Assessment of macrozoobenthic communities in the lagoon of Obidos, western coast of Portugal

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SUMMARY: A benthic and sedimentological survey undertaken in the lagoon of Obidos, western coast of Portugal, based on 57 faunal samples and 61 grain-size analysis provided initial data for the assessment of the bio-sedimentological gradients in that system. Five sediment types were characterized and charted, ranging from clean coarse sand, in the vicinity of the lagoon mouth, to fine mud in the inner areas with a mean silt percentage of 98 %. The 68157 individuals collected were distributed among 119 species characteristic of both Atlantic and Mediterranean lagoons. Species richness was higher at those intermediate sampling stations, where more diverse surface sediments occur. Faunal abundance was higher in the center of the lagoon, on fine muds, and on the intertidal sand-banks. The correspondence analysis shows that both surface sediments and benthic communities were distributed along a gradient normal to the longitudinal axis of the lagoon, evolving from an outer marine community, occupying 4 % of the lagoon bottom and settled on clean coarse unstable sand, to an inner lagoon community, corresponding to 85 % of the lagoon bottom and located on fine muds. Transition occurred within a central ecotone area, where species richness was higher, which occupied the remaining 11 % of the bottom surface and was located on slightly silty medium sand. A cenotic model proposed for this lagoon is discussed in relation to hydrological and sedimentological data, and compared with both the faunistically similar lagoon of Albufeira located 140 km south of Obidos, and the general model proposed for Mediterranean lagoon systems.

Key words: benthic macrofauna, surface sediments, bio-sedimentological gradients, coastal lagoons.

INTRODUCTION

The lagoon of Obidos is located on the western coast of Portugal, 100 km north of Lisbon (39° 26′ N to 39° 23′ N; 9° 11′ W to 9° 14′ W). It is a shallow semi-enclosed body of water with northwest-southeast orientation, and its longitudinal axis perpendicular to the coast line. It has an area of ≈ 7.0 km^2 and a maximal depth of 5 m, located in an inner area, the Bom Sucesso (Fig. 1). The lagoon communicates with the ocean by a shallow and narrow channel which may be obstructed by sand deposition following storms. Intertidal sand-banks extend from the lagoon mouth inwards, for up to one third of maximal lagoon length. Besides the delta channels, there is only a single northern navigation channel crossing the sand-banks (Fig. 1).

On a topographical basis, three regions will be distinguished and referred in the text as the outer area, comprising the delta channels near the entrance of the lagoon, the intermediate region, comprising the navigation channel and the sand-banks, and the inner basin, located inward of the sand-banks (Fig. 1).

Physico-chemical data taken monthly from May 1985 to May 1986 (CALDEIRA *et al.*, 1986) have shown that surface and bottom temperatures increase inwards in summer (18 °C near the entrance to 25 °C in the inner basin) but are more uniform in winter, when they average 13 °C throughout. Salinity is always higher near the bottom. It increases inwards in summer (from 35.8 to 36.2) and decreases in winter, due to fluvial inputs (mean surface value near the entrance of 33.6, and 24.9 in the inner

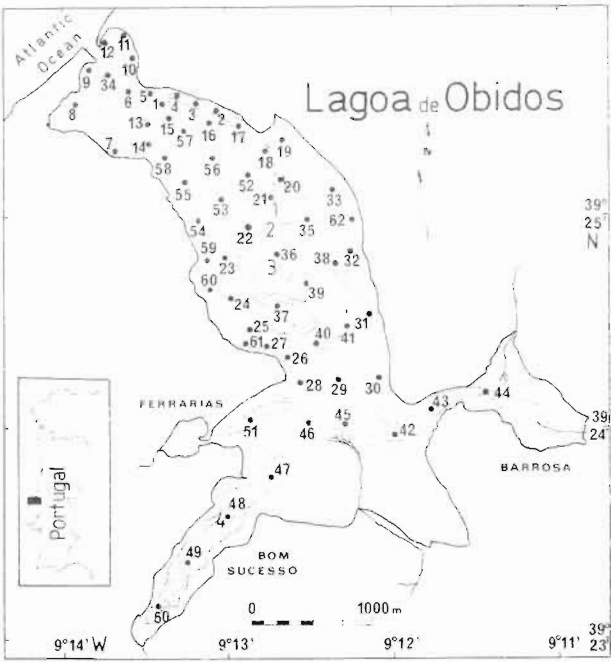

FIG. 1. — The lagoon of Obidos showing positions of the sampling stations. Depth in meters shown by isobaths (continuous line and numbers 1 to 4; the interrupted line is the 0m contour).

basin). Dissolved oxygen is always higher at the surface. From the outer to the inner regions, mean annual values increase at the surface (from 6.31 ml l^{-1} to 7.80 ml l^{-1}) and decrease at the bottom (from 6.31 ml l^{-1} to 4.58 ml l^{-1}). Temporary oxygen depletion has only been found near the bottom in the inner deeper regions (Bom Sucesso). Particulate suspended matter is always higher in the inner basin than near the entrance, with greater differences at the bottom (mean annual value of 20.2 mg l^{-1} in the navigation channel and 34.5 mg l^{-1} near Bom Sucesso).

