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The Effect of Aquaculture Practices on the Benthic Macroinvertebrate Community of a Lagoon System in the Bay of Cádiz (Southwestern Spain)

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ABSTRACT: Monthly quantitative Ekman-Birge grab sampling was used to characterize and compare the composition and structure of the benthic macroinvertebrate community inhabiting semi-enclosed polyculture lagoons (SPL) (three sampling sites) and enclosed monoculture ponds (EMP) (two sampling sites) of a lagoonal system of the Bay of Cádiz. The two areas differed considerably in habitat characteristics and aquaculture management. The SPL area was characterized by low rates of water exchange, low fish densities, and the presence of a macroalgal cover. In the EMP area, there was a complete exchange of water daily (by pumping) and a supply of food pellets, density of fish was high, and no vegetative cover was present. There were considerable differences in species composition between habitats with different culture methods: 11 of the 21 most abundant species were exclusive to one or the other. Several epibenthic species were abundant in the polyculture lagoon but were low in density or were absent in monoculture ponds. Some infaunal species, on the other hand, were more abundant in the monoculture ponds. Univariate measures of community structure (abundance and biomass, Margalef's species richness, Shannon-Wiener diversity, and Pielou's evenness indices) did not indicate significant differences between the SPL and EMP areas. Conversely, the abundance-biomass comparison (ABC) method indicated that, on average, the macrobenthic community was moderately disturbed in the SPL and undisturbed in the EMP areas. Multidimensional scaling (MDS) ordination and hierarchical cluster analysis (Bray-Curtis similarity measure) revealed the occurrence of two main benthic assemblages that corresponded to the aquaculture methods. The different rates of water exchange for the two aquaculture practices seem to have contributed to differences in the composition and structure of the benthic communities.

Introduction

Coastal lagoons are often highly productive and suitable for aquaculture practices but are, at the same time, stressed by anthropogenic activities (Kjerfve 1994). The management of lagoonal environments for extensive aquaculture is a traditional activity in the Mediterranean region (Labourg 1976; Ardizzone et al. 1988; Arias and Drake 1993). In recent decades, there has been an intensification of aquaculture practices to increase lagoonal production and, consequently, there has been an additional input of organic pollutants (uneaten food and feces). Lagoonal systems themselves are considered an important environmental asset and the management of lagoons urgently needs a balance between economic exploitation and ecological protection (Philomena 1994; DeFur and Rader 1995). The saltmarsh area surrounding the Bay of Cádiz is a good example of such a situation. Presently, most aquaculture in this system is fish polyculture in semi-enclosed areas, but, increasingly, monocultures of sea bream (*Sparus aurata*) fed on artificial pellets are being implemented in ponds, with a consequent change of environmental conditions and possible habitat degradation and eutrophication.

Macrobenthos are considered a suitable group for detecting the effects of pollution (Warwick 1993), and its response to organic enrichment is relatively well documented (Pearson and Rosenberg 1978). It is generally assumed that a macrobenthic community under increased organic enrichment will exhibit a general reduction in species richness, biomass, and body size, and an increase in total number of individuals (opportunistic species). Based on these assumptions, several methods have been proposed to assess the disturbance status of a community (Warwick and Clarke 1991; Warwick 1993). For analyzing changes in benthic community structure, univariate methods that are species independent, such as faunal density and diversity, do not respond consistently to environmental stress. Graphical methods such as

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ABC curves (Warwick 1986) seem to be inappropriate for assessing the disturbance status in areas where small-size species occur (Beukema 1988). Nevertheless, Reizopoulu et al. (1996) have concluded recently that the ABC curves are sensitive enough to discriminate between different levels of disturbance in temperate coastal lagoons. Species dependent multivariate methods are more sensitive in discriminating between different communities (Warwick and Clarke 1991), both perturbed and unperturbed.

The main aim of this study was to analyze changes in benthic macroinvertebrate community composition and structure associated with varying aquaculture practices in a lagoonal system of the Bay of Cádiz, and to assess the disturbance status for each aquaculture method. We determined differences between communities using several statistical methods to test which method was more appropriate in defining community changes.

Lagoonal System

The study was carried out in the San Francisco de Asis lagoon system, a shallow coastal enclosed ecosystem located in the saltmarsh area of the Bay of Cádiz, southwestern Spain (36°23′–36°37′N, 6°8′–6°15′W). The lagoon is divided into two main areas on the basis of the hydrodynamic regime and aquaculture method: the main water body and the fish-pond battery (Fig. 1 and Table 1). The former is a semi-enclosed, shallow, 12.5-ha pan used for fish polyculture (SPL = Semi-enclosed Polyculture Lagoon). Gates of this pan remain open between February and April to permit the passive entrance of fish larvae and free exchange of water with the adjacent tidal channel. During the remaining 9 mo, exchange is possible only at spring tides, with a mean exchange rate of about 25% of the water volume per high tide. The area closest to the gates (sites A and B) experiences higher rates of water exchange than the area further away from the gates (site C). The fish-pond battery (sites D and E), seven ponds of 0.4 ha each, is used for monoculture (EMP = Enclosed Monoculture Pond) of sea bream, *Sparus aurata*. Complete exchange of water in the ponds (about 160% d^{-1}) is made possible by continuous pumping of seawater from the tidal channel. Thus, the enclosed ponds actually receive more water exchange than the semi-enclosed lagoon. Bottled oxygen was used to aerate the monoculture ponds, especially during the warmest period.

When the gates of the polyculture lagoon were open (February–April), 91% of their total surface (sites A and C) was exposed, except at high spring tides. Submerged channels (site B) were always flooded. The upper sediment layer at site B was periodically removed (February 1992) to prevent the submerged channels from filling up. Monoculture ponds were always submerged unless the ponds were emptied to clean the bottom (March 17 to April 21 and September 8 to October 6 of 1992 in site D). Macroalgal cover (mainly *Ulva lactuca* and *Cladophora* sp.) was present in the polyculture lagoon during most sampling occasions but never in the monoculture ponds. During the sampling period, the polyculture lagoon supported an average fish density of 17 g wet wgt m^{-2}, and the fish fed exclusively on natural food found in the lagoon, mainly benthic macroinvertebrates (Table 1). The monoculture ponds supported an average sea bream density of 1.9 kg wet wgt m^{-2} and 1.8 kg wet wgt $^{-2}$ (sites D and E, respectively), and the fish fed mainly on artificial pellets. On average, 22 g dry wgt m^{-2} and 18 g dry wgt m^{-2} of pellets were supplied daily to ponds D and E, respectively.

