) between the land and the sea. Although, they are generally small in size compared to the size of the catchment areas they are embedded, their niche in the landscape enables them unique contribution to habitat, species and genetic diversity, regulation of fluxes of materials between the terrestrial and the marine environment, and coastal defense (Boorman, 1999). These attributes are, in turn, responsible for economically valued environmental services, such as high biological production, provision of nursery and spawning grounds, and assimilation of nutrients and toxins (Valiela *et al*., 2004). The provision of these environmental services is threatened given the world-wide trend of loss and/or degradation of coastal wetlands through reclamation, filling, and sediment-interception and the uncertainties involved with climate change, such as sea level rise and alteration in precipitation patterns (Levin *et al*., 2001; Adam, 2002; Valiela *et al*., 2004; Lotze *et al*., 2006).

Numerous studies on the ecology of coastal wetlands have demonstrated zonation patterns in plant and sediment-associated macroinvertebrate communities that seem to be dictated by abiotic factors, such as frequency and degree of inundation, or else elevation, and salinity (Netto and Lana, 1997; Sanchez *et al*., 1998; Ungar, 1998; Tagliapetra *et al*., 2000; Álvarez Rogel *et al*., 2001; Bockelmann *et al*., 2002; Irmler *et al*., 2002; Ross *et al*., 2003; Pennings *et al*., 2005; Silvestri *et al*., 2005), biotic interactions, such as competition, synergy, and positive interactions (Callaway and Pennings, 1998; Levine *et al*., 1998; Emery *et al*., 2001; Pennings *et al*., 2005), anthropogenic affects, such as livestock grazing (e.g. Andersen *et al*., 1990) and alterations in the hydrological regime (e.g. de Leeuw *et al*., 1995; Seys *et al*., 1995; Kingsford, 2000).There are few studies on the transition zones between coastal wetlands/uplands (Álvarez Rogel *et al*., 2001; Traut, 2005) and coastal wetlands/oceans (Cardinale *et al*., 1998; Lefeuvre *et al*., 2000).

Description of spatial heterogeneity in abiotic and biotic constituents of coastal wetlands is a prerequisite for the establishment of long-term monitoring programs and a first step in elucidating their functional role in the landscape; both of particular significance to management. In order to account for their transitional role in the landscape, however, management at spatial scales larger than those defined by the physical boundaries of salt marshes has been advocated (Whigham *et* al., 1988). Furthermore, differences in floristic composition and in flooding regime of coastal wetlands from different geographic regions make difficult the comparison or/and adoption of results of studies from different regions (e.g. North America vs. Europe see Lefeuvre et *al*., 2000). Coastal wetlands in the Mediterranean are protected habitats under the NATURA 2000 network of protected areas. To our knowledge, there has been as yet no published work on the structure or/and function of an entire gradient encompassing the marine, the coastal wetland and the land component, named heteroforth the coastal wetland system, in the Mediterranean.

This study aims to describe spatial distribution of environmental variables and macrofauna along a sea-coastal wetland-land gradient and to describe the repeatability of patterns across five coastal wetland systems in North East Aegean utilizing transects that originate at sea, intersect coastal wetlands, and end up on land. Specifically, we aimed at: (i) describing the spatial distribution of water, substratum, and macrofauna and (ii) determining their utility in discriminating among the sea, coastal wetland, and land components of the five coastal wetland systems studied.

Methods

Study Sites

We studied five wetlands within the coast of Kalloni bay (560 km^2 catchment area): Apothika estuarine lagoon (1.38 km^2; 6.2 km^2 catchment), Parakoila swamp (0.18 km^2; 1.2 km^2 catchment), Kalloni salt meadows (0.5 km^2; 15.8 km^2 catchment), Vouvaris estuarine lagoon (0.08 km^2; 25.3 km^2 catchment), and Polihnitos salt pan (1.2 km^2; 3.7 km^2) (Fig. 1). These wetlands were selected because they were in relatively pristine condition, easily accessible, and of manageable size. The coast of Kalloni bay constitutes an ecological network of wetlands. It has been incorporated into the European Network of protected areas Natura 2000 (GR4110004; Mandylas and Kardakari, 1998), the list of CORINE biotopes, the list of important areas of avian fauna of Greece (SPPE), and the 20 national Ecological Hot Regions (Hotspots) for avian fauna (Troumbis and Dimitrakopoulos, 1998).

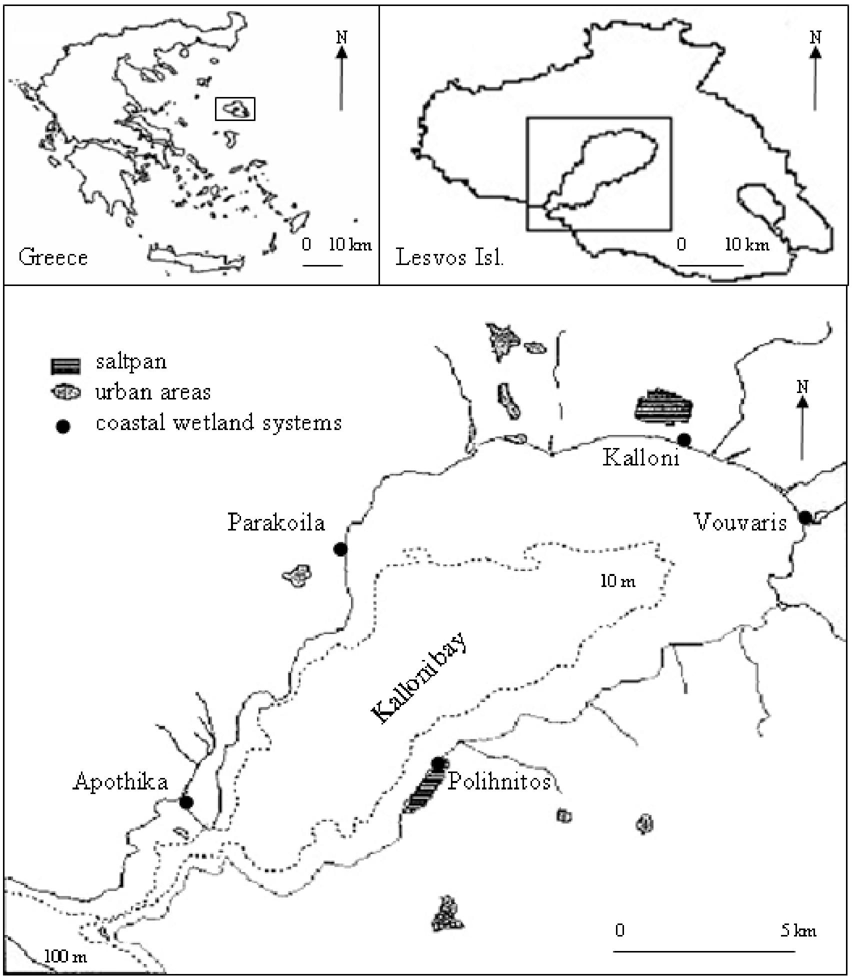

Figure 1. Location of the five studied coastal wetland systems of Kalloni bay, Lesvos Island, Greece.