These four parameters showed higher annual amplitudes in the inner areas than around the lagoon mouth.

In order to characterize the general ecology of this system, a survey was undertaken between February 1984 and December 1986. In this contribution we present the results concerning the sedimentological and macrozoobenthic baseline data.

MATERIAL AND METHODS

Sampling

Surface sediment description was based on grain-size analysis from 61 samples: Stations 1 to 21 and 23 to 62 (Fig. 1).

Macrozoobenthic communities composition and distribution were assessed from 57 faunal samples taken during two weeks in February-March 1984: Stations 1 to 8 and 10 to 58 (Fig. 1). Subtidal sampling (Stations 1 to 13, 17, 18 and 20 to 51) was performed with a Rallier du Baty dredge, a semi-quantitative anchor sampler. It is a small scale model adapted from those used by CABIOCH (1968), LARSONNEUR (1971) and RETIERE (1979) in sedimentological and benthic studies in the English Channel. It has a circular mouth of 0.30 m diameter, maximal capacity of 50 l and collecting bag with a mesh size < 1 mm. Intertidal samples were collected on foot, from a surface of 0.5 m^2 to a depth of 0.15 m.

Samples for faunal studies were sieved through a 1 mm mesh screen and the material fixed in 10 % buffered formalin (stained by Rose Bengal). In the laboratory macrofauna was enumerated and identified to species level whenever possible.

Analysis

Grain-size analysis consisted of three major steps: i) Chemical destruction of organic matter with H_2O_2; ii) Measurement of the total dry weight (P_1), followed by chemical dispersion of the sediment in tetra-sodium pyrophosphate (30 g/l) and wet sieving through a 63 μm mesh screen. Measurement of a second dry weight of the material left on the mesh (P_2) and calculation of the weight of the fraction < 63 μm by difference (P_1-P_2); iii) Dry mechanical sieving of the remaining sediment with mesh screens ranging from 63 μm (4ø) to 8000 μm (−3ø), at 1 ø intervals.

Final total dry weight of a sample, P_t, is given by P_1 exclusive of its biogenic fraction (mostly molluscs shells) retained by a mesh screen ⩾ 1 mm. This fraction was removed manually under microscope. For a given sample, the values of each of the 9 grain-size classes thus obtained is a percentage of P_t.

Data treatment

Surface sediments and faunal data were both treated by correspondence analysis (BENZECRI *et al.*, 1973), with interpretation aided by ascendent hierarchical classification (LEBART *et al.*, 1977; JAMBU, 1978; JAMBU & LEBEAUX, 1978). This methodology for the analysis of numerical data concerning grain-size classes and benthic ecology has been used and discussed by CHARDY *et al.* (1976a and b), MALMGREN *et al.* (1978), CREVEL (1983), PLANTE *et al.* (1983) and QUINTINO *et al.* (1987).

Affinity groups obtained from sediment data were further characterized by some classical grain-size parameters, the median (P_{50}) (TRASK, 1930), mean (M_z) (FOLK & WARD, 1957), sorting coefficient (Γ_I) (FOLK & WARD, 1957) and mean percentages of silt (< 63 μm), sand (< 2000 μm; ⩾ 63 μm) and gravel (⩾ 2000 μm). Given the fact that the silt + clay content was not analysed, the sorting coefficient was not calculated in those samples where this content was above 5 %.

RESULTS

Sediments

The raw data consisted of a 9 grain-size classes × 61 samples matrix. The final analysis considered a 7 × 60 matrix, by the omission of the coarser grain-size classes, almost absent in the samples (4000 to 8000 μm) and the omission of sampling station 27, due to its heterogeneous sediment (pebbles and silt).

Axes 1 and 2 of the correspondence analysis explains 87 % of the total inertia. The distribution of affinity groups among the sampling stations and the grain-size classes in Plane 1-2 is shown in figure 2. Due to the large number of points simultaneous representation has been avoided. Both figures are, however, drawn to the same scale.