Materials and Methods

Sampling Procedures

Five areas were sampled (A, B, and C in the semi-enclosed polyculture lagoon and D and E in the enclosed monoculture ponds). Benthic samples were collected monthly between January 1991 and December 1992 at sites A and C, between April 1991 and December 1992 at site B, between January 1992 and September 1993 at site D, and between July 1992 and September 1993 at site E. Three to six replicate samples were taken randomly at each site, with an Ekman-Birge grab (15 cm × 15 cm) modified to close by hand. After a presieving (0.3 mm mesh) to eliminate the finest fraction of the sediment, samples were preserved using 5% formalin in seawater. Later, each sample was resieved through a nested series of sieves (6 mm, 5 mm, 4 mm, 3 mm, 2 mm, 1 mm, 0.5 mm, and 0.3 mm mesh). Animals were sorted by species and counted. For elongate organisms, body length (chironomid larvae) or body width (polychaetes) was estimated. Faunal biomass was estimated using regression equations for these species that relate mean faunal ash-free dry weight (AFDW) to sieve mesh size, body length, or body width (Arias and Drake 1994).

Data Analysis

Benthic macroinvertebrate community structure was described for each sampling occasion on the basis of total density and biomass, and Margalef's species richness (S), Shannon-Wiener diversity (H′), and Pielou's evenness (J′) indices (using ln) (Ludwig and Reynolds 1988). Values of these variables were always estimated on abundance and biomass data per grab (225 cm^{-2}) to standardize the sample size. The effect of the aquaculture method

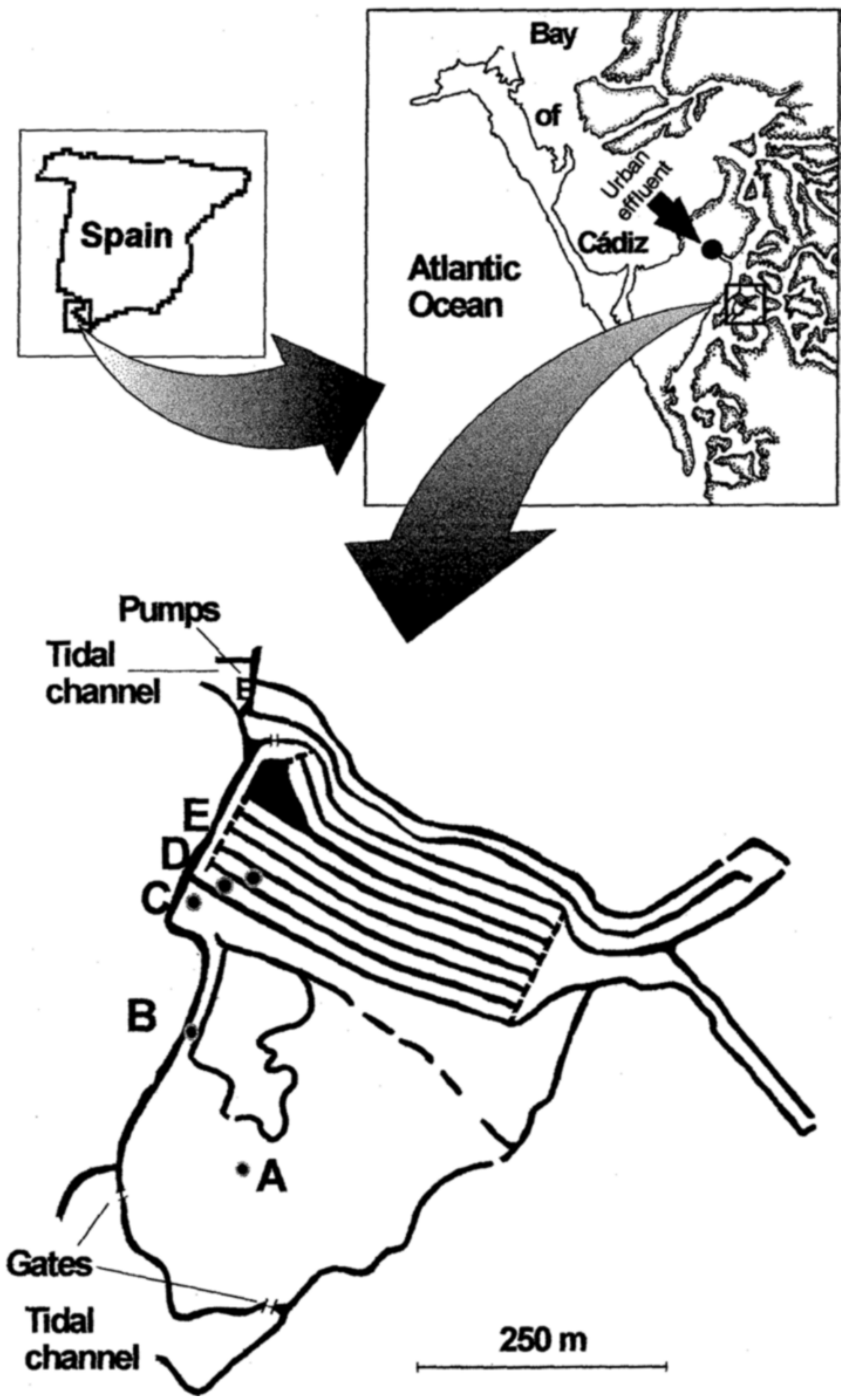

Fig. 1. San Francisco de Asís lagoon system and its location in the Bay of Cádiz, Spain. A, B, C, D and E: sampling sites.

