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FAUNAL INTERRELATIONSHIPS BETWEEN LAGOONAL AND MARINE AMPHIPOD CRUSTACEAN COMMUNITIES OF THE PO RIVER DELTA (NORTHERN ADRIATIC)

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RESUMEN

Una serie de investigaciones sobre las comunidades bentónicas de la laguna salobre «Sacca del Canarin» (delta del río Po) y el área marina adyacente han permitido la identificación de cuatro biocenosis diferentes. Los fondos blandos de la laguna son habitados por una biocenosis eurihalina y euritérmica: los anfípodos están representados principalmente por *Corophium orientale* y *Echinogammarus pungentoides*. La última especie también se encuentra en los sustratos duros de la laguna, junto a *Leptocheirus pilosus, Corophium insidiosum, Gammarus aequicauda*, y otros. En los fondos blandos de la zona marina adyacente se encuentra una típica biocenosis de arenas finas, con *Urothoe poseidonis, Atylus massiliensis* y otras. En los sustratos marinos duros se encuentra una comunidad de *Mytilus galloprovincialis* algo empobrecida en la que los anfípodos están representados por *Caprella equilibra* y otros. El intercambio de especies de anfípodos entre estas biocenosis se ha detectado mediante técnicas de análisis multivariante (análisis de correspondencia y análisis jerárquico de «cluster»), basadas en un conjunto de 16 especies y 16 estaciones de muestreo. La mayoría de intercambios faunísticos (*Jassa marmorata, Echinogammarus olivii*, etc.) se observó entre las dos comunidades de sustrato duro, que en consecuencia, muestran composiciones específicas similares. Casi ninguna especie marina penetra en la laguna; por el contrario, las áreas marinas más someras soportan una importante intrusión de especies de la laguna cuando se dan condiciones de «stress» hidrológico o sedimentológico. En el primer caso, algunas especies eurioicas (*Gammarus crinicornis, Echinogammarus pungentoides, Melita palmata*, etc.) procedentes de fondos duros o con barro, tienden a perder la especificidad del sustrato y colonizan arenas. En el segundo caso, la especie limícola *Corophium orientale* puede extender su distribución en el espacio.

SUMMARY

Extensive investigations on the benthic communities of the brackish lagoon «Sacca del Canarin» (Po river delta) and the adjacent marine area allowed the identification of four different biocenoses. The soft bottoms of the lagoon are inhabited by an euryhaline and eurythermic lagoonal biocenosis: amphipods are represented mainly by *Corophium orientale* and *Echinogammarus pungentoides*. The latter occurs also on the hard substrates of the lagoon, together with *Leptocheirus pilosus, Corophium insidiosum, Gammarus aequicauda* and others. On the soft bottoms of the adjacent marine area a typical biocenosis of fine sands is found, with *Urothoe poseidonis, Atylus massiliensis* and others. On the marine hard substrates there is a somewhat impoverished *Mytilus galloprovincialis* community in which amphipods are represented by *Caprella equilibra* and others. Amphipod species interchanges among these biocenoses were detected by multivariate techniques (correspondence analysis and hierarchical cluster analysis), based on a set of 16 species per 16 sampling stations. The largest number of faunal exchanges (*Jassa marmorata, Echinogammarus olivii*, etc.) turned out to occur between the two hard substrate communities, which therefore exhibit similar species composition. Almost no marine species enter the lagoon; on the contrary the shallowest marine areas undergo a large intrusion of lagoonal species when hydrological or sedimentological stresses occur. In the first case some euryoecious species (*Gammarus crinicornis, Echinogammarus pungentoides, Melita palmata*, etc.), coming from hard or muddy bottoms, tend to lose substrate specifity and colonize sands. In the second case the limicolous species *Corophium orientale* can extend its distribution.

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INTRODUCTION

In the last few years, the Po river delta has been the subject of a large number of naturalistic studies (PARISI, 1973; AMBROGI *et al.*, 1985); many concerned the lagoon called «Sacca del Canarin» where a large thermoelectric power plant was being built (BORGESE *et al.*, 1981).

Several papers considered the benthic communities of the lagoon itself (BEDULLI & PARISI, 1978; BEDULLI & PERETTI, 1979; MATRICARDI *et al.*, 1980; RELINI *et al.*, 1981, 1985; MATRICARDI & BIANCHI, 1982; PARISI *et al.*, 1985) and of the sea in front of it (AMBROGI and BEDULLI, 1981; AMBROGI *et al.*, 1983; BEDULLI *et al.*, 1983, 1984; PARISI *et al.*, 1985). The large amount of data collected allows the identification of the biocenoses present in the area and a first attempt to inquire into faunal exchanges between the sea and the lagoon; similar investigations have already been carried out on planktonic species (FERRARI *et al.*, 1981) and ichthyofauna (GANDOLFI *et al.*, 1985), but not on benthic invertebrates. The present contribution takes this topic into account, dealing in particular with the distribution of amphipod crustaceans, one of the most important macrobenthic taxa of this area (DIVIACCO, 1981a; DIVIACCO & PINKSTER, 1982; DIVIACCO *et al.*, 1983). They include strictly benthic species and others, such as the gammarids, which, having a bentho-pelagic life, are part of the so-called «suprabenthos» (BACHELET *et al.*, 1983). Like other members of the vagile fauna, they are a key element in the spatial dynamics of estuarine ecosystems (MUUS, 1979). Their importance in brackish-water food webs is widely recognized (MUUS, 1979; BACHELET *et al.*, 1981; KIRN *et al.*, 1986); furthermore they are generally considered as good «biocenosis indicators» (BELLAN-SANTINI, 1971).