Among samples, four major affinity groups were obtained: Aa, Ab, Ba and Bb, the latter being split into subgroups Bb_1 and Bb_2. They correspond to groups Ia, Ib, IIa and IIb, obtained among the grain-size classes. The succession from group Aa (quadrant $1^- 2^-$) to group Bb (centred in quadrant $1^+ 2^-$) is made by the groups Ab ($1^- 2^+$) and Ba ($1^+ 2^+$). The transition represented by Aa → Ab → Ba → Bb corresponds to a spatial sucession of sampling stations located from the vicinity of the lagoon mouth (Aa), to the intertidal sand-bank and navigation channel (Ab), to the inner northern margin (Ba) and to the center and innermost regions of the lagoon (Bb). Within this group, the sampling stations belonging to subgroup Bb_1 are located between the intertidal sand-bank and subgroup Bb_2, which comprises the majority of the sampling stations in the inner parts of the lagoon.

The grain-size classes affinity groups show a similar transition, Ia → Ib → IIa → IIb, corresponding to a gradually increasing silt content of the surface sediments. Thus, axis 1 opposes the coarser fractions predominating at the outer stations (groups Ia and Aa) to the finer fractions of the innermost stations (groups IIb and Bb). Axis 2 isolates a few intermediate stations (group Ba) with a grain-size class corresponding to fine sand (IIa).

The increasing silt content towards the inner

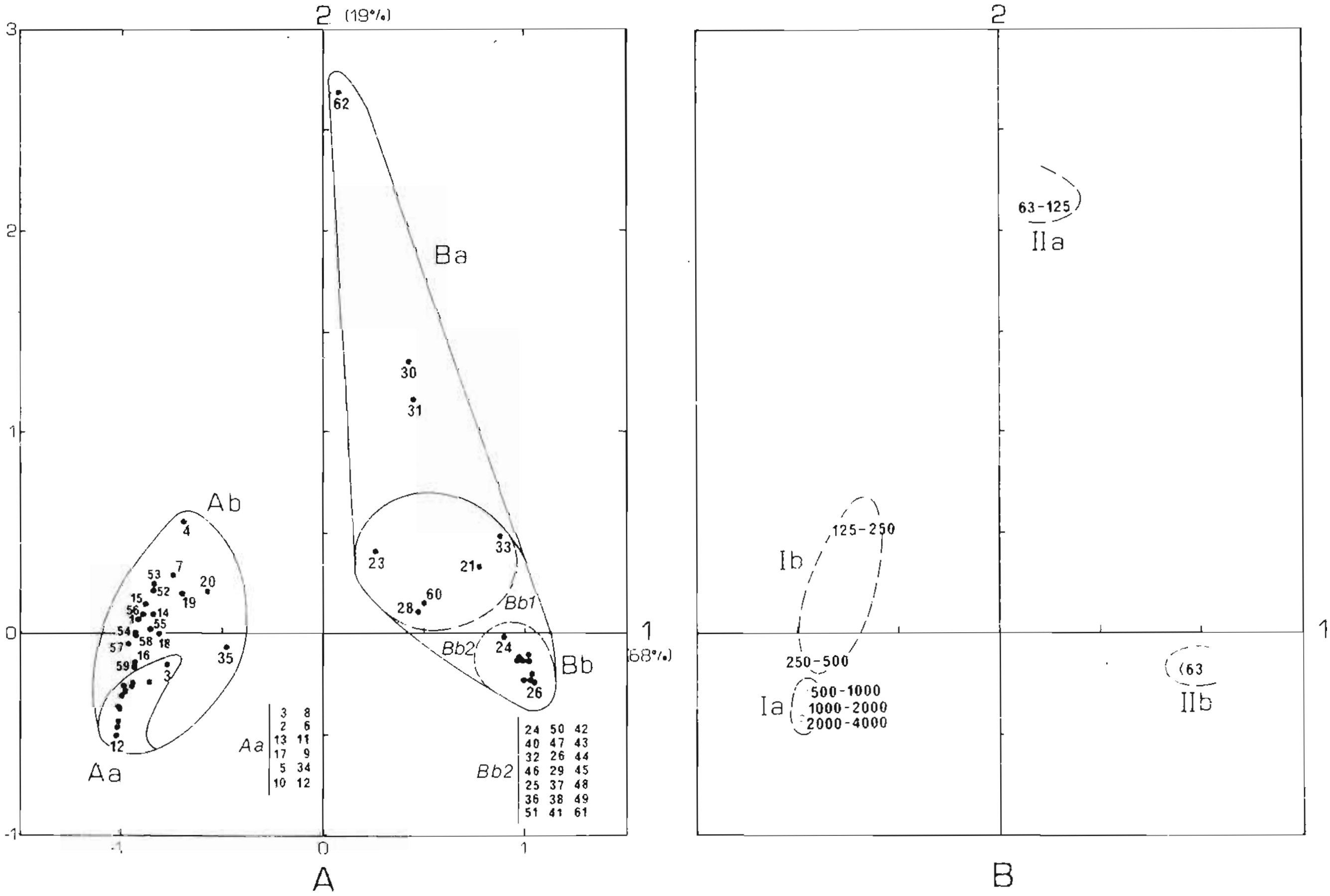

FIG. 2. — Affinity assemblages among sampling stations (A) and grain-size classes (B), according to the partition obtained in plane 1-2 of the correspondence analysis. Grain-size classes in μm.