TABLE 1. A summary of the main differences in habitats and aquaculture practices.

	Semi-enclosed Polyculture Lagoon	Enclosed Monoculture Ponds
Water surface	12.5 ha (total for A, B, and C)	0.4 ha (each)
Water depth	February–April: 91% of surface exposed, except at high spring tides. May–January: submerged (25–70 cm)	submerged (180–200 cm)
Rate of water exchange (% of total volume)	February–April: free tidal exchange. May–January: 25% fortnightly	≈160% d^{-1} (by pumping)
Water aeration	wind	bottled oxygen
Vegetative cover	macroalgae (*Ulva* and *Cladophora*)	absent
Reared fish species	sea bream, sea bass (two species), sole, eel, mullet (five species)	sea bream
Fish biomass density	17 g wet wgt m^{-2}	1,850 g wet wgt m^{-2}
Fish food	natural food	pellets (≈20 g dry wgt m^{-2} d^{-1})

(SPL or EMP) on these variables was ascertained using two-way nested (top factor = aquaculture method; nested factor = site) analysis of variance (ANOVA). Because significant differences were not found between aquaculture methods ($p > 0.05$), one-way ANOVA and a posteriori Student-Newman-Keuls (SNK) tests were performed to determine significant differences between sites. Homogeneity of variances was tested by Bartlett tests. Abundance and biomass data were $\ln(x + 1)$-transformed prior to analysis to reduce heteroscedasticity.

To ascertain the stress on the macroinvertebrate benthic community, abundance-biomass comparison (ABC) curves (Warwick 1986) were constructed for each grab and the corresponding W statistic was calculated (Clarke 1990). W statistic differences between aquaculture methods were tested by two-way nested ANOVA (top factor = aquaculture method; nested factor = site).

Community structure differences were also analyzed by multivariate approaches, using the computer software package PRIMER (Plymouth Routines In Multivariate Ecological Research). Multivariate data analysis was by group-average sorting classification and nonmetric multidimensional scaling (MDS) ordination with the Bray-Curtis similarity measure calculated on root-root transformed abundance and biomass data (Clarke 1993). SIMPER was used to determine the contribution of individual species to dissimilarity between the communities of both aquaculture methods. Two-way nested (top factor = aquaculture method; nested factor = site) ANOSIM permutation tests (Clarke and Green 1988) were carried out to determine if there were significant differences between the sample similarities of the aquaculture methods. Since significant differences ($p < 0.05$) were always found between aquaculture methods and between sites (within aquaculture method), a posteriori pairwise ANOSIM tests were used to test for differences between sites within each method. The BIOENV program was implemented to test which combinations of the environmental variables matched better the observed benthic community patterns. This program quantifies the degree of concordance between the biotic (community MDS ordinations) and abiotic ordinations of samples. The abiotic ordination of samples was conducted on the correlation-based PCA (Principal Component Analysis) configurations of environmental factors (Clarke and Ainsworth 1993). The environmental variables considered in the ordination analysis were water temperature, salinity and depth, rate of water exchange, log (1 + macroalgal biomass), and log (1 + organic matter in sediment). The weighted Spearman rank coefficient (r) was used as a matching coefficient between the biotic and abiotic ordinations of samples. Because sediment organic matter data were not available for site E, BIOENV was implemented the first time excluding site E and a second time excluding the variable sediment organic matter.

There was considerable spatial (among replicates) and seasonal (among dates) variation within each sampling site (Arias and Drake 1994). In this study, we focused on testing the effect of aquaculture methods on the benthic macroinvertebrate community. Thus, both spatial and seasonal sources of variation, within each sampling site, were included in the error term of the ANOVA. Because the timing of sample collections at the polyculture lagoon and monoculture ponds differed, we tested to determine if differences observed between both communities for the whole sampling period agreed with the results provided by samples taken during the coincident sampling period (July–December 1992).

Results

Environmental Conditions

Water temperature (8.1–24.3°C) and salinity (18–65 ‰) varied seasonally (Table 2). While intersite differences in annual mean water tempera-

TABLE 2. Mean water temperature (°C), salinity (‰), water depth (cm), macroalgal biomass (g DW m^{-2}), organic matter in the sediment (%), and sediment grain size characteristics (%) at the five sampling sites (A, B, C, D, E). Monthly ranges of variables are shown in parentheses.

Site	Temperature	Salinity	Depth	Algal Biomass	Organic Matter	Grain Size		
						Sand	Silt	Clay
A	17.1 (11.1–24.3)	46.5 (18–65)	27.5 (0–40)	81.3 (0–643)	8.8 (7.1–12.1)	11.2	4.3	84.5
B	17.0 (8.1–23.6)	47.2 (18–64)	55.2 (60–70)	64.5 (0–461)	9.1 (6.8–13.9)	3.1	11.1	85.8
C	17.1 (11.0–24.1)	47.3 (19–62)	23.8 (0–35)	134.1 12–540	10.0 (6.3–12.7)	2.0	13.8	84.2
D	16.7 (9.6–23.0)	41.4 (36–44)	189 (185–200)	0	7.7 (4.9–11.6)	1.1	9.6	89.3
E	17.8 (10.7–23.6)	41.5 (36–45)	190 (180–200)	0	—	1.0	9.8	89.2

ture were negligible, annual mean salinity was lower in the monoculture ponds (sites D and E).

The clay fraction predominated in the sediment at all sites, with slightly higher clay content in the monoculture ponds (Table 2). Organic content in the sediment, estimated as percentage weight loss on ignition, ranged between 4.9 % and (site D) 13.9 % (site B) (Table 2), with a maximum annual mean value of 10.0 % (site C) and a minimum of 7.7 % (site D).

When the gates of the polyculture lagoon remained open (February–April), the water level at site B was ≃ 10 cm and sites A and C were exposed most of the time. Every fortnight for 5 d on average, the whole SPL was completely flooded at high spring tides. From May to January the water level was constant in the SPL (≃ 35 cm, 65 cm, and 30 cm at sites A, B, and C, respectively). The water depth in the monoculture ponds was constant during the year (189 cm and 190 cm on average at sites D and E, respectively).