Anthropogenic pressures in the coastal area of Kalloni bay include: partial drainage of wetlands, fragmentation of biotopes, illegal construction in swamps, sand extraction, sewage and olive presses' discharge in torrents, unauthorized disposal of solid waste, grazing, and illegal hunting.

Sampling

In each wetland, sampling took place along transects that originated from the sea and reached the land. All transects were perpendicular to the coastline. Stations were placed 50 m apart along each transect. There were 12, 11, 9, 8 and 6 stations (S) at Apothika, Parakoila, Kalloni, Polihnitos and Vouvaris, respectively. The first station (S0) was always at sea and the last station was always on land. Sampling took place in March 2005.

At each station, 5 surface (0-2 cm) substratum samples were scooped, dried in room temperature, crashed and sieved through 2mm mesh size siever. These samples were used to determine Bulk Density (BD), Electrical Conductivity (EC), pH, Total Phosphorus (TP), Total Nitrogen (TN), and percent Organic Matter (OM). Bulk density is a structural property of the substratum expressed as the weight of soil per unit volume. It gives an indication of the porosity of the soil medium. Pores affect the ability of soils to support plant, animal and microbial life. Spaces hold water and allow drainage, entry of O_2 and removal of CO_2 from the soil, roots and fauna to penetrate, and microbes to decompose. Electrical conductivity and pH are chemical properties of the substratum. Electrical conductivity measures the sum of anions and cations and is the net result of many hydrodynamic factors, including tides, rainfall, freshwater and groundwater inputs. Substratum pH is a measure of soil acidity. Soil pH most markedly affects plant growth through control of nutrient availability and also the major groups of soil decomposing fauna. Total nitrogen concentration, total phosphorus concentration, and percent organic matter are properties of nutrient status of substratum. The organic matter content of the soil, which consists of plant, animal and microbial residues at various stages of decay, represent the dominant source of microbial nutrition. During decomposition of organic matter by micro-organisms, plant nutrients are liberated in forms which can readily be absorbed by plants. Thus, many plant nutrients, particularly nitrogen, phosphorus and sulphur, are involved in cycles from decaying plant and animal debris, through soil organic matter and back to the plant. All soil properties were assessed in the aerobic/oxidized surface layer (0-2cm). Electrical conductivity and pH were measured in saturated solutions of 1:5 soil to water ratio, after centrifugation and filtration through 47 mm filters, with the use of a portable electrometric unit Consort 932. Total phosphorus concentration was measured using Olsen's method (Olsen *et al.*, 1954). Total nitrogen concentration was measured using wet Kendjal's method (Bremner and Mulvaney, 1982). Percent organic content was measured with the method of wet oxidation. Bulk density of substratum samples (n=5 at each station) was measured after drying at 100^0 C for 24 hours of steady sample volume (40.10 cm^3; brass ring liner of core sampler), weighting, and dividing their weight by the steady volume.

At each station, measurements of water Temperature (T), Dissolved Oxygen (DO), pH, and Electrical Conductivity (EC) were obtained with a portable electrometric unit Consort 932.

At each station, another 5 surface (0-2 cm) substratum samples of 250 cm^3 each were scooped and placed in self-sealing plastic bags. They were then left to dry at room temperature, crashed and examined using magnifying lenses for the presence of macroinvertebrates (whole individuals or parts of them). Animals were stored in vials containing ethanol, sorted, identified and counted. Substratum macroinvertebrates were classified at class level.

Statistical analysis

Relationships among water and substratum properties were explored using Spearman correlations (r_s). A one-way Multivariate Analysis of Variance (MANOVA; Huberty, 1994; Hair *et al.*, 1998; Tabachnick and Fidell, 2000) was employed to test the equality among stations at each wetland of vectors (means) of the six substratum variables after transformations. Standard (with all dependent variables entered simultaneously), one-way (between subjects, linear) Discriminant function Analysis (DA) was carried out for each wetland (i.e. analysis of main effects) to: (i) evaluate station differences based on Wilk's lambda (StatSoft, 1996), and (ii) assess the contribution of each dependent variable in differentiating among sites based on a potency index (Hair *et al.*, 1998); a relative measure, which includes both the contribution (correlation) of a variable in a discriminant function (its discriminant loading) and the relative contribution of the function to the overall solution (a relative measure among the eigenvalues of the functions).

Numerical abundance of substratum macroinvertebrate fauna at class level was analyzed using multivariate techniques. Dissimilarity matrices based on Bray-Curtis dissimilarity index were calculated using raw data. The dissimilarity matrices were then used as a basis to group successive stations into clusters using Hierarchical Agglomerative Clustering. Taxa responsible for the dissimilarity between clusters were identified using SIMPER. Dissimilarity matrices, Hierarchical Agglomerative Clustering and SIMPER were performed using the PRIMER software package (Clarke and Warwick, 2001).

Relationships among physicochemical variables of substratum and abundances of macroinvertebrate taxa were explored with Spearman correlations.

Table 1. Variation in water variables across the five coastal wetland systems studied. T: temperature (^{0}C); EC: electrical conductivity (mS/cm); DO: dissolved oxygen (mg/lt).

			STATIONS											
		Variables	S0	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11
WETLANDS	Apothika	T	14.8	-	20.8	21.6	-	21.4	10.0	10.8	14.0	15.0	19.0	15.0
		pH	8.1	-	9.1	8.8	-	9.1	8.3	8.1	6.8	8.8	8.0	7.9
		EC	37.6	-	30.8	32.0	-	1.8	0.6	4.9	0.0	0.2	0.2	0.2
		DO	6.2	-	8.0	8.4	-	9.3	6.4	5.6	3.6	3.7	3.3	3.2
	Parakoila	T	14.5	-	18.4	18.4	17.6	18.8	19.3	13.1	10.8	11.3	-	
		pH	8.1	-	8.0	8.2	8.1	8.1	8.0	7.2	6.6	6.5	-	
		EC	56.7	-	16.1	15.6	15.1	13.8	0.0	0.5	0.4	0.3	-	
		DO	11.2	-	9.4	9.2	10.3	11.00	12.0	9.5	4.2	5.4	-	
	Kalloni	T	15.8	-	-	23.0	25.5	26.4	-	22.1	16.7			
		pH	8.3	-	-	8.4	9.5	9.2	-	9.2	7.3			
		EC	53.7	-	-	4.3	6.0	5.4	-	3.1	2.9			
		DO	13.5	-	-	11.3	11.3	11.4	-	10.9	10.1			
	Polihnitos	T	15.0	19.1	-	-	-	-	-	-	-			
		pH	8.3	9.4	-	-	-	-	-	-	-			
		EC	55.7	16.8	-	-	-	-	-	-	-			
		DO	8.4	7.9	-	-	-	-	-	-	-			
	Vouvaris	T	14.3	14.0	-	23.6	-	-						
		pH	8.2	8,3	-	8.6	-	-						
		EC	23.6	14.4	-	13.1	-	-						
		DO	10.9	10.1	-	11.6	-	-						