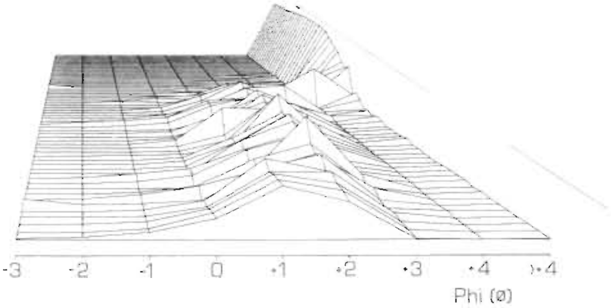

FIG. 3. — Succession of the sampling stations according to their projection on axis 1 of the correspondence analysis. Direction of silting up is given by arrow.

areas, expressed by axis 1, is represented on figure 3, obtained by projecting both the sampling stations and the grain-size classes on that axis. This shows the marked distinction of sandy sediments (foreground) from muddy sediments (background). Table I summarizes the results for each of the affinity groups established among the sampling stations.

According to Wentworth's system (MORGANS, 1956; DOEGLAS, 1968), LARSONNEUR (1977) and to the FOLK & WARD (1957) sorting coefficient scale, the stations of group Aa comprise moderately sorted coarse sands, group Ab corresponds to moderately sorted slightly silty medium sands, group Ba comprises silty very fine sands and group Bb corresponds to muds. Within this latter group, stations of assemblage Bb_1 correspond to slightly sandy muds and Bb_2 to fine muds.

The spatial distribution of these five sediment types is charted in figure 4, where it is shown that muddy sediments predominate. Muds with a silt percentage > 95 % correspond to 80 % of the subtidal bottom of this lagoon.

Macrofauna

FAUNAL ANALYSIS

The 68157 individuals collected were distributed among 119 species. Annelids, Molluscs and Arthropods together comprise more than 95 % of the individuals and more than 85 % of the species. Table II shows the distribution of species and specimens among the major taxa.

TABLE I. — Grain-size parameters for each of the affinity groups established by the correspondence analysis. Mean percentage of silt+clay (Si), sand (Sa) and gravel (G) and mean values for percentile 5 (P5), median (Md), mean (Mz) and sorting coefficient (Γ_1).

Affinity groups	*No. of stations*	*Si*	*Sa* %	*G*	*P5*	*Md* φ	*Mz*	Γ_1
Aa	12	2.5	92.7	4.8	-0.98	0.95	0.89	0.96
Ab	18	6.1	93.5	0.4	0.23	1.57	1.60	0.99
Ba	3	40.9	58.4	0.7	1.57	3.75	-	-
Bb	27	92.8	7.0	0.2	3.20	>4.0	-	-
Bb1	5	70.6	29.3	0.1	1.68	>4.0	-	-
Bb2	22	97.9	1.9	0.2	>4.0	>4.0	-	-

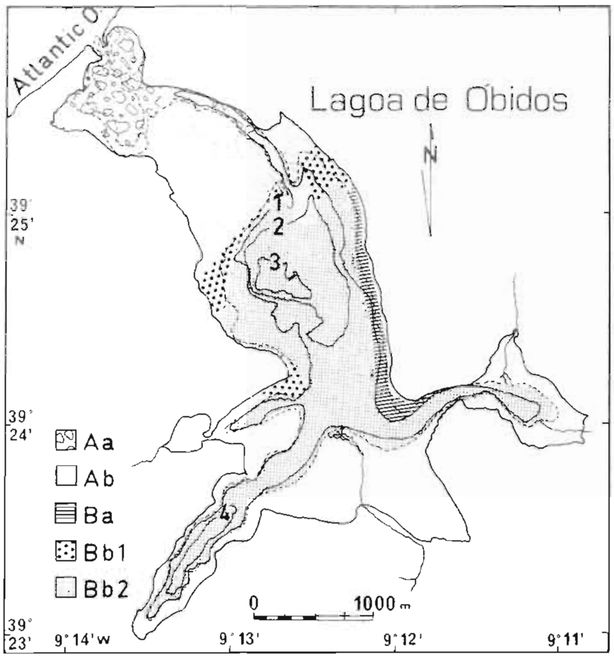

FIG. 4. — The lagoon of Obidos showing the spatial distribution of surface sediments. Aa, clean coarse sand; Ab, slightly silty medium sand; Ba, silty very fine sand; Bb_1 slightly sandy mud; Bb_2, fine mud.