Macroalgal biomass varied seasonally in the polyculture lagoon, ranging between 0 g dry wgt m^{-2} and 643 g dry wgt m^{-2}. The maximum annual mean of macroalgal biomass was observed in the most confined area of the SPL (site C) (Table 2). *Ulva lactuca* was the predominant macroalgal species at sites A and B, while the filamentous *Cladophora* sp. predominated at site C.

Dominant Macrobenthic Species

The composition and abundance of dominant species (based on the most abundant at each site) differed between SPL and EMP sites (Table 3). The polychaetes *Syllides* sp., *Alkmaria* sp., and *Oriopsis* sp., the cumacean *Iphinoe trispinosa*, and the amphipods *Corophium acherusicum*, *Pariambus typicus*, and *Perioculodes longimanus* were exclusive to the monoculture ponds (sites D and E). Oligochaetes, the mysidacean *Diamysis bahirensis*, the amphipod *Microdeutopus gryllotalpa*, and the chironomid *Halocladius varians* were observed only in the polyculture lagoon (sites A, B, and C). On the other hand, the mean density of several common species, such as the molluscans *Hydrobia minoricensis*, *Hydrobia ventrosa*, and *Abra ovata*, and the chironomid *Chironomus salinarius*, varied greatly between aquaculture methods. The intersite density differences of benthic macroinvertebrate species within each aquaculture method were also considerable.

Community Structure

Macrobenthos abundance and biomass, and species richness, diversity, and evenness indices did not differ significantly between the SPL and EMP areas (two-way nested ANOVA; $p > 0.05$). Significant intersite differences, however, were observed for all five variables (Table 4). The greatest biomass was found at the polyculture lagoon (sites B and C), while the highest values for species richness, diversity, and evenness indices were observed in the monoculture ponds (site E).

According to criteria proposed by Warwick (1986) for detecting the severity of disturbance in a macrobenthic community, the average ABC curves (Fig. 2) at sites A and C, where the abundance curves begin slightly above those for biomass, suggested a moderate state of disturbance. In the case of sites D and E, the ABC curves indicated an undisturbed condition. The community at site B was an intermediate situation. When the apparent differences between the ABC curves were tested using the W statistic value estimated for each sample, it was found that significant differences existed between both aquaculture methods (two-way nested ANOVA, $F_{1,3} = 47.8$, $p < 0.01$), while the differences between sampling sites within each aquaculture method were not significant ($F_{3,387} = 1.0$, $p > 0.05$). For the polyculture lagoon (sites A, B, and C), mean W values were close to 0 for most sampling dates (Fig. 3), with some exceptions, but not clear seasonal trend. Conversely, at the mono-

TABLE 3. Mean densities (no. individuals 225 cm^{-2}) and, in parentheses, mean biomass (mg AFDW 225 cm^{-2}) of the 10 most abundant benthic species for at least one sampling site (A, B, C, D, E). Po = polychaete; Mo = molluscan; My = mysidacean; Cu = cumacean; Am = amphipod; Di = dipteran.

	Semi-enclosed Polyculture			Enclosed Monoculture	
	A	B	C	D	E
Nereis diversicolor (Po)	78.6 (99.6)	45.5 (637.4)	14.6 (618.0)	61.9 (162.6)	70.3 (120.1)
Syllides sp. (Po)	0 (0)	0 (0)	0 (0)	3.4 (0.1)	15.0 (0.8)
Polydora sp. (Po)	4.0 (5.3)	4.8 (6.1)	2.8 (3.6)	11.1 (9.2)	9.4 (7.8)
Streblospio srhubsolii (Po)	61.6 (3.3)	25.0 (1.6)	0.1 (0.0)	114.9 (5.6)	104.6 (4.4)
Alkmaria sp. (Po)	0 (0)	0 (0)	0 (0)	13.8 (0.5)	207.0 (7.3)
Capitella capitata (Po)	6.5 (1.3)	16.8 (3.7)	75.1 (20.8)	2.1 (0.2)	11.8 (2.5)
Oriopsis sp. (Po)	0 (0)	0 (0)	0 (0)	164.3 (0.9)	200.6 (0.8)
Oligochaetes	18.5 (1.8)	1.3 (0.1)	0 (0)	0 (0)	0 (0)
Abra ovata (Mo)	2.6 (18.9)	1.5 (32.3)	0.8 (9.0)	47.7 (16.2)	68.9 (27.3)
Cerastoderma glaucum (Mo)	12.7 (42.7)	1.7 (32.9)	4.5 (54.3)	0.3 (0.5)	0.4 (0.3)
Hydrobia minoricensis (Mo)	307.7 (46.7)	559.2 (113.5)	294.5 (76.1)	0.4 (0.1)	0 (0)
Hydrobia ulvae (Mo)	6.7 (6.8)	6.7 (8.4)	3.8 (10.3)	0.6 (0.2)	0.1 (0.1)
Hydrobia ventrosa (Mo)	40.8 (7.1)	92.1 (13.0)	62.6 (10.3)	0.1 (0.1)	0 (0)
Diamysis bahirensis (My)	4.8 (1.4)	1.6 (0.6)	0.3 (0.2)	0 (0)	0.0 (0.0)
Iphinoe trispinosa (Cu)	0 (0)	0 (0)	0 (0)	25.3 (0.8)	22.9 (0.9)
Corophium acherusicum (Am)	0 (0)	0 (0)	0 (0)	68.8 (3.0)	15.1 (0.9)
Microdeutopus gryllotalpa (Am)	418.3 (43.0)	183.5 (17.2)	129.9 (15.2)	0 (0)	0 (0)
Pariambus typicus (Am)	0 (0)	0 (0)	0 (0)	5.4 (0.2)	41.8 (1.4)
Perioculodes longimanus (Am)	0 (0)	0 (0)	0 (0)	4.0 (0.3)	7.4 (0.5)
Chironomus salinarius (Di)	3.2 (1.1)	29.8 (13.2)	151.1 (51.8)	0.0 (0.0)	1.3 (0.2)
Halocladius varians (Di)	1.8 (1.1)	5.1 (0.4)	35.4 (1.9)	0.0 (0.0)	0 (0)

culture ponds (sites D and E) the W statistic was frequently positive and was maximal in summer.