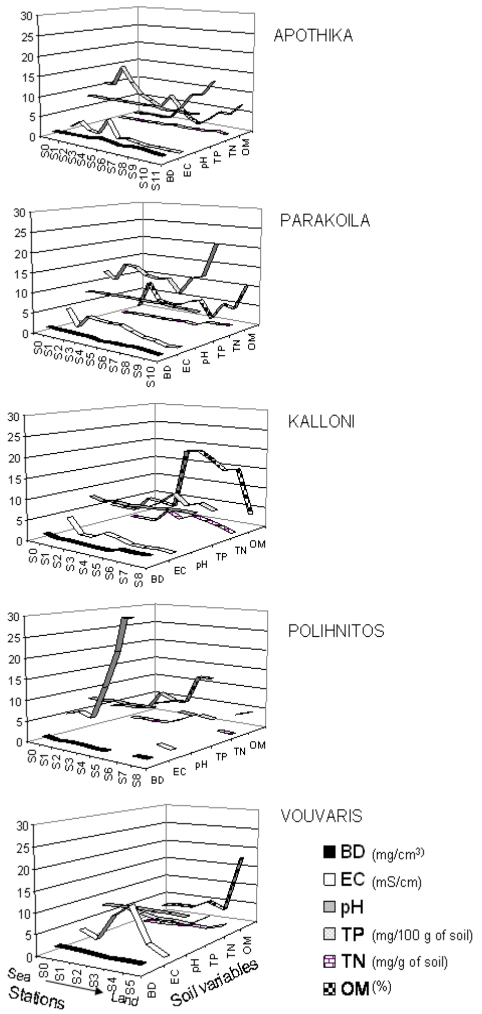

Figure 2. Variation in substratum physicochemical variables across the five coastal wetland systems studied during March 2005. BD: bulk density in mg/cm^3; EC: electrical conductivity in mS/cm; TP: total phosphorous in mg/100 gr of soil; TN: total nitrogen in mg/gr of soil; OM: percent organic matter. Stations (S) are 50 m apart across each gradient from sea towards land.

Results

Physicochemical variables of water and substratum

Trends in physicochemical variables of water were uniform among the coastal wetland systems studied (Tab. 1). Stations within the wetland portion of all five coastal wetland systems studied showed higher temperatures compared to the seaward stations. Alkaline conditions prevailed within wetland stations compared to conditions closer to neutral at landward stations. Dissolved oxygen seemed to increase within wetland stations compared to seaward and landward stations. Electrical conductivity showed the highest values at seaward stations, decreased towards wetland stations and obtained the lowest values at landward stations.

In contrast, trends in substratum physicochemical variables varied among the coastal wetland systems studied (Fig. 2). Bulk density seemed to increase within wetland stations at Apothika compared to seaward and landward stations; the reverse trend appeared in the other four coastal wetland systems. Salt influence varied at stations within wetlands. Thus, hypersaline conditions prevailed within Polihnitos saltpan and Vouvaris estuarine lagoon; mild saline conditions appeared within Parakoila and Apothika; the influence of salt within Kalloni salt meadow appeared incremental. Alkaline conditions prevailed across all wetland systems studied with values varying slightly above and below pH=8. Total phosphorous concentration showed peaks at ecotonal stations between the sea and the wetland and between the wetland and the land of Apothika and Parakoila and reached highest values at land stations. It showed higher concentrations within wetland stations of Parakoila and Kalloni and lower concentrations within wetland stations of Vouvaris compared to seaward and landward stations. Total nitrogen concentration gradually increased from the sea, across the wetland and towards the land stations of Apothika, Parakoila and Vouvaris. It exhibited higher concentrations, however, within wetland stations of Kalloni and Polihnitos compared to seaward and landward stations. Percent organic matter gradually increased from the sea, across the wetland and towards the land stations of Apothika, Parakoila and Vouvaris. It showed

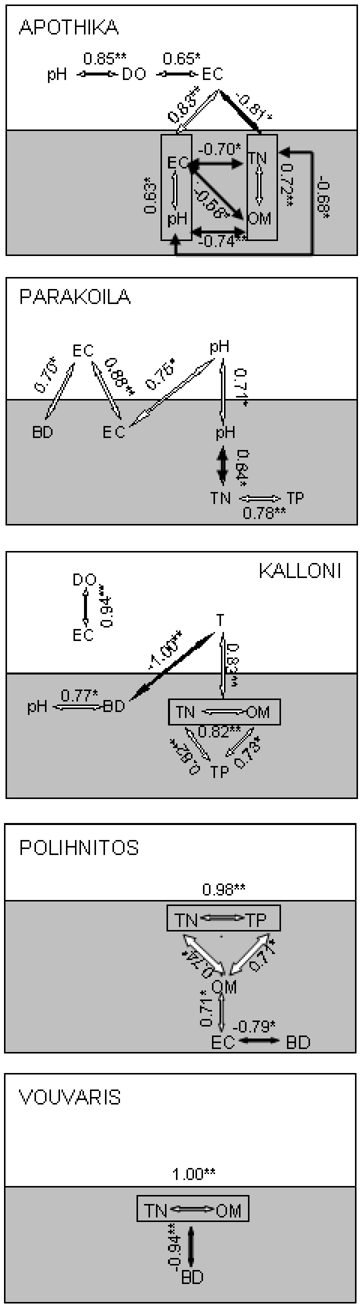

Figure 3. Schematic representation and values of the significant Spearman correlations between water and substratum physicochemical variables across the five studied coastal wetland systems. Apothika, substratum-substratum relationships n=12, substratum-water relationships n=10, water-water relationships n=10; Parakoila, substratum-substratum relationships n=11, substratum-water relationships n=9, water-water relationships n=9; Kalloni, substratum-substratum relationships n=9, substratum-water relationships n=6, water-water relationships n=6; Polihnitos, substratum-substratum relationships n=8; Vouvaris, substratum-substratum relationships n=6. BD: bulk density in mg/cm^3; EC: electrical conductivity in mS/cm; TP: total phosphorous in mg/100 gr of soil; TN: total nitrogen in mg/gr of soil; OM: percent organic matter; T: temperature; DO: dissolved oxygen. White arrows: positive relationships; black arrows: negative relationships; white background: water; grey background: soil. *: significant at p=0.05; **: significant at p=0.01.

Table 2. Summary results of linear discriminant function analysis of transformed physicochemical variables of substratum for the five studied coastal wetland systems. Substratum variables as described in Figure 2.