Of the 119 species, 21 (17 %) were collected once comprising 31 individuals (0.05 %), and 61 (51 %) had a frequency ≤ 10 % (sampled in less than 6 stations) and comprising only 489 individuals (0.72 %); 39 species (33 %) were sampled in 12 or more stations (frequency ≥ 20 %) and were represented by 66782 individuals (98 %), showing the strong disproportion of the distribution of individuals among

TABLE II. — Distribution of species and individuals among the major taxa.

Taxa	*No. of species*	*No. of individuals*
Bivalves	22	8170
Gasteropods	16	9753
Polyplacophores	2	28
Polychaetes	38	13525
Oligochaetes	2	2817
Amphipods	7	24725
Peracarids*	7	1722
Decapods	7	35
Chironomids**	1	4345
Echinoderms	2	32
Phoronids	1	1617
Chordates	6	44
Other groups***	8	1344
Total	119	68157

* Mysidaceans and Isopods
** larval stage
*** Nemerteans, Platyhelminthes and Anthozoans

TABLE III. — Macrozoobenthic fauna list. The code number given to each species is used in figure 7.

	ANNELIDA		
9	*Aonides oxycephala* (Sars, 1862)	82	*Pholoe* sp.
12	*Cirriformia tentaculata* (Montagu, 1808)	84	*Phylo foetida* (Claparède, 1870)
16	*Capitella capitata* (Fabricius, 1780)	85	*Anaitides groenlandica* (Oersted, 1843)
25	*Diopatra neapolitana* delle Chiaje, 1841	86	*Platynereis dumerilii* (Audouin & M.-Edwards, 1833)
33	*Eteone foliosa* Quatrefages, 1865	87	*Pseudopolydora antennata* (Claparède, 1870)
34	*Mysta picta* (Quatrefages, 1865)	88	*Polydora ciliata* (Johnston, 1838)
35	*Eulalia viridis* (Linnaeus, 1767)	90	*Pomatoceros lamarkii* (Quatrefages, 1865)
36	*Eumida sanguinea* (Oersted, 1843)	91	*Prionospio malmgreni* Claparède, 1878
41	*Glycera convoluta* Keferstein, 1862	93	*Pygospio elegans* Claparède, 1863
43	*Heteromastus filiformis* (Claparède, 1864)	96	*Saccocirrus papillocercus* Bobretzky, 1872
48	*Lagis koreni* Malmgren, 1866	97	*Scoloplos armiger* (Müller, 1776)
54	*Malacoceros ciliata* (Keferstein, 1862)	101	*Spiophanes bombyx* (Claparède, 1870)
55	*Malacoceros fuliginosa* (Claparède, 1870)	102	*Spio martinensis* Mesnil, 1896
56	*Mediomastus capensis* Day, 1961	103	*Spio* sp.
66	*Nephtys cirrosa* Ehlers, 1868	104	*Spionidae* sp.
67	*Nephtys hombergii* Savigni, 1818	107	*Sthenelais boa* (Johnston, 1839)
68	*Nereis diversicolor* Müller, 1776	108	*Streblospio shrubsolii* (Buchanan, 1890)
69	*Ophelia bicornis* Savigny, 1818	109	*Syllidia armata* Quatrefages, 1865
70	*Ophelina modesta* Stop-Bowitz, 1958	113	*Tubificoides benedeni* (Udekem)
71	*Owenia fusiformis* delle Chiaje, 1841	114	*Tubificidae* sp.
	MOLLUSCA		
1	*Abra alba* (Wood, 1801)	49	*Lepidochitona cinereus* (Linnaeus, 1769)
2	*Abra ovata* (Philippi, 1836)	50	*Littorina littorea* (Linnaeus, 1758)
3	*Acantochitona fascicularis* (Linnaeus, 1767)	51	*Loripes lacteus* (Linnaeus, 1758)
4	*Akera bullata* Müller, 1776	59	*Mytilus galloprovincialis* Lamarck, 1819
13	*Bittium reticulatum* (da Costa, 1778)	60	*Nassarius reticulatus* (Linnaeus, 1758)
15	*Calyptraea chinensis* (Linnaeus, 1758)	78	*Parvicardium exiguum* (Gmelin, 1790)
19	*Cerastoderma edule* (Linnaeus, 1758)	79	*Parvicardium* sp.
22	*Corbula gibba* (Olivi, 1792)	80	*Pharus legumen* (Linnaeus, 1758)
26	*Donax trunculus* Linnaeus, 1758	81	*Philine aperta* (Linnaeus, 1758)
27	*Dosinia exoleta* (Linnaeus, 1758)	94	*Rissoa labiosa* (Montagu, 1803)
29	*Ensis siliqua* (Linnaeus, 1758)	95	*Rissoa parva* (da Costa, 1778)
30	*Epitonium clathratulum* (Kanmacher, 1797)	98	*Scrobicularia plana* (da Costa, 1778)
32	*Ervilia castanea* (Montagu, 1859)	105	*Spisula solida* (Linnaeus, 1758)
38	*Gibbula cineraria* (Linnaeus, 1758)	106	*Spisula subtruncata* (da Costa, 1778)
39	*Gibbula pennanti* (Philippi, 1836)	111	*Tellina donacina* Linnaeus, 1758
40	*Gibbula umbilicalis* (da Costa, 1778)	112	*Tellina tenuis* da Costa, 1778
42	*Haminea navicula* (da Costa, 1778)	115	*Chrysallida terebelum* (Philippi, 1844)
44	*Hiatella arctica* (Linnaeus, 1758)	117	*Venerupis decussata* (Linnaeus, 1758)
45	*Hydrobia ulvae* (Pennant, 1777)	118	*Venerupis pullastra* (Montagu, 1803)
46	*Hydrobia ventrosa* (Montagu, 1803)	119	*Venus striatula* (da Costa, 1778)
	ARTHROPODA		
10	*Atelecyclus* sp.	52	*Macropodia rostrata* Linnaeus, 1761
11	*Atylus swammerdami* (Milne-Edwards, 1830)	53	*Macropipus* sp.
17	*Caprella acanthifera* Leach, 1814	57	*Melita palmata* (Montagu, 1804)
18	*Carcinus maenas* (Linnaeus, 1758)	58	*Microdeutopus gryllotalpa* Costa, 1853
20	*Chironomidae* sp.	72	*Palaemon elegans* Rathke, 1837
23	*Corophium insidiosum* Crawford, 1937	73	*Palaemon serratus* (Pennant, 1777)
24	*Cyathura carinata* (Krøyer, 1847)	74	*Palaemonetes varians* (Leach 1814)
28	*Dynamene bidentata* Adams, 1800	75	*Paramysis bacescoi* Labat, 1953
31	*Ericthonius difformis* Milne-Edwards, 1830	77	*Paramysis nouveli* Labat, 1953
37	*Gammarus insensibilis* Stock, 1966	99	*Sphaeroma hookeri* Leach, 1814
47	*Idotea chelipes (=viridis)* (Slabber, 1778)	100	*Sphaeroma monodi* Bocquet, Hoestland Lévi, 1954
	ECHINODERMATA		
76	*Paracentrotus lividus* (Lamarck, 1816)	92	*Psammechinus miliaris* (Gmelin, 1807)
	VARIA		
5	*Ammodytes tobianus* Linnaeus, 1758)	62	Nemertea sp. B
6	*Anguilla anguilla* (Linnaeus, 1758)	63	Nemertea sp. C
7	*Anemonia* sp.	64	Nemertea sp. D
8	Anthozoan sp. indet.	65	Nemertea sp. E
14	*Branchiostoma lanceolatum* (Pallas, 1778)	83	*Phoronis psammophila* Cori, 1889
21	*Ciona intestinalis* (Linnaeus, 1767)	89	*Pomatoschistus microps* (Krøyer, 1838)
61	Nemertea sp. A	110	*Syngnathus acus* (Linnaeus, 1758)
		116	Platyhelminthes sp. indet.