Ordination (MDS) and hierarchical cluster analysis on abundance and biomass data (Fig. 4) revealed the occurrence of two clearly dissimilar benthic macroinvertebrate assemblages, coinciding with the two aquaculture methods: the semi-enclosed polyculture lagoon (Cluster II = sites A, B, and C) and enclosed monoculture ponds (Cluster I = sites D and E). Two-way nested ANOSIM results (Table 5) supported this conclusion, showing the maximal possible R statistic value (R = 1) for differences between the community for the two aquaculture methods. Despite this feature, the significance level was p = 0.10, which is the maximal significance level at which ANOSIM tests can reject the null hypothesis under the situation of only nine possible permutations. SIMPER results indicated an average dissimilarity between Cluster I and II of 77% and 68% for abundance and biomass data, respectively. The main differences between assemblages were the lack of the amphipod *M. gryllotalpa* and the cumacean *I. trispinosa* in the EMP and SPL areas, respectively, and the high density of the gastropods *H. minoricensis* and *H. ventrosa* in the SPL, area, when were only recorded occasionally in the EMP area. On the other hand, results of pairwise tests (Table 5) for differences between sites, within each aquaculture method, indicated that the maximal intersite community dif-

TABLE 4. Mean values (standard errors) of density, biomass, and Margalef's species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') indices of the macroinvertebrate benthic community at the five sampling sites (A, B, C, D, E). Means followed by different letters within the same row are significantly different (Student-Newman-Keuls tests; $p < 0.05$).

	Semi-enclosed Polyculture			Enclosed Monoculture	
	A	B	C	D	E
Density (no. individuals 225 cm^{-2})	696[ab] (91)	980[a] (116)	780[ab] (51)	528[b] (67)	780[ab] (91)
Biomass (mg AFDW 225 cm^{-2})	245[a] (22)	882[b] (148)	874[b] (159)	201[a] (33)	179[a] (25)
Species richness (S)	1.32[ab] (0.04)	1.41[a] (0.04)	1.28[b] (0.02)	1.43[a] (0.04)	1.57[c] (0.04)
Diversity (H')	1.24[ab] (0.03)	1.16[a] (0.04)	1.28[ab] (0.02)	1.30[b] (0.05)	1.56[c] (0.5)
Evenness (J')	0.59[a] (0.01)	0.52[b] (0.02)	0.60[a] (0.01)	0.60[a] (0.02)	0.66[c] (0.02)

ferences existed for the polyculture lagoon between the area farthest from the gates (site C) and the area closest to the gates (sites A and B).

BIOENV results indicated that rate of water exchange was the single environmental variable which best grouped the sites according to the macroinvertebrate benthic community (excluding site E: $r = 0.659$ and 0.625 for abundance and biomass, respectively; excluding organic matter: $r = 0.704$ and 0.666 for abundance and biomass, respectively). No other environmental variable or combination of variables provided such a good match between biotic and abiotic ordinations.

When only samples from July to December 1992 (coincident sampling period for all the sites) were included in statistical analyses, the differences observed between the communities in both aquaculture methods were concordant with the results obtained for the whole sampling period. Univariate measures of the community structure did not differ significantly between aquaculture methods (two-way nested ANOVA; $p > 0.05$). W statistic values and MDS ordinations differed significantly between the two aquaculture methods (two-way nested ANOVA ($p < 0.05$) and ANOSIM ($p = 0.10$), respectively).

Discussion

The benthic communities of the polyculture lagoon and monoculture ponds were similar in that they were composed mainly of a few pollution-tolerant opportunistic species, there was a strong dominance by a few species, the diversity was very low, and they reached a relatively high abundance and a moderate biomass. According to the species-abundance-biomass (SAB) curves for a gradient of organic enrichment proposed by Pearson and Rosenberg (1978), the communities correspond to the zone between the "peak of opportunists" and "the ecotone point" (transition region between disturbed and undisturbed zones). Maximal biomass observed in this study (sites B and C at the polyculture lagoon) occurred in the region where organic material provided a rich food source for benthic macrofauna, but its input level was insufficient to cause continuous oxygen depletion and, consequently, an azoic zone (Brown et al. 1987). Nevertheless, at the monoculture ponds (especially site E), the benthic community structure was a slightly less disturbed status (Table 4 and Fig. 3). This feature was also observed when species abundances were compared (Table 3): species typical of organically enriched environments, such as *C. capitata* (Brown et al. 1987; Weston 1990; Tsutsumi et al. 1991), *C. salinarius* (Ferrarese and Ceretti 1986), and *M. gryllotalpa* (Diviacco and Relini 1981; Taramelli and Pezzali 1986), were more abundant in the polyculture lagoon, while slightly less tolerant polychaetes, such as *Polydora, Syllides,* and *Streblospio* (Grassle and Grassle 1974; Llansó 1991), were more abundant in the monoculture ponds.

In the salt marsh area adjacent to the culture ponds (Fig. 1), the content of organic matter in the water column and sediment was strongly affected by urban sewage effluents (Sales et al. 1983; Establier et al. 1984). In general, mean values of organic matter in the sediment obtained inside the lagoonal systems were lower than those observed in the tidal channels that supply seawater to them. Blasco et al. (1987) suggested that organic matter was not accumulated within the lagoonal systems because it was removed from the system in the annual yield of reared fish. It appears as if urban effluents were fertilizing the lagoonal area and contributing to its high productivity (Arias and Drake 1995; Drake and Arias 1995a,b,c) but leading to environmental conditions tolerated only by opportunistic (small-size) species. While external organic loading may be the case for the polyculture lagoon, in the monoculture ponds there is an additional input of organic matter (food pellets). The results of the present study, however, with a lower average concentration of organic matter in the sediment (Table 2) and less stressful benthic conditions (suggested by the W statistics) at the monoculture ponds, is not inconsistent with the excessive organic loading. The higher rate of water exchange at the monoculture ponds ($\simeq 160\%\ d^{-1}$) removes a considerable amount of the organic residues from the ponds (Jambrina et al. 1995), avoiding its accumulation in the sediment.