Variable	Wilk's lambda	Partial lambda	F-remove	p-level	Tolerance
(Apothika) Wilks' Lambda: 0.00027, approximate F (66, 203)=11.226, p<0.0001					
BD	0.001	0.465	3.868	0.0009	0.885
1/sqrt(EC)	0.002	0.124	23.633	0.0001	0.962
pH^3.046	0.001	0.514	3.177	0.0041	0.868
Sqrt(TP)	0.001	0.220	11.948	0.0001	0.934
log(TN)	0.001	0.248	10.167	0.0001	0.807
OM^0.456	0.001	0.379	5.520	0.0001	0.844
(Parakoila) Wilks' Lambda: 0.00001 approximate F (60, 193)=23.833 p<0.0001					
BD	0.001	0.317	7.750	0.0001	0.799
sqrt(EC)	0.001	0.154	19.786	0.0001	0.813
arcsin(pH)	0.001	0.213	13.322	0.0001	0.840
log(TP)	0.001	0.488	3.777	0.0015	0.797
log(TN)	0.001	0.067	49.773	0.0001	0.793
sqrt(OM)	0.001	0.121	26.120	0.0001	0.725
(Kalloni) Wilks' Lambda: 0.00400 approximate F (48, 156)=6.7598 p< 0.0001					
BD	0.007	0.546	3.221	0.0088	0.973
arcsin(EC)	0.017	0.227	13.185	0.0001	0.829
arcsin(pH)	0.008	0.469	4.390	0.0012	0.833
TP	0.009	0.454	4.663	0.0008	0.920
arcsin(TN)	0.005	0.815	0.879	0.5445	0.907
OM	0.009	0.443	4.871	0.0006	0.948
(Polihnitos) Wilks' Lambda: 0.00476 approximate F (42, 130)=6.5882 p<0.0001					
BD	0.011	0.443	4.841	0.0012	0.776
log(EC)	0.017	0.276	10.110	0.0001	0.857
pH	0.009	0.526	3.476	0.0087	0.948
TP	0.009	0.544	3.237	0.0126	0.751
log(TN)	0.011	0.458	4.561	0.0018	0.592
log(OM)	0.009	0.528	3.450	0.0091	0.552
(Vouvaris) Wilks' Lambda: 0.00267 approximate F (30, 66)=7.4797 p< 0.0001					
BD	0.012	0.224	11.099	0.0001	0.588
log(EC)	0.016	0.167	15.929	0.0001	0.667
pH	0.007	0.389	5.0280	0.0059	0.731
TP^0.223	0.004	0.591	2.218	0.1031	0.852
arcsin(TN)	0.003	0.790	0.851	0.5337	0.805
log(OM)	0.006	0.438	4.100	0.0138	0.757

highest values, however, within wetland stations of Kalloni and Polihnitos.

The nodal factor determining the chemistry of water and substratum at Apothika was electrical conductivity (Fig. 3). Electrical conductivity of water correlated positively and significantly with dissolved oxygen of water, electrical conductivity and pH of substratum and negatively and significantly with total nitrogen and organic matter of substratum. In substratum, electrical conductivity correlated significantly and positively with pH and significantly and negatively with total nitrogen and organic matter. At Parakoila, pH of water appeared the nodal factor linking water to substratum properties (Fig. 3). Water pH correlated positively with electrical conductivity and pH of substratum. Water temperature linked water with substratum properties at Kalloni (Fig. 3); it correlated negatively with bulk density, total nitrogen and organic matter of substratum. In the substratum of all wetland systems studied, total nitrogen concentration showed positive and significant correlations with either organic matter or total phosphorus

Table 3. Potency index based on potency values of the first two discriminant functions of substratum variables at each studied coastal wetland system. Substratum variables explained in Figure 2.

Soil variables*	WETLANDS				
	Apothika	Parakoila	Kalloni	Polihnitos	Vouvaris
BD	0.028	0.012	0.152	0.100	0.090
EC	0.643	0.082	0.170	0.350	0.194
pH	0.045	0.034	0.137	0.013	0.088
TP	0.186	0.008	0.109	0.037	0.033
TN	0.006	0.379	0.003	0.088	0.001
OM	0.004	0.122	0.152	0.054	0.075

*transformations of variables are presented in Table 2

concentration or both of them.

Means of the six transformed substratum variables differed across the stations of Apothika (Wilk's Lambda=0.000; $p<0.001$), Parakoila (Wilk's Lambda=0.000; $p<0.001$), Kalloni (Wilk's Lambda=0.000; $p<0.001$), Polihnitos (Wilk's Lambda=0.001; $p<0.001$), and Vouvaris (Wilk's Lambda=0.003; $p<0.001$) coastal wetland systems. Summary results of discriminant function analyses for each coastal wetland system studied showed that all six variables examined contributed significantly to the discrimination among stations at all five coastal wetland systems except total nitrogen concentration at Kalloni and total phosphorous concentration, total nitrogen concentration and percent organic matter at Vouvaris (Tab. 2). It is worth noting that in all five linear discriminant models, all six variables showed high values of tolerance denoting large contribution of unique information by each variable or low colinearity among variables. Yet, potency index values (Tab. 3) indicated that electrical conductivity was the most important variable in discriminating among stations within four of the five studied coastal wetland systems, i.e. Apothika, Kalloni, Polihnitos and Vouvaris. Total nitrogen concentration appeared the most important discriminatory variable among stations at Parakoila. The second, most important variable in discriminating among stations was bulk density at Kalloni, Polihnitos and Vouvaris, and total phosphorus and organic matter at Apothika and Parakoila, respectively.

Distribution and abundance of substratum macroinvertebrates

Twelve macroinvertebrate classes were identified in surface substratum samples from the five studied coastal wetland systems, namely gasteropoda, bivalvia, scaphopoda, polyplacophora, polychaeta, oligochaeta, crustacea, insecta (discriminated into mature and immature individuals), arachnida, echinoidea, asteroidea, and anthozoa. Generally, there was apparent dominance of gasteropoda at seaward stations and of insecta at landward stations across all five sea-wetland-land transects (Fig. 4). At Apothika, gasteropoda dominated with progressively reduced abundances the first six stations (0-250m); oligochaeta and insecta (including larvae) prevailed at the rest six stations in far lower abundances, however, compared to those of gasteropoda. At Parakoila, marine gasteropoda dominated the first station (0 m) while insecta prevailed with fluctuating abundances at all other stations (50-450m) but the last one (500 m), where land gasteropoda was the most abundant taxon. At Kalloni, the first station (0 m) showed comparable abundances of gasteropoda and bivalvia, which were considerably lower than those of the equivalent stations at all other wetland systems. All stations of Kalloni (0-400m) contained insecta, which abundance peaked at intermediate stations within the gradient. At Polihnitos, all stations (0-400m) and