Many works have been published on the ecology of estuarine amphipods of both the Mediterranean (BRIAN, 1939; GIORDANI SOIKA, 1949; DRIDI & PRUNUS, 1980; DIVIACCO, 1979, 1981b, 1982a, 1982b, 1983; JANSSEN *et al.*, 1979; SCONFIETTI, 1983; etc.) and other seas (GOODHART, 1941; BASSINDALE, 1942; DEN HARTOG, 1964; SORBE, 1978; NAIR *et al.*, 1983; KUKERT, 1984; RODRÍGUEZ & DAUVIN, 1985; FREDETTE & DÍAZ, 1986; etc.), but interrelations between

TABLA 1. List of species collected and their distribution in sampling stations and the corresponding four communities: lhsa=lagoonal hard substrates assemblages, mb=mussel bed, SFBC=«biocoenosis of fine well-sorted sand», LEE= «euryhaline and eurythermal biocoenosis in brackish waters» (see text).

Lista de especies recolectadas y su distribución en las estaciones de muestreo y las cuatro comunidades respectivas: lhsa=conjuntos de sustratos de laguna duros, mb=lechos de mejillones, SFBC=«biocenosis eurihalinas y euritérmicas de aguas salobres» (ver texto).

	lhsa						mb	SFBC						LEE		
AORIDAE																
Leptocheirus pilosus Zaddach	+	+	+	+	+	+	+									
COROPHIIDAE																
Corophium acherusicum Costa	+	+	+	+	+	+	+	+	+	+	+	+				
C. insidiosum Crawford	+	+	+	+	+	+	+									
C. orientale Schellenberg			+						+					+	+	+
DEXAMINIDAE																
Atylus massiliensis Bellan-Santini								+	+	+		+				
GAMMARIDAE																
Echinogammarus olivii (Milne-Edwards)	+	+		+	+		+									
E. pungens (Milne–Edwards)		+	+	+	+	+	+									
E. pungentoides Diviacco & Pinkster	+	+	+	+	+	+	+				+	+		+	+	+
Gammarus aequicauda (Martynov)	+			+	+											
G. crinicornis Stock	+	+		+						+						
Melita palmata (Montagu)		+	+	+	+	+	+	+		+				+		+
HAUSTORIIDAE																
Bathyporeia guilliamsoniana (Bate)								+								
Urothoe poseidonis Reibish								+	+		+	+	+			
ISAEIDAE																
Microprotopus maculatus Norman								+					+			
ISCHYROCERIDAE																
Jassa marmorata Holmes			+		+	+	+									
CAPRELLIDAE																
Caprella equilibra Say							+									

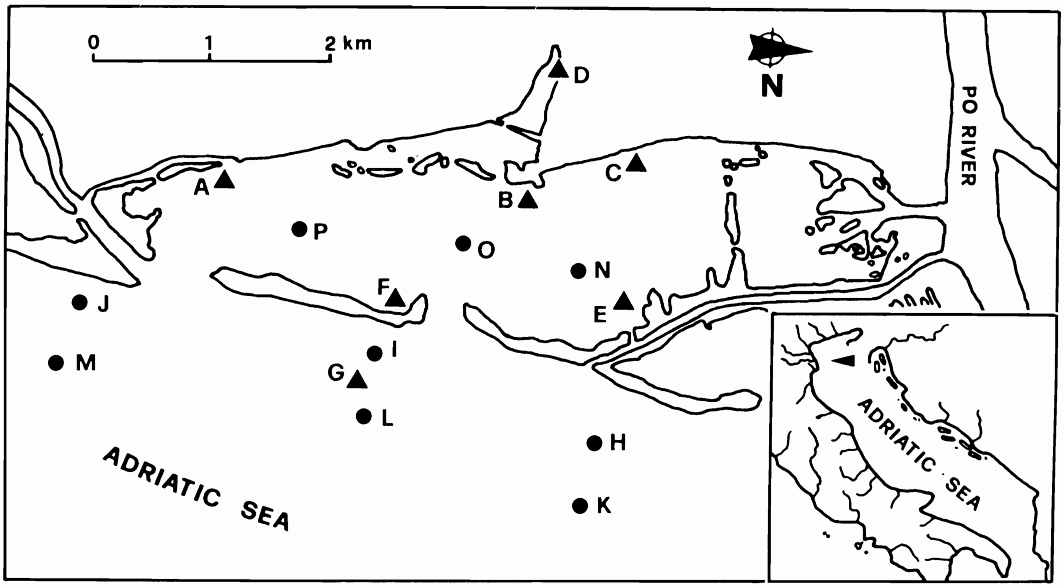

FIGURE 1. Sampling sites in the lagoon «Sacca del Canarin» and in the adjacent marine area. Circles represent soft-bottom stations, triangles hard-substrate stations.