species. A species list with taxonomic authorities is given in table III.

The distribution of species per sampling station shows an enrichment gradient, directed from the outer and inner stations towards intermediate ones, located along the navigation channel and bordering the intertidal sand-bank (Fig. 5). The distribution of the abundance of individuals (Fig. 5) also shows that the poorest regions comprise the outermost and innermost sampling stations. However, the sampling stations with the highest total abundances are located further from the channel sand-bank area than those with the highest species richness.

Thus along the axis of the lagoon from the entrance to the inner basin, the species enrichment reaches a maximum before the highest densities are found. Similar results are known from the Lagoon of Albufeira (QUINTINO & RODRIGUES, 1985) and the Ria of Alvor (RODRIGUES & QUINTINO, 1986), western and southern coast of Portugal. Perimediterranean lagoon systems show similar gradients (AMANIEU *et al.*, 1977; 1979; GUELORGET & PERTHUISOT, 1983), the major difference being the absence of an initial inwards enrichment. This could be caused by the stronger tidal currents along the entrance channel in Atlantic lagoons which induces a coarse and moving sedimentation, thus inhibiting the settlement of species in the vicinity of the lagoon mouth.

BENTHIC COMMUNITIES

The raw data consisted of a binary matrix (presence-absence) of station × species. The final treatment considered a 57 stations × 98 species matrix, by the omission of species sampled once.