Fish are stocked at a high density (1.8–1.9 kg wet wgt m^{-2}) in the monoculture ponds and the aquaculture management of ponds (high water ex-

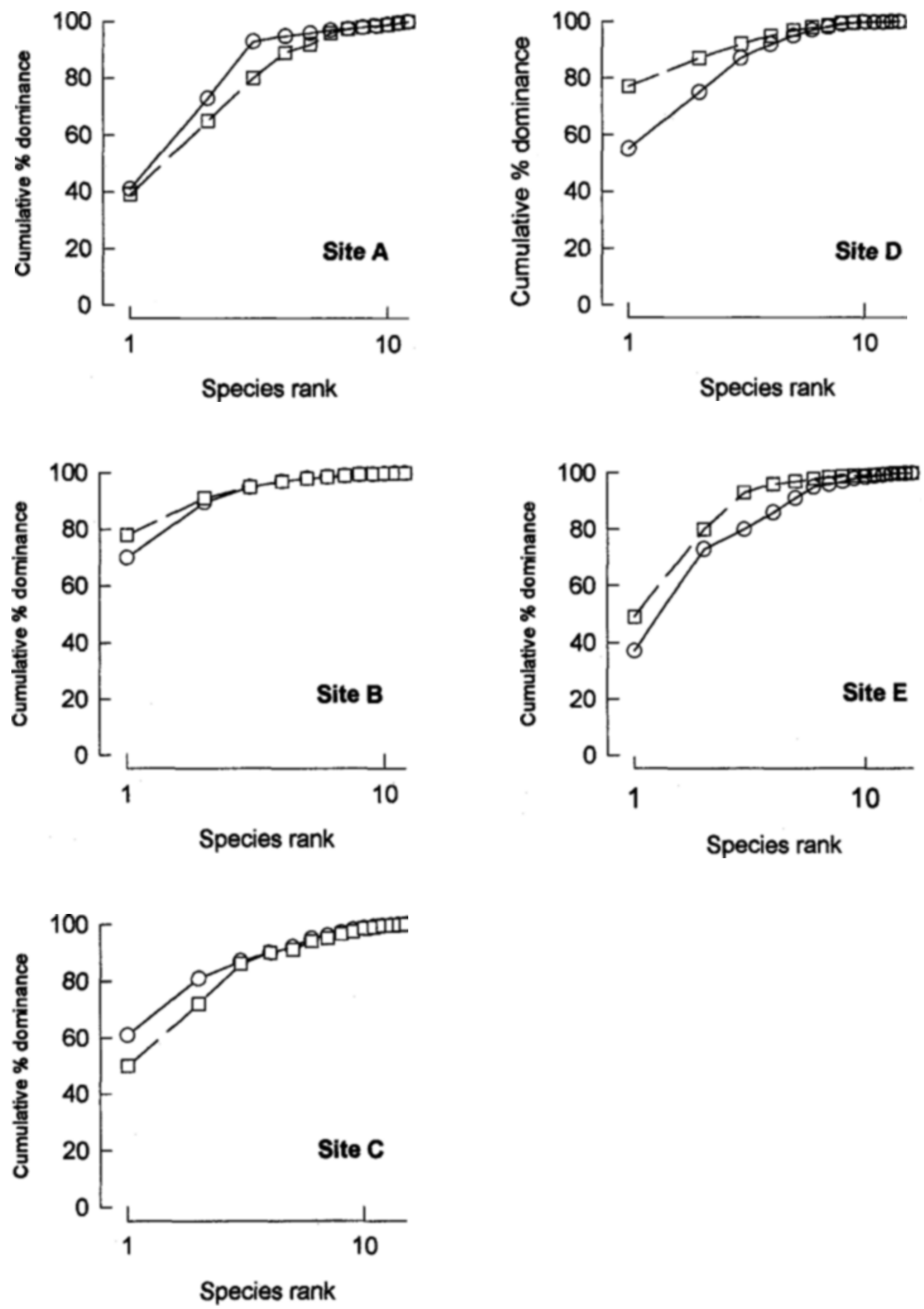

Fig. 2. Average abundance-biomass comparison curves at all the five sampling sites. ○ abundance; □ biomass.

change) prevents macroalgae from proliferating. Both the high density of epibenthic predators and the lack of an algal refuge may have contributed to the low density or lack in the EMP area of species such as *Hydrobia* species, *C. salinarus*, and *M. gryllotalpa*, whose abundances seem to be positively affected by macroalgal biomass (Arias and Drake 1994; Drake and Arias 1996). Conversely, infaunal species such as *A. ovata*, *I. trispinosa*, and *S. srhubsolii* may have been positively affected by the lack of macroalgae, because macroalgae may form a physical barrier between infauna and the oxygenated water column (Everett 1994). On the other hand, there was a proliferation at the EMP sites of small, suspension-feeding polychaetes (*Alkmaria* sp. and *Oriopsis* sp.). Both the higher water exchange rates and the lack of small predators (crabs, shrimps, large individuals of *Nereis diversicolor*) at