Estaciones de muestreo en la laguna «Sacca del Canarin» y en el área marina adyacente. Los círculos indican estaciones de fondo blando y los triángulos estaciones de sustrato duro.

the faunas of brackish waters and of the neighbouring marine areas are usually neglected; some interesting observations can be found in LEINEWEBER (1985).

Some aspects of these general problems were examined, in the Mediterranean region, by PICARD (1983), for soft bottom communities, and by LEDOYER (1968), for different taxa of the vagile fauna on both hard and soft bottoms.

MATERIALS AND METHODS

Material comes from a research project carried out between 1977 and 1981, on the benthos of the lagoon and of the adjacent marine area, over a total of 16 stations (fig. 1): six stations (A to F) represent the hard substrates of the lagoon (stones, reeds, serpulid-reefs, piers etc.), one (G) the marine ones (the pillars of a tide-gauge station, at 1 m depth), six the marine soft bottoms at 2.5 m (H to J) and 5 m (K to M) and three (N to P) the lagoonal soft bottoms at about 1 m depth. A Van Veen grab was used on soft bottoms, whereas on hard bottoms samples were collected by scraping off or removal of the whole substrate; in both cases the sampled area was of about 0.1 m^2. Further information on methods and sampling sites, together with environment descriptions, can be found in the above-mentioned papers.

The biocenoses present in these stations were identified on the basis of previously published faunal data and of direct field observations; they were named according to the system of PERES (1967), taking into account also further revisions or integrations (AUGIER, 1982; BELLAN-SANTINI, 1985). Although originally conceived for the Mediterranean Sea, such a system has been generalized on a world-wide scale by PERES (1982), while a specific adaptation for the Adriatic Sea can be found in GAMULIN-BRIDA (1974).

Amphipod species have been considered as typical of a given biocenosis on the basis of present knowledge of their bionomics (LEDOYER, 1968; BELLAN-SANTINI & LEDOYER, 1973; RUFFO, 1982).

Species distribution in the 16 stations was examined by multivariate techniques, applied to a presence/absence matrix. Ordination was performed by means of the factorial analysis of correspondences (BENZECRI, 1980); the significance of the axes was evaluated through comparison with the tables of LEBART (1975). Classification was done by hierarchical cluster analysis, based on Sorensen's index; the similarity matrix was resolved in a dendrogram, with the group average sorting algorithm (SOKAL & SNEATH, 1963).

RESULTS AND DISCUSSION

Four different communities can be recognized in the 16 stations examined, where 16 amphipod species were found (table 1).

A typical «euryhaline and eurythermal biocoenosis in brackish waters» (LEE) characteri-