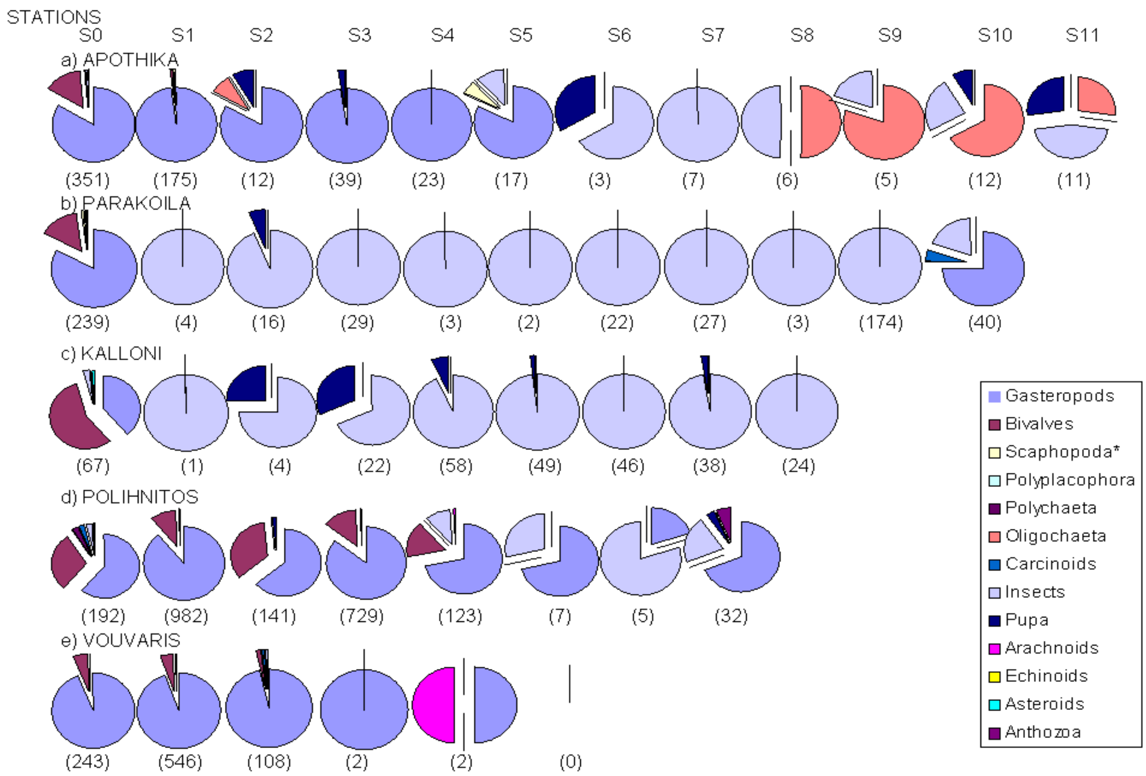

Figure 4. Variation in substratum macroinvertebrates abundance across the five studied coastal wetland systems during March 2005. Total number of macroinvertebrates encountered in 5 samples (250 cm^3 volume each) at each station (S) is noted inside parenthesis.

the first four stations (0-150m) contained gasteropoda and bivalvia, respectively, at fluctuating abundances. Insecta (either adults or immature individuals) were encountered at all stations but at far lower abundances compared to gasteropoda and bivalvia. At Vouvaris, the first three stations (0-100m) were dominated by gasteropoda, which abundance was considerably higher than that of bivalvia and scaphopoda. Abundances of gasteropoda and crustacea were very low at the next two stations (150-200m) while no invertebrate was encountered at the last station (250m). Insecta were found in very low abundance only at the third station (100m).

Also, there was a trend of decreasing total abundance of macroinvertebrates from the sea and towards the land although exact patterns differed across the five sea-wetland-land gradients (Fig. 4). At Apothika and Vouvaris there was a sharp decline in substratum macroinvertebrates abundance after the first stations (0-50m) while their abundance remained low at all other stations. At Polihnitos, there were large variations in substratum macroinvertebrates abundance within the first five stations (0-200m) while abundances remained low at the rest stations. At Parakoila there was a sharp decline in substratum macroinvertebrates abundance after the first station (0m), it remained low within wetland stations (50-400m) and gained higher values at the three last terrestrial stations (450-550m). At Kalloni there was a sharp decline in substratum macroinvertebrates abundance after the first station (0m), which gradually gained higher values and

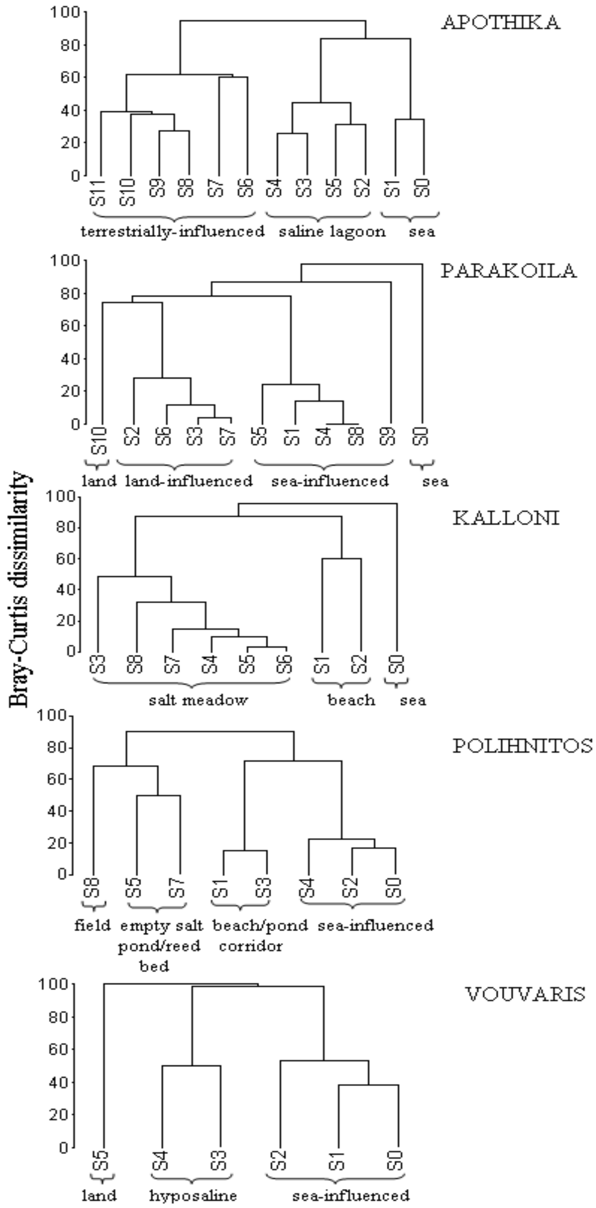

Figure 5. Results of group-average clustering based on a ranked Bray-Curtis dissimilarity matrix of the abundance of substratum macroinvertebrate taxa (n=5) across the five studied coastal wetland systems.

peaked at the fifth station (200m), after which it declined smoothly till the last station (250-400m). The highest and the lowest total macroinvertebrates abundances were found at Polihnitos and Kalloni systems, respectively.

Successive stations across the sea-wetland-land gradients of Apothika, Kalloni and Vouvaris were grouped in three clusters while successive stations across the sea-wetland-land gradients of Parakoila and Polihnitos were grouped in five and four clusters, respectively (Fig. 5). In almost all cases, stations within a cluster exhibited more than 50% similarities in taxa composition and abundance. In all cases, there were two

Table 4. Results of similarity percentages ( ) among stations { } within a cluster (C), dissimilarity percentages [ ] among clusters, and % substratum macro-invertebrate taxa contributions among clusters, composed of one or more stations across the five coastal wetland systems studied.