The first ten eigenvalues of the correspondence analysis explained 57.1 % of the total inertia, with axes 1 and 2 comprising 24.5 %. The results showed three major affinity groups among both stations and species, distributed in plane 1-2 according to figures 6 (stations) and 7 (species). Again, the simultaneous representation of samples and species has been avoided; figures 6 and 7 are, however, drawn to the same scale.

Among the sampling stations the groups Aa, Ab and B, with Ba and Bb, were obtained. Subgroup Bb comprised three further divisions represented in figure 6 by assemblages Bb_1, Bb_2 and Bb_3. Axis 1 opposes assemblage Aa (quadrant $1^+ 2^-$) to assemblage Bb ($1^- 2^-$). The transition from Aa to Bb is made by groups Ab ($1^+ 2^+$) and Ba (mainly $1^- 2^+$), by the positive pole of axis 2. The succession Aa → Ab → B (Ba → Bb) shows a clear spatial correspondence represented by the outermost sampling stations located in the vicinity of the lagoon mouth (Aa) to the stations of the navigation channel (Ab) and to the stations comprising the intertidal sand-bank (Ba) and the remaining stations located inwards of any of the previous groups (Bb).

The subgroups Bb_1, Bb_2 and Bb_3 maintain this geographical coherence; Bb_1 comprises 4 stations located inwards to the intertidal sand-bank; Bb_2 is a group of 17 stations inward to Bb_1 and located in the shallow regions of the center of the lagoon, and Bb_3 concerns 10 stations occupying both the deeper regions of the center of the lagoon and the innermost

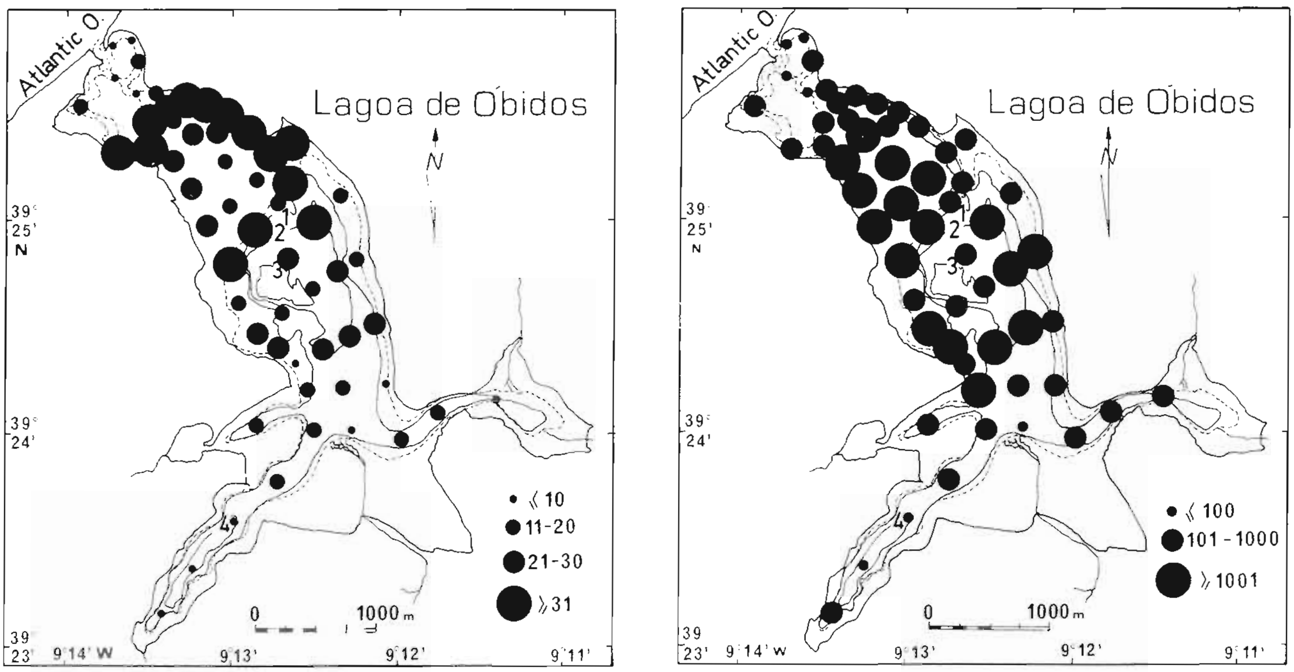

FIG. 5. — Number of species (left) and number of individuals (right) per sample in the Obidos lagoon.