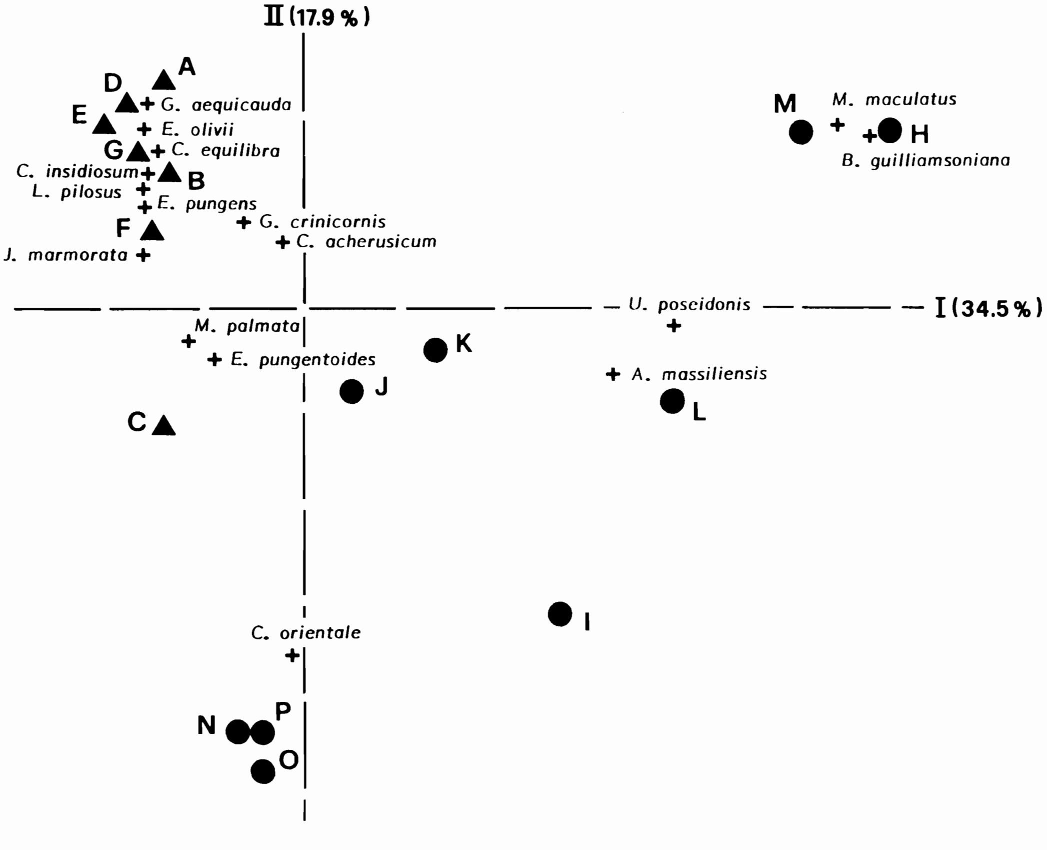

FIGURE 2. Factorial analysis of correspondence: projection of species-points and station-points on the plane formed by the first two axes (in brackets the percent variance explained by each axis). Circles represent soft-bottom stations, triangles hard-substrate stations.

Análisis factorial de correspondencia: proyección de los puntos especies y los de estaciones en el plano formado por los dos primeros ejes (entre paréntesis, el porcentaje de varianza explicado por cada eje). Los círculos indican estaciones de fondo blando y los triángulos estaciones de sustrato duro.

zes the muddy bottoms inside the lagoon (stations N to P): three amphipod species were present, but only *Corophium orientale* was characteristic.

The lagoonal hard substrate community (stations A to F) exhibits a remarkable richness in amphipod species: *Leptocheirus pilosus, Corophium insidiosum, Echinogammarus olivii, E. pungens* and *E. pungentoides* were the most important species, while other typical euryhaline species —like *Gammarus aequicauda* and *G. crinicornis*— were less common.

Two communities can be recognized on the marine sediments in front of the lagoon: the «biocoenosis of the fine sands in very shallow waters» (SFHN) at 2.5 m (stations H to J) and the «biocoenosis of fine well-sorted sand» (SFBC) at 5 m depth (stations K to M). According to LEDOYER (1968), however, the vagile fauna of these two biocenoses constitutes a single assemblage (SFBC *sensu lato*). Many amphipod species were present, but some of them clearly represent invading species from deeper communities, due to sedimentological stress (DIVIACCO *et al.*, 1983); so that, if only the fauna typical of the stations within 5 m depth is taken into consideration (BIANCHI *et al.*, 1984), *Atylus massiliensis, Urothoe poseidonis, Bathyporeia guilliamsoniana* and *Microprotopus maculatus* can be cited as the more characteristic species.

Finally, in the only hard-substrate station (G)

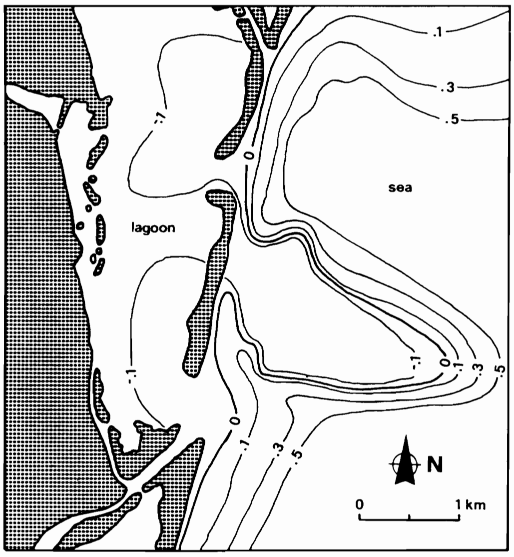

FIGURE 3. Map of the isopleths of the factor-scores of station-points on the first axis from correspondence analysis.

Mapa de isopletas de los factor-scores de los puntos estación en el primer eje a partir del análisis de correspondencia.

of the marine area a mussel bed (mb) —formed by *Mytilus galloprovincialis* together with an impoverished accompanying fauna— was found, showing affinity for both the «biocoenosis of the lower mediolittoral rock» (RMI) and the «biocoenosis of the photophilic algae» (AP): amphipods were represented by *Caprella equilibra, Corophium acherusicum, Melita palmata* and other less important species.

Many species appeared in more than one community: among these *Echinogammarus pungentoides* and *Melita palmata* were found in all the four biocenoses.