			CLUSTERS			
			C1	C2	C3	C4
WETLANDS	Apothika	C1 {S0,S1} (65.78)				
		C2 {S2-S5} (60.57)	GAST: 89.58 BIV: 8.79 [83.62]			
		C3 {S7-S11} (48.13)	GAST: 88.83 BIV: 7.72 [99.30]	GAST: 72.97 INS: 11.86 OLIG: 10.86 [92.74]		
	Parakoila	C1 {S0}				
		C2 {S1,S4,S5,S8} (83.02)	GAST: 81.82 BIV: 15.29 [100.0]			
		C3 {S2,S3,S6,S7} (81.31)	GAST: 75.46 BIV: 14.10 [100.0]	INS: 98.28 [76.56]		
		C4 {S9}	GAST: 47.94 INS: 42.13 [100.0]	INS: 100.0 [96.61]	INS: 99.83 [76.58]	
		C5 {S10}	GAST: 76.71 BIV: 16.89 [78.49]	GAST: 81.06 INS: 13.54 [86.10]	GAST: 63.71 INS: 31.44 [74.64]	INS: 83.84 GAST: 15.15 [92.52]
	Kalloni	C1 {S0}				
		C2 {S1,S2} (40.00)	BIV: 57.15 GAST: 39.10 [95.71]			
		C3 {S3-S8} (70.47)	BIV: 37.68 INS: 33.32 GAST: 25.78 [96.19]	INS: 92.87 [87.94]		
	Polihnitos	C1 {S0, S2, S4} (79.18)				
		C2 {S1,S3} (84.75)	GAST: 90.04 [71.42]			
		C3 {S5,S7} (50.0)	GAST: 64.79 BIV: 28.11 [94.55]	GAST: 87.40 BIV: 12.27 [98.88]		
		C4 {S8}	GAST: 58.79 BIV: 32.14 [71.74]	GAST: 86.80 BIV: 12.50 [94.30]	GAST: 79.31 INS: 16.53 [66.80]	
	Vourvuris	C1 {S0,S1,S2} (51.47)				
		C2 {S3,S4} (50.00)	GAST: 94.95 [98.50]			
		C3 {S5}	GAST: 94.95 [100.0]	GAST: 75.00 ARACH: 25.00 [100.0]		

Table 5. Results of Spearman rank correlations of gasteropoda (a) and insecta (b) abundances with substratum physicochemical variables across the five coastal wetland systems. Number of stations in parenthesis. Substratum variables explained in Figure 2.

a) gasteropoda abundance

Wetland	BD	EC	pH	TP	TN	OM
Apothika (n=12)	0.34	0.28	0.85*	0.10	-0.75*	-0.45
Parakoila	-	-	-	-	-	-
Kalloni	-	-	-	-	-	-
Polihnitos (n=8)	-0.05	0.50	0.52	-0.62	-0.36	0.38
Vouvaris (n=6)	-0.08	0.09	0.71	-0.31	-0.89*	-0.89*

b) insects abundance

Wetland	BD	EC	pH	TP	TN	OM
Apothika (n=12)	-0.66*	-0.36	-0.52	0.01	0.43	0.53
Parakoila (n=11)	0.29	-0.08	-0.04	0.46	0.20	-0.07
Kalloni (n=9)	-0.45	0.57	-0.72*	-0.07	0.78*	0.48
Polihnitos (n=8)	-0.28	-0.12	-0.71*	0.39	-0.06	-0.16
Vouvaris	-	-	-	-	-	-

*all correlations significant at p=0.05

antipode clusters of stations corresponding to the marine (“sea”) and the terrestrial (“land”) environments and one or more clusters of stations with varying influence of salinity in between. Gasteropoda, insecta, and bivalvia were primarily responsible for differentiating among successive clusters in 8, 4 and one pair-wise comparisons, respectively, of a total of 13 pair-wise comparisons of clusters across the five sea-wetland-land gradients based on their absolute abundances (Tab. 4). Specifically, gasteropoda was the most important taxon in differentiating among clusters of Apothika, Polihnitos and Vouvaris; gasteropoda and insecta were primarily responsible for differentiating among clusters of Parakoila; bivalvia, gasteropoda and insecta were the taxa responsible for differentiating among clusters of Kalloni (Tab. 4).

Substratum physicochemical variables and macroinvertebrates

The few significant correlations established among substratum physicochemical variables and either gasteropoda or insecta abundances differed among the five sea-wetland-land gradients studied (Tab. 5). Thus, gasteropoda abundance was positively related with pH and total phosphorus concentration at Apothika and negatively related with total nitrogen concentration at Apothika and Vouvaris. On the other hand, insecta abundance was positively related with total nitrogen concentration at Kalloni and negatively related with bulk density at Apothika and with pH at Kalloni and Polihnitos.

Discussion

The studied wetlands develop on an alluvial flat plain of mineral soils as indicated by low values of percent organic matter, circumneutral pH, and high values of bulk density (Mitch and Gosselink, 2000). Trends in physicochemical variables of substratum varied among the five sea-wetland-land gradients even when the same variable was examined. Thus, there were increased values of bulk density at Apothika, electrical conductivity at Apothika, Polihnitos and Vouvaris, pH at Parakoila, Polihnitos, and Vouvaris, total phosphorus concentration at Kalloni and Polihnitos, total nitrogen concentration at Kalloni and Polihnitos, and percent organic matter at Kalloni and Polihnitos within wetland stations compared to seaward and landward stations. The reverse trend was exhibited by bulk density at Parakoila, Kalloni, Polihnitos and Vouvaris, pH at Kalloni, total phosphorus concentration at Apothika, Parakoila, and Vouvaris, and percent organic matter at Parakoila. A gradual decrease from seaward towards landward stations was shown by pH at Apothika and electrical conductivity at Parakoila and Kalloni. A gradual increase from seaward towards landward stations was shown by nitrogen concentration at Apothika, Parakoila and Vouvaris, and percent organic matter at Apothika. A similar trend was shown by percent total nitrogen with distance inland from tidal stream in a Louisiana salt marsh, USA (Buresh et al., 1980 in Mitsch and Gosselink, 2000). However, there were no unimodal and apparently inconsistent trends in total nitrogen concentration (gr/kg) across two gradsects extending from the lagoon towards land at La Mata salt marsh, Spain (Álvarez Rogel *et al*., 2001). The coastal marsh/upland zones in the Pt Reyes area, California, USA, had greater total nitrogen concentrations than the adjacent upland (Traut, 2005). In coastal wetlands of Saginaw Bay, Lake Huron, USA, there have been documented gradual reductions in turbidity, dissolved oxygen, and pH with distance from the open water/wetland edge (Suzuki *et al*., 1995).

The aforementioned spatial patterns may give an indication of the functional role of the studied wetlands in the landscape. Kalloni and Polihnitos may function as "sinks" of nutrients and organic matter since the latter were found to accumulate at wetland stations. Apothika, Parakoila, and Vouvaris may function either as "exporters" or "transformers" of nutrients and organic matter since the latter did not appear to accumulate at wetland stations. Long-term studies of nutrients and organic matter budgets are necessary to confirm the functional role of these wetlands in the landscape taking under consideration factors such as wetlands' age, ecological maturity, runoff, human activities and coastal influence (Mitsch and Gosselink, 2000). A decadal study of organic matter and nutrient fluxes between saltmarshes and marine waters at Mont-Michel bay, northwest France, concluded that saltmarsh production enhances the production of the whole bay via export of organic matter; the same conclusion was reached for studied salt marshes in the Netherlands (Lefeuvre *et al*., 2000).