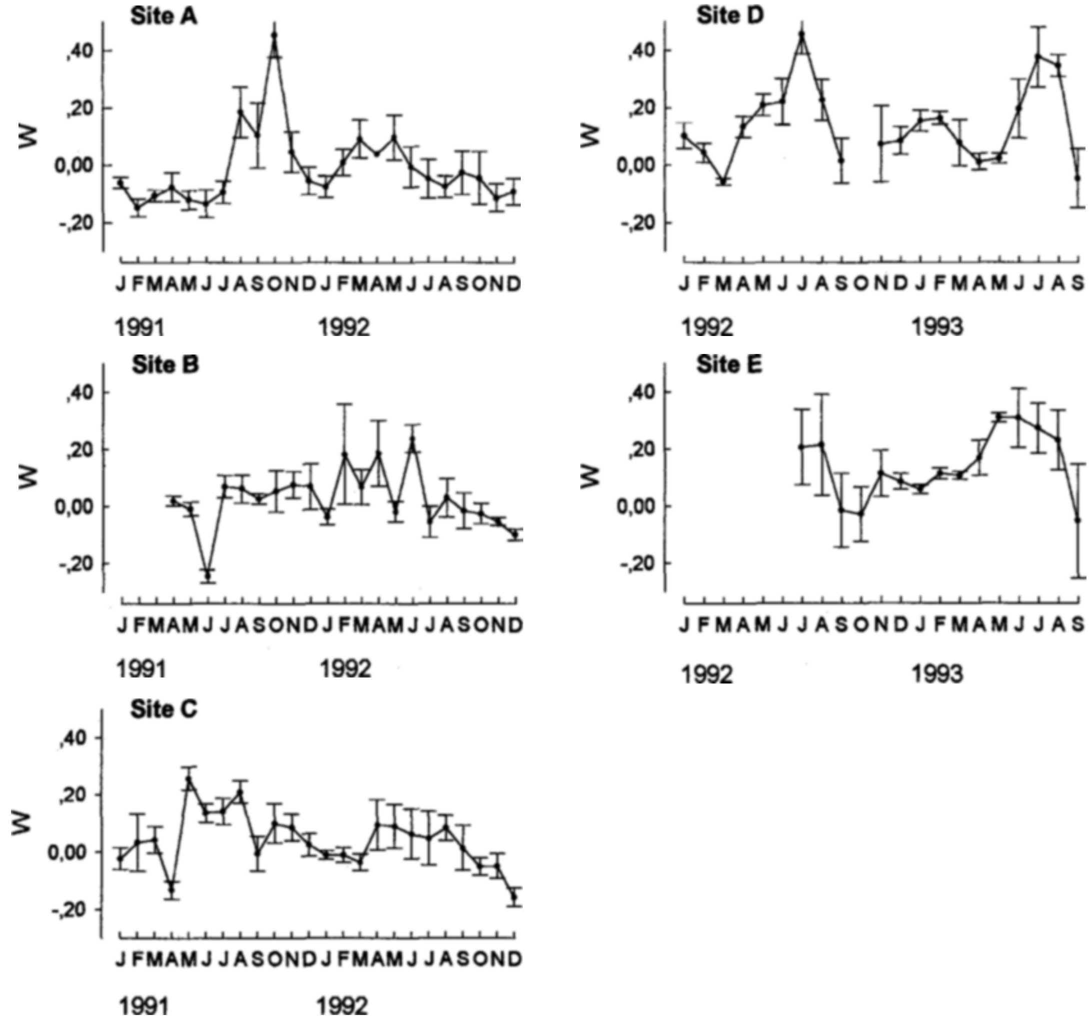

Fig. 3. Monthly mean values (± 1 standard error) of the W statistic at all the five sampling sites.

the EMP sites may have contributed to their high density. It is surprising that, although the same tidal channel supplied seawater to the polyculture lagoon and monoculture ponds (Fig. 1), 11 of the 21 most abundant macroinvertebrate species (Table 3) were exclusive to one of the aquaculture methods. It is interesting to note that the aquaculture methods in this study are good examples of the two most extreme situations (fish density, water exchange, pellet supply, water depth, macroalgal cover) of aquaculture practices in the area. In fact, under intermediate situations of aquaculture methods, it is possible to find co-occurring species that in this study were always found separately. For example, from July to November 1993 juveniles of Senegalese sole (*Solea senegalensis*) were stocked (3–6 g wet weight m^{-2}) in 0.1 ha ponds whose seawater input (50–100% d^{-1}) was from the same tidal channel that supplied seawater to the studied lagoonal system. On average, 2 g dry wgt m^{-2} of pellets were supplied daily to each pond. Under these conditions, species such as *M. gryllotalpa*, *C. acherusicum*, *I. trispinosa*, *H. varians*, and *D. bahirensis* co-occurred in the fish ponds (personal observations).

Environmental conditions in semi-enclosed environments, such as the lagoonal systems, are restrictive and fluctuating. The successful colonization of these lagoons by macrofauna is hampered by two features: dispersal of individuals within and between systems and persistence of populations within a given area. We hypothesize that in the polyculture lagoon the dominant species are those typical of "lagoonal" environments (Barnes 1989, 1994), with a lower dispersal rate within the area but able to persist under suboptimal conditions. Their restricted and sporadic distributions within the monoculture ponds could result from low