Factorial analysis of correspondences disposes species-points and station-points in a parabolic cloud on the plane formed by the first two axes, which altogether account for 52.4% of total variance (fig. 2): such a conformation (Guttman effect) is typical of situations where a strong polarizing factor exists (FRESI & GAMBI, 1982). Along the first axis a clear sea-lagoon gradient (fig. 3) is recognizable, with the «pure» SFBC stations (H and M) at the positive end and the lagoon stations at the negative one; some of the marine sandy stations (e.g., J and K) have a central position and the only marine hard substrate station (G) lies among the lagoonal ones (A to F). Along the second axis the cloud formed by station-points is split into two distinct parabolas (fig. 4): thus the second axis —altough not significant ($P>0.05$)— is likely to represent a factor inversely correlated to the siltation amount. The sequence of the stations proceeds from relatively pure hard (A, B, D, E, F and G) or sandy (H and M) substrates, through muddy hard (C) or sandy (I) substrates, to entirely muddy bottoms (N, O and P).

On the whole, three main groups of stations are recognizable.

A first very homogeneous group includes the lagoonal stations A, B, D and E and the marine station G: they represent the hard substrate complex and are distinguished by a great number of species, among which *Leptocheirus pilosus, Corophium insidiosum* and *Echinogammarus olivii* are the most frequent ones.

A second homogeneous group is formed by the muddy-bottom lagoonal stations N, O and P, characterized by the presence of *Corophium orientale:* they correspond to the LEE biocenosis.

Finally, the third group has a lower inner affinity, but it can include at least stations H and M of the marine sandy bottoms, which are inhabited by typical SFBC species *(Atylus massiliensis, Bathyporeia guilliamsoniana, Urothoe poseidonis* and *Microprotopus maculatus).*

The remaining stations exhibit intermediate positions and cannot be attributed to one of the previous groups (fig. 5). For example, station C (lagoonal hard substrate) is intermediate between the first and the second group, and station I (marine sandy bottom) is intermediate between the second and the third group; in both cases this is probably due to a high siltation rate that allows for colonisation by *Corophium orientale,* a strictly limicolous species. Communities at stations J, K and L (marine sandy bottoms) are even less defined, because of the presence of hard substrate species *(Echinogammarus pungentoides, Melita palmata, Corophium acherusicum* and *Gammarus crinicornis);* such a situation, as well as the «brackish aspect» of the marine hard substrate station G (fig. 4), could indicate a hydrological influence of the river that displaces to the sea a number of estuarine species: *G. crinicornis,* in particular, is considered by SORBE (1978) as a species indicating displacement of estuarine water masses.

Cluster analysis also shows three station groups (fig. 6), which are broadly consistent with those seen in the ordination model; some differences arise as regards the above-mentioned «intermediate» stations, especially K and J.

CONCLUSIONS

The high environmental instability, typical of

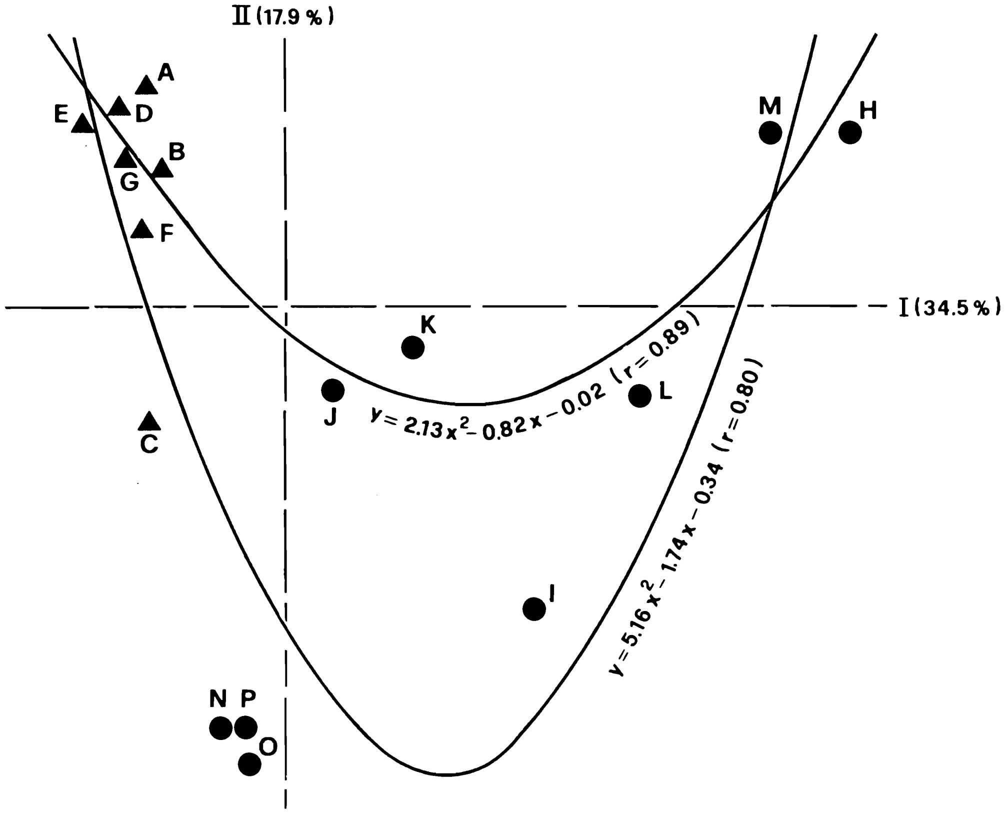

FIGURE 4. The double parabolic shape of the station-points ordination model.