The correlations established among substratum variables revealed links among substratum structure, chemistry and production. Bulk density correlated with electrical conductivity, pH or nutrients concentration. Electrical conductivity was positively correlated with pH, which is related to redox-potential, availability of nutrients, and plant growth. It was also positively or negatively correlated with nutrients concentrations and/or organic matter. Similar with Polihnitos saltpan but contrary to Apothika estuarine lagoon, there was a strong and positive relationship (r_s=0.943, p=0.005; use of published data) between organic carbon (g/kg) and electrical conductivity at a coastal saltmarsh in Spain (Álvarez Rogel *et al*., 2001). It is possible that differences in slope and vegetation biomass may be responsible for differences in the direction of this relationship. The direction of this relationship may indicate differences in plant composition; positive direction indicating the presence of halophytes, which are well-adapted to salinity effects. Interdependence of nutrients and organic matter in the substratum of all five coastal wetland systems studied was apparent. Total nitrogen concentration of substratum developed positive relationships with either total phosphorus concentration or percent organic matter of substratum in all coastal wetland systems studied; high values of total nitrogen concentration coincided with the presence of vegetation. Positive correlations among total nitrogen, total phosphorus and percent organic matter may indicate that production is nitrogen limited and that the systems have poor imports and are basically self-sustaining.

The composition and abundance of substratum macroinvertebrate taxa across the sea-wetland-land gradients studied reflected the interaction between the marine and terrestrial environment. At sea and sea-influenced stations, groups, such as gasteropoda, bivalvia and schaphopoda, were found in higher abundances, which gradually decreased towards land. On the other hand, groups, such as insecta, appeared at stations further away from the shore and their abundances progressively increased towards land. No typical or exclusive wetland taxon existed. Similarly, Plum (2005) concluded in her review that there were no typical species found in substratum macroinvertebrate fauna of seasonal freshwater grasslands but only tolerant hydrophilous species. Generally, there was a trend of lower abundances of substratum macroinvertebrates within wetland compared to sea stations, probably due to numerical dominance of gasteropoda at seaward stations, and higher or comparable abundances of substratum macroinvertebrates within land compared to wetland stations across the five sea-wetland-land gradients.

Gasteropoda and insecta were the taxa responsible for the identification of at least three clusters of stations across all five sea-wetland-land gradients studied. Two clusters contained clearly "terrestrially-influenced" or "sea-influenced" stations while intermediate clusters contained stations with varying degree of salinity influence. Similarly, Tagliapetra *et al*. (2000) identified three different zones a "Landward Zone", a "Central zone", and a "Seaward Zone", according to the composition of macrobenthic communities at a shallow eutrophic saltmarsh pond located inside the Venetian lagoon, Italy. They noted that the features observed at the "Central Zone" and in part of the "Landward Zone" were typical of organically-enriched environments in contrast to those observed at the "Seaward Zone", which presented a higher diversity and a more balanced community. On the other hand, analyses of distribution of benthic macrofauna along an unvegetated tidal gradient in Paranagua Bay, Brazil, demonstrated that, despite its sediment homogeneity, the tidal flat was divided into a superior and an inferior zone, which were characterized by similar species composition but clearly distinct faunal densities (in Netto and Lana, 1997).

The most important substratum variable in discriminating among stations across the five coastal wetland systems was total nitrogen concentration at Parakoila and electrical conductivity at the other four systems studied. Yet, electrical conductivity of substratum was not directly correlated with abundance of either gasteropoda or insecta, which were the main taxa characterizing the marine and the terrestrial habitat, respectively, at any of the five sea-wetland-land gradients studied. Rather, the distribution of these taxa across the five sea-wetland-land gradients studied seems to be more directly dictated by other aspects of soil chemistry, such as pH, and by soil nutrients status.

The relative influence of marine processes on abiotic and biotic components of the five sea-wetland-land gradients studied may be reflected in variations of electrical conductivity and gasteropoda abundance. According to (i) the potency index values, (ii) the presence/absence and the significance of relationships of electrical conductivity with other substratum and/or water physicochemical variables, and (iii) the presence/absence and relative abundance of gasteropoda, the studied wetlands may be grouped with decreasing influence of salt as follows: Polihnitos and Apothika, which receive seawater directly and periodically; Vouvaris, which receives limited volume of seawater or less frequently; and Kalloni and Parakoila, which are influenced by brackish groundwater and salt infusion. On the other hand, the relative influence of terrestrial processes may be reflected in variations of total nitrogen, percent organic matter and insecta abundance.

Conclusions

The five coastal wetland systems of Kalloni bay studied during spring 2005 experience differential influence of salt, which, however, was shown to be the prevailing substratum property among the ones studied across wetland-land gradients.

Spatial distributions of nutrients and organic matter indicated that Kalloni salt meadows and Polihnitos salt pan may function as "sinks" while Apothika estuarine lagoon, Parakoila swamp and Vouvaris estuarine lagoon may function either as "exporters" or "transformers". Biological monitoring of these sea-coastal wetland-land gradients necessitates the use of both marine and land taxa, namely gasteropoda and insecta, whose distribution and abundance was directly related to nutrient status of substratum.

Acknowledgments

We would like to thank the Directors and staff of the Chemistry, Biology and Remote Sensing Laboratories of the Dept. of Environment, University of the Aegean for providing advice on materials and methods and space for the realization of this study. We would also like to thank Christoforos Mandylas for generously providing his work and study experience on Kalloni bay. The study was funded by EPEAEK II-PYTHAGORAS: Metro 2_6. Supporting Science Groups at Universities, Greek Ministry of Education and Religious Affairs and the European Union.

References

Adam P 2002. Saltmarshes in a time of change. *Environmental Conservation* **29**: 39-61. DOI: 10.1017/S0376892902000048.

Álvarez Rogel JA, Silla RO, Ariza FA 2001. Edaphic characterization and soil ionic composition influencing plant zonation in a semiarid Mediterranean salt marsh. *Geoderma* **99**: 81-98. DOI: 10.1016/S0016-7061(00)00067-7.

Andersen H, Bakker JP, Brongers M, Heydemann B, Irmler U 1990. Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* **89**: 137-148. DOI: 10.1007/BF00032166.

Bockelmann AC, Bakker JP, Neuhaus R, Lage J 2002. The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. *Aquatic Botany* **73**: 211-221. DOI: 10.1016/S0304-3770(02)00022-0.

Boorman LA 1999. Salt-marshes-present functioning and future change. *Mangroves and Salt Marshes* **3**: 227-241. DOI: 10.1023/A:1009998812838.

Bremner JM, Mulvaney CS 1982. Nitrogen – total. In Page AL (ed.), *Methods of Soil Analysis, Part 2*. American Society of Agronomy and Soil Science Society of America, Madison, 595–624.

Buresh RJ, Delaune RD, Patrick WH 1980. Nitrogen and phosphorus distribution and utilization by *Spartina alterniflora* in a Louisiana gulf coastal marsh. *Estuaries* **3 (2)**: 111-121. DOI: 0180-8347/80/02011 l-l 1 $01 SO/O.