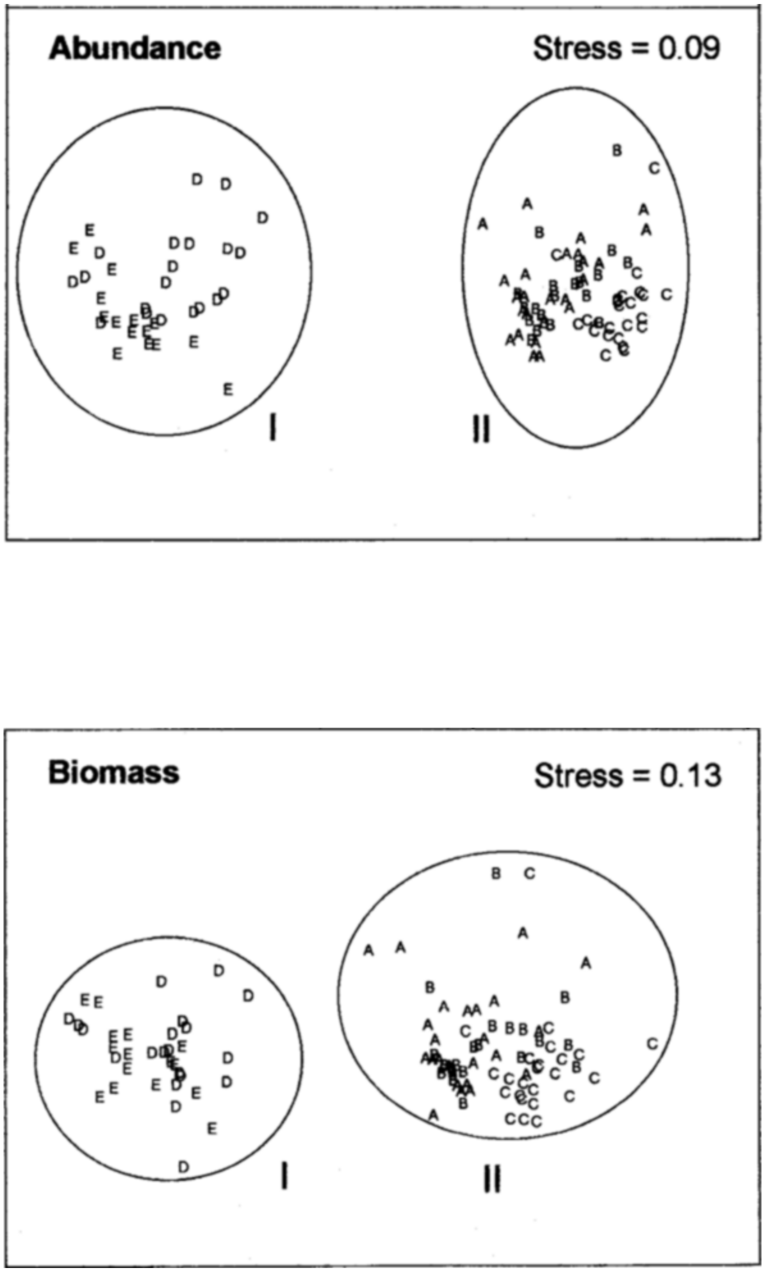

Fig. 4. Multidimensional scaling (MDS) ordination plots of benthic macroinvertebrate community at the different sampling sites (A, B, C, D, and E). Encircled points represent sample groups with an average dissimilarity between clusters of 77% and 68% for abundance and biomass data, respectively. The stress values indicate good success of the MDS in preserving the sample relationships (Bray-Curtis dissimilarity ranks) as Euclidean distances in the two-dimensional ordination plots.

probabilities of colonization (low density in tidal channel water column) and/or persistence (high large predator density, lack of macroalgal cover, periodical removal of sediment). Conversely, at the monoculture ponds there could be a proliferation of species which are more abundant in the tidal channel water column, because they are either components of the tidal channel benthic community or species with a pelagic larval stage, and are easily drifted into the ponds with the continuous seawater input. These species may fail to colonize the SPL area due mainly to a lower probability of persistence (fluctuating conditions, higher density of small predators, algal cover as a physical barrier), and also because of a lower chance of recolonization when the gates remain closed. BIOENV results seem to support the hypothesis that the different degree of water confinement in the poly-

TABLE 5. Summary of results from two-way nested ANOSIM. Value of ANOSIM statistic (R) and significance level (P) for global tests for differences in the macroinvertebrate benthic community (abundance and biomass) between sites (within culture types) and between culture types, and results of pairwise tests between sites (within culture types).

	Abundance		Biomass	
	R	P	R	P
Between sites (global)	0.234	<0.01	0.190	0.01
A, B (pairwise)	0.020	0.17	0.110	0.04
A, C	0.432	<0.01	0.317	<0.01
B, C	0.339	<0.01	0.218	<0.01
D, E	0.112	0.02	0.094	0.04
Between culture types	1.00	0.10[a]	1.00	0.10[a]

[a] With only nine possible permutations, P = 0.10 is the maximal significance level at which ANOSIM tests can reject the null hypothesis.

culture lagoon and monoculture ponds was an important factor in explaining the differences in benthic assemblages observed between aquaculture methods.

The lagoonal systems are naturally stressed, and we need statistical methods to detect increased stress from anthropogenic sources in such disturbed communities. In this study, univariate (species independent) methods, such as total density and biomass, and Margalef's species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') indices seemed to be insensitive to the changes in benthic community structure between aquaculture methods. Similar insensitivity of univariate methods has been observed previously in other areas (Austen et al. 1989). Multivariate approaches, however, indicated clearly two different macrobenthic assemblages (Fig. 4).

The ABC technique was used successfully to identify areas disturbed by organic enrichment (Warwick 1986; Ritz et al. 1989; Reizopoulou et al. 1996), but in other studies (Beukema 1988; Weston 1990; Dauer et al. 1993) it failed to characterize disturbance of some sites. In our study, the W statistic (for the whole sampling period) gave results consistent with those of the multivariate approach. The high temporal variation shown by the statistic (Fig. 4), however, suggested that the method would lead to an over- or underestimation of disturbance state of the community in short-term studies. The prolonged reproductive periods of the macrofaunal populations (Arias and Drake 1995; Drake and Arias 1995a,b,c), which resulted in fluctuations of new recruits (small individuals) during the whole year, may have contributed to the considerable seasonal variation observed for the W statistic. Recruitment events have been reported previously as a possible cause of disturbance misclassifications by the ABC method (Dauer et al. 1993).

Conclusions

The intensification of aquaculture practices from semi-enclosed polyculture lagoons to enclosed monoculture ponds in a lagoonal system did not produce more stressful life conditions for macroinvertebrates living in the monoculture ponds. A slightly less disturbed macrofaunal community was observed in monoculture ponds. Several epibenthic species, which were abundant in the polyculture lagoon, were low in density or were absent in monoculture ponds, while some infaunal species had an increased density in monoculture ponds. Univariate methods such as total density and biomass, and Margalef's species richness (S), Shannon-Wiener diversity (H'), and Pielou's evenness (J') indices seemed to be insensitive to changes in benthic community structure between the aquaculture methods. Conversely, and despite the fact that communities were composed mainly by small species, the ABC curves (W statistic) were useful for detecting slight changes in the disturbance status of the benthic community, provided that seasonal variations were considered when establishing the duration of the sampling program. Finally, the multivariate approach reflected successfully the changes in benthic community composition and structure associated with varying aquaculture practices, primarily differences in water exchange rates.

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