La forma parabólica doble del modelo de ordenación de los puntos de las estaciones.

the examined area, greatly influences the faunal composition; this is characterized by a considerable heterogeneity, essentially achieved by means of mutual exchanges of amphipod species between neighbouring communities.

The greatest number of exchanges (fig. 7) occurred between the two hard-substrate assemblages, through highly euryecious species: *Jassa marmorata* and *Corophium acherusicum* penetrated deeply into the lagoon, while five lagoonal species were able to invade the marine hard substrate. Thus, the amphipod faunas of the two assemblages were not well distinguishable, although *Caprella equilibra* is exclusive of the mussel bed (mb) and *Gammarus aequicauda* is exclusive of lagoonal hard-substrate asemblages (lhsa). Such a situation is favoured by low salinity due to freshwater coming from the Busa di Bastimento, and flowing up to station G: a depression of salinity by continental waters is a general characteristic of these shallow-water habitats (GAGE, 1974). Some «bionomical analogies» in the amphipod fauna of brackish and neighbouring marine hard substrates were already noted by FEDOTOV (1985) in a region as far from the Mediterranean as the eastern Kamchatka.

Faunal exchanges occuring with the other benthic communities and between them, follow two main ways, corresponding to the two parabolas showed in the ordination model (fig. 4).

The first is represented by the ability to lose substrate specificity showed by some species, as previously seen in brackish water fauna (COGNETTI, 1982). Species coming from hard substrates are able to colonize both the lagoonal muddy bottom and the marine sands when some hydrological stress decreases competition pressures. According to DIVIACCO *et al.* (1983), this occurs especially in spring *(E. pungentoides)*, when the higher river flow causes a fall in the salinity values, and in summer *(M.*