Callaway RM, Pennings SC 1998. Impact of a parasitic plant on the zonation of two salt marsh perennials. *Oecologia* **114**: 100-105. DOI: 10.1007/s004420050425.

Cardinale BJ, Brady VJ, Burton TM 1998. Changes in the abundance and diversity of coastal wetland fauna from the open water/macrophyte edge towards shore. *Wetlands Ecology and Management* **6**: 59-68. DOI: 10.1023/A:1008447705647.

Clarke KR, Warwick RM 2001. *Changes in Marine Communities: an Approach to statistical analysis and interpretation*. Second edn, PRIMER-e, Plymouth, U.K.

De Leeuw J, de Munck W, Apon LP, Herman PMJ, Beeftink WG 1995. Changes in saltmarsh vegetation following the construction of the Oosterscheldt storm surge barrier. In McLusky DS (ed.) *Coastal Zone Topics: Process, Ecology and Management* 1, 35-40.

Emery NC, Ewanchuk PJ, Bertness MD 2001. Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology* **82 (9)**: 2471-2485. DOI: 10.1890/0012-9658(2001)082[2486:FAPPEO]2.0.CO;2.

Hair JF Jr, Anderson RE, Tatham RL, Black WC 1998. *Multivariate Data Analysis*. Fifth ed., Prentice-Hall Inc.

Huberty CJ 1994. *Applied Discriminant Analysis*. John Wiley and Sons Inc., New York, USA.

Irmler U, Heller K, Meyer, Reinke H-D 2002. Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the North and the Baltic Sea and the impact of the predicted sea level increase. *Biodiversity and Conservation* **11**: 1129-1147. DOI: 10.1023/A:1016018021533.

Kingsford RT 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology* **25**: 109-127. DOI: 10.1046/j.1442-9993.2000.01036.x.

Lefeuvre J-C, Bouchard V, Feunteun E, Grare S, Laffaille P, Rdureau A 2000. European salt marshes diversity and functioning: The case study of the Mont Saint-Michel bay, France. *Wetlands Ecology and Management* **8**: 147-161. DOI: 10.1023/A:1008440401950.

Levin L, Boesch D, Covich A, Dahm C, Erséus C, Ewel C, Kneib R, Moldenke A, Palmer M, Snelgrove P, Strayer D, Weslawski J 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* **4**: 430–451. DOI: 10.1007/s10021-001-0021-4.

Levine JM, Brewer JS, Bertness MD 1998. Nutrients, competition and plant zonation in a New England salt marsh. *Journal of Ecology* **86**: 285-292. DOI: 10.1046/j.1365-2745.1998.00253.x.

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* **312 (5781)**: 1806-1809. DOI: 10.1126/science.1128035.

Mandylas C, Kardakari N 1998. *Special Environmental Study: Conservation and promotion of wetlands of Kalloni bay, Lesvos Island- Part A*. Ministry of Environment and Public Works, Athens, Greece.

Mitsch JW, Gosselink G 2000. *Wetlands*. Third edn, John Wiley & Sons, New York, USA.

Netto SA, Lana PC 1997. Intertidal zonation of benthic macrofauna in a subtropical salt marsh and nearby unvegetated flat (SE, Brazil). *Hydrobiologia* **353**: 171-180. DOI: 10.1023/A:1003090701675.

Olsen SR, Cole CV, Watanabe FS, Dean LA 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. U.S. Dep. Agr. Circ. 939.

Pennings SC, Grant MB, Bertness MD 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *Journal of Ecology* **93**:159-167. DOI: 10.1111/j.1365-2745.2004.00959.x.

Plum N 2005. Terrestrial invertebrates in flooded grassland: a literature review. *Wetlands* **25 (3)**: 721-737. DOI: 10.1672/0277-5212-(2005)025[0721:TIIFGA]2.0.CO;2.

Ross MS, Reed DL, Sah JP, Ruiz PL, Lewin MT 2003. Vegetation: environment relationships and water management in Shark Slough, Everglades National Park. Wetlands *Ecology and Management* **11**: 291-303. DOI: 10.1023/B:WETL.0000005541.30283.11.

Sanchez JM, Otero XL, Izco J 1998. Relationships between vegetation and environmental characteristics in a salt-marsh system on the coast of Northwest Spain. *Plant Ecology* **136**: 1-8. DOI: 10.1023/A:1009712629733.

Seys J, Meire P, Loosen J, Craeymeersch J 1995. Long-term changes in the intertidal macrobenthos fauna at eight permanent sites in the Oosterschedlt: effects of the construction of the storm surge barrier – preliminary results. In McLusky DS (ed) *Coastal Zone Topics: Process, Ecology and Management* 1, 51-60.

Silvestri S, Defina A, Marani M 2005. Tidal regime, salinity and salt marsh plant zonation. *Estuarine, Coastal and Shelf Science* **62**: 119-130. DOI: 10.1016/j.ecss.2004.08.010

StatSoft Inc 1996. STATISTICA *for Windows* (Computer Program Mannual). Tulsa, OK, USA.

Suzuki N, Endoh S, Kawashima M, Itakura Y, McNabb CD, D'Itri FM, Batterson TR 1995. Discontinuity bar in a wetland of Lake Huron's Saginaw Bay. *Journal of Freshwater Ecology* **10**: 111-123. DOI: 10.1046/j.1440-1770

.2002.00202.x.
Tabachnick BG, Fidell LS 2000. Using Multivariate Statistics. Fourth edn, Allyn and Bacon, Boston, MA, USA.
Tagliapietra D, Pavan M, Wagner C 2000. Benthic patterns in a salt marsh basin: a snapshot of Palude della Rosa (Venetian Lagoon, Italy). *Wetlands Ecology and Management* **8**: 287-292. DOI: 10.1023/A:1008450804196.
Traut BH 2005. The role of coastal ecotones: a case study of the salt marsh/upland transition zone in California. *Journal of Ecology* **93**: 279-290. DOI: 10.1111/j.1365-2745.2005.00969.x.
Troumbis AY, Dimitrakopoulos PG 1998. Geographic coincidence of diversity threat spots for three taxa and conservation planning in Greece. *Biological Conservation* **84 (1)**: 1-6. DOI: 10.1016/S0006-3207(97)00093-1.
Ungar IA 1998. Are biotic factors significant in influencing the distribution of halophytes in saline habitats? *Botanical Review* **64**: 176-199. DOI: 10.1086/324047.
Valiela I, Rutecki D, Fox S 2004. Salt marshes: biological controls of food webs in a diminishing environment. *Journal of Experimental Marine Biology and Ecology* **300**: 131-159. DOI: 10.1016/j.jembe.2003.12.023.
Wellborn GA, Skelly DK, Werner EE 1996. Mechanisms creating structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* **27**: 337-363. DOI: 10.1046/j.1472-4642.2003.00038.x.
Whigham DF, Chitterling C, Palmer B 1988. Impacts of Freshwater Wetlands on Water Quality: A Landscape Perspective. *Environmental Management* **12 (5)**: 663-671. DOI: 10.1007/BF01867544.
Wiggens GB, MacKay RJ, Smith IM 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Archives fur Hydrobiologia Supplement* 58, 97-206.