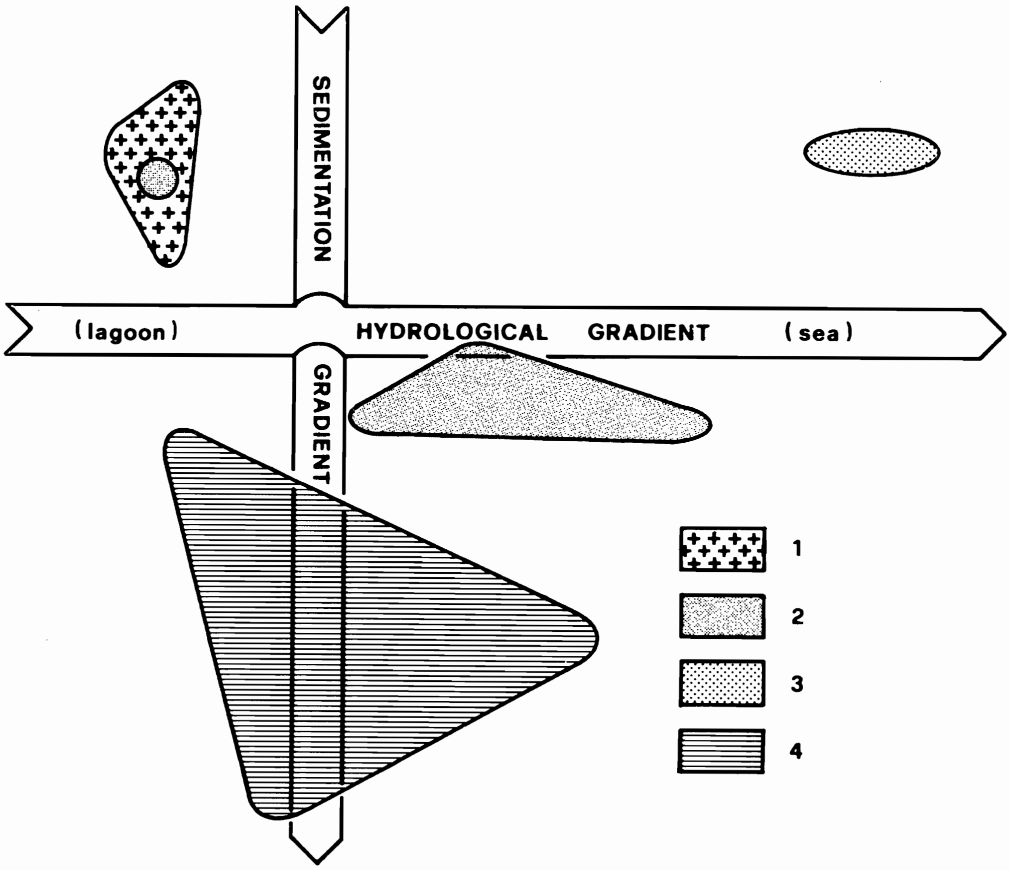

FIGURE 5. Ecological interpretation of the ordination model (see text and fig. 2). 1=community of «pure» lagoonal hard substrates, 2=faunal assemblages of zones under the hydrological influence of the river, 3=biocenosis of «pure» marine sandy bottoms (SFBC), 4=faunal assemblages of zones with high silt deposition, included the typical lagoonal biocenosis (LEE).

Interpretación ecológica del modelo de ordenación (ver texto y fig. 2). 1=comunidad de sustratos duros de la laguna «puros», 2=conjuntos faunísticos de zonas sometidas a la influencia hidrológica del río, 3=biocenosis de los fondos marinos arenosos «puros» (SFBC), 4=conjuntos faunísticos de zonas con elevada sedimentación de limo incluidas las típicas biocenosis de laguna (LEE).

palmata, *G. crinicornis* and *C. acherusicum*), during the period of water stratification.

The second way is mainly related to sedimentary disequilibrium events: an increase in silt deposition allows for colonisation of both hard substrates and sandy bottoms by the limicolous species *C. orientale*. Thus, the SFBC biocenosis is simultaneously subjected to two opposite trends, both due to increased siltation: the invasion of species from deeper marine bottoms (DIVIACCO *et al.*, 1983) and the invasion of species from the lagoonal muds.

On the whole, the faunal exchanges occur mostly in the lagoon-sea direction, and much less in the opposite way (fig. 7); while in other Italian coastal lagoons amphipod marine species penetrate into the parts under sea influence (DIVIACCO, 1981b, 1983), in the Po river delta area it is the lagoon that exports species to the adjacent marine area.

Such a situation does not seem to be so unusual in the Adriatic coastal lagoons. A movement of species from the lagoon of Grado to the sea has been observed for the plancton (FONDA UMANI & SPECCHI, 1979), but examples can be found even in the case of sessile benthos: by means of the seawards displacement of larvae from the lagoons of the Po river delta, the cirriped *Balanus improvisus* colonizes the nearby marine bottoms in great abundance

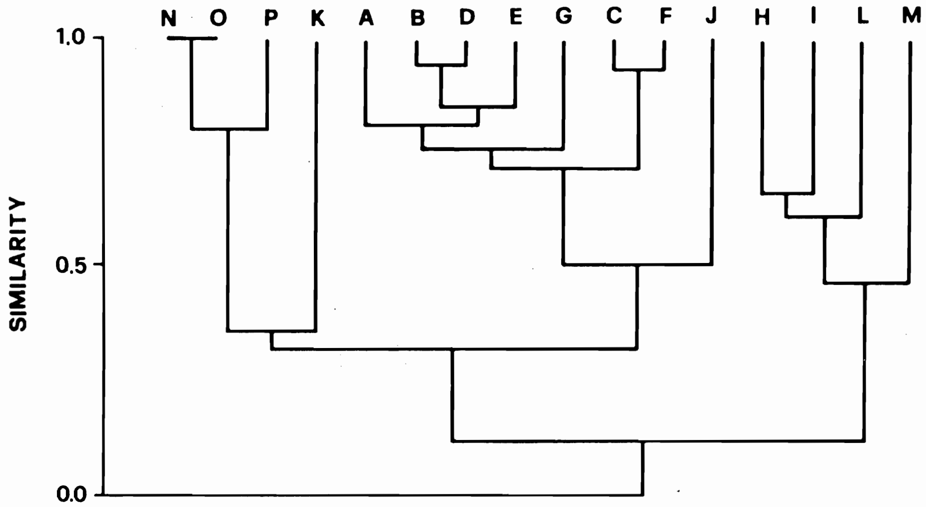

FIGURE 6. Dendrogram of similarity among sampling stations (Sorensen index).

Dendrograma de similaridad entre las estaciones de muestreo (índice de Sorensen).

(AMBROGI *et al.*, 1983). Similarly, the brackish-water serpulid *Ficopomatus (=Mercierella) enigmaticus* has been recorded from an offshore platform 6 km off Ravenna (RELINI *et al.*, 1977).

These results do not fit into the classical concept of marine «vivification» of lagoons, usually supported by Mediterranean ecologists (SACCHI, 1979). Such a concept implies that coastal laggons are primarily colonized by euryecious marine species, which can survive more or less stably to form the so-called «prelethal climax» (PETIT, 1962). This point of view has recently been criticized by GUELORGET & PERTHUISOT (1983), but their «confinement» theory again emphasizes the prevalent influence of the sea on the lagoon.

On the contrary, the distribution patterns we observed evidence that faunal interrelationships between marine and brackish environments cannot be described under a single scheme. As stressed by BIANCHI (1987), coastal lagoons are complex ecosystems interfacing marine, fresh water and terrestrial domains at the same time: depending on the specific situation, a different interface component can play the major role in affecting structural and functional aspects (biocenotic gradients, biomass transfer, etc.) of lagoonal ecosystems.

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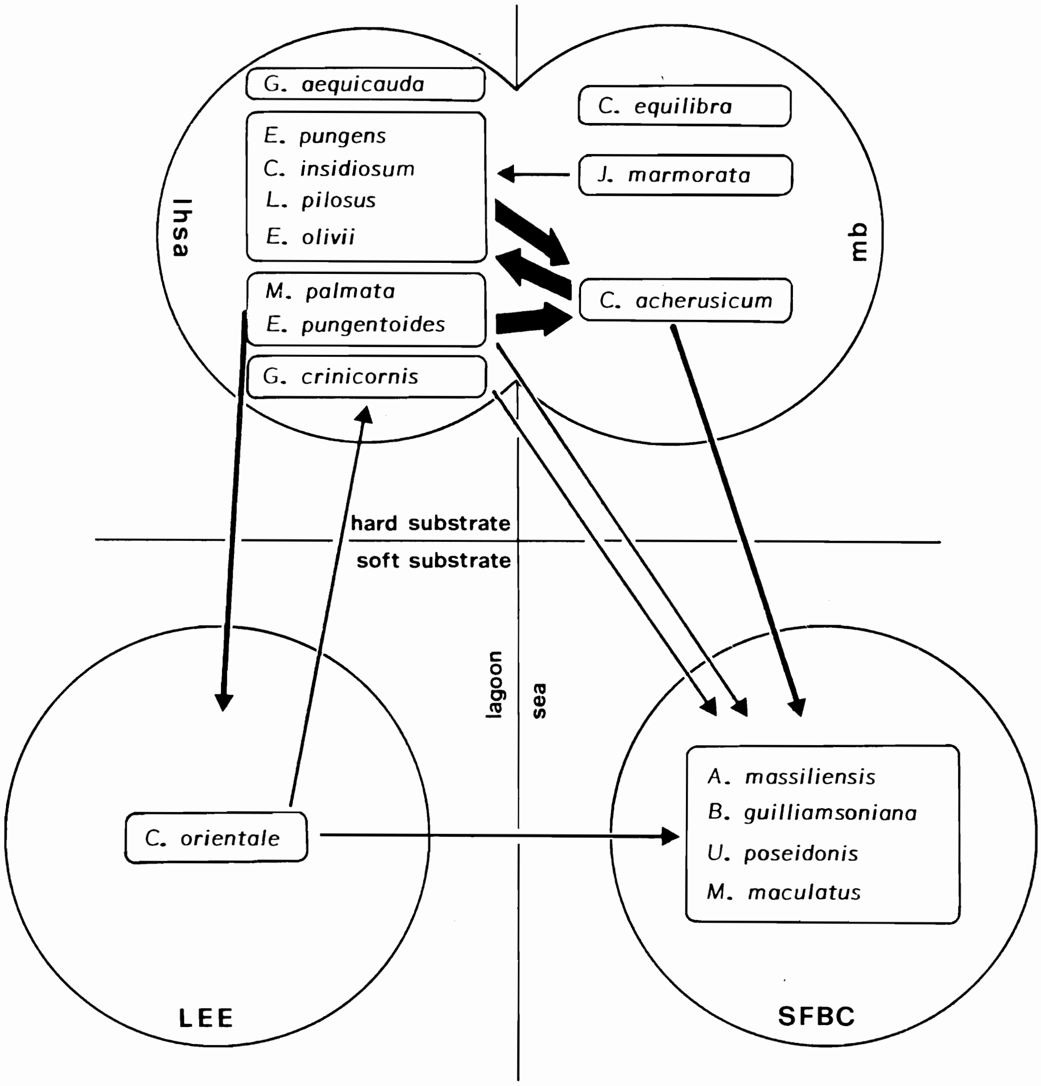

FIGURE 7. Summarizing scheme of Amphipod species translocations among the four identified benthic communities (see text); lhsa=lagoonal hard substrates assemblages, mb=mussel bed, LEE=«euryhaline and eurythermal biocoenosis in brackish waters», SFBC=«biocoenosis of fine well-sorted sand».

Esquema comprensivo de las translocaciones de especies de anfípodos entre las cuatro comunidades de bentos identificadas (ver texto); lhsa=conjuntos de sustrato duro de laguna, mb=lecho de mejillones, LEE=«biocenosis de aguas salobres eurihalinas y euritérmicas», SFBC=«biocenosis de arena fina bien seleccionada».

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