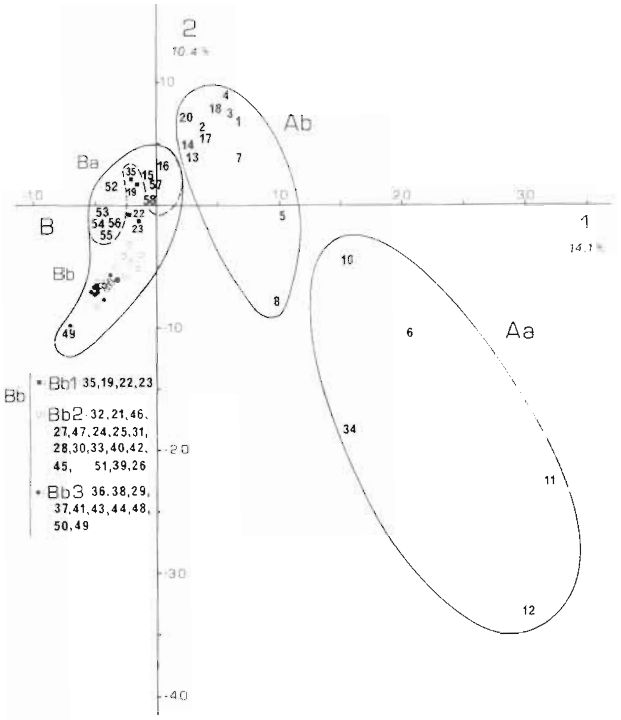

FIG. 6. — Affinity assemblages among sampling stations according to the partition obtained in plane 1-2 of the correspondence analysis.

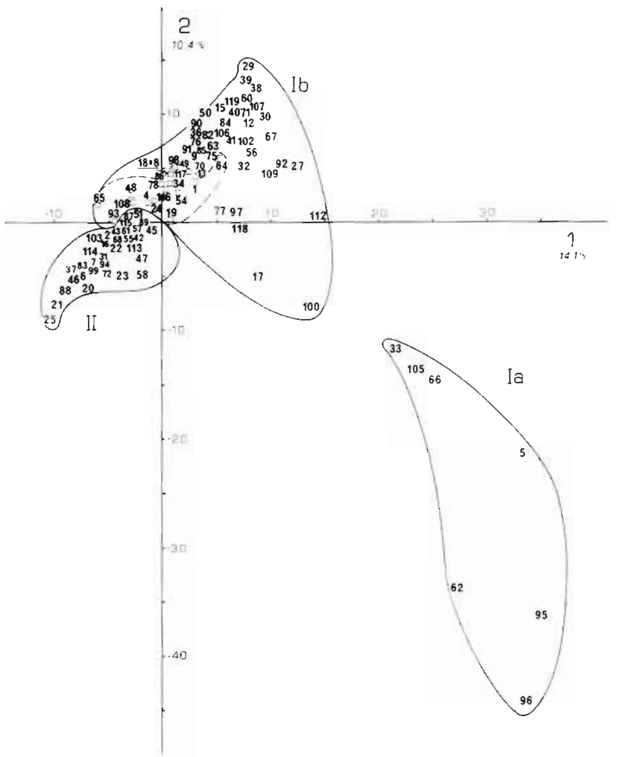

FIG. 7. — Affinity assemblages among species according to the partition obtained in plane 1-2 of the correspondence analysis. For correspondence of code numbers with species names refer to Table III.

sampling stations located in Barrosa and Bom Sucesso.

Among the species the affinity groups Ia (quadrant $1^+ 2^-$), Ib ($1^+ 2^+$) and II ($1^- 2^-$) were obtained (Fig. 7). Axis 1 opposes the group Ia, comprising 7 species, to the group II, of 33 species. The transition is made by the group Ib, of 58 species, by the positive pole of axis 2.

Assemblages Ia, Ib and II agree with the former partition into groups Aa, Ab and B.

Group Ia consists of a few characteristic marine species (*Spisula solida, Nephtys cirrosa, Ammodytes tobianus, Saccocirrus papillocercus,* etc.) and group II contains several characteristic lagoon and estuarine species (*Abra ovata, Loripes lacteus, Rissoa labiosa, Hydrobia ventrosa, Heteromastus filiformis, Nereis diversicolor, Capitella capitata, Polydora ciliata, Tubificoides benedeni, Corophium insidiosum, Gammarus insensibilis, Microdeutopus gryllotalpa, Sphaeroma hookeri, Idotea chelipes, Phoronis psammophila,* etc.).

Thus, axis 1 opposes the outermost stations together with a group of marine species, to the innermost stations and a group of characteristic lagoonal species. Axis 2 isolates a group of intermediate stations together with the richest affinity group of species.

These results suggest the presence of two distinct benthic communities, one located near the lagoon mouth and the other in inner areas, connected by a transition area characterized by high species richness.

The macrozoobenthic community structure of the lagoon of Obidos, illustrated in figure 8, is described as follows:

OI: marine community located on clean coarse unstable sand (mean = 0.78ø; median = 0.83ø; sorting coefficient = 0.82ø; mean silt percentage = 1.1 %). Geographically identified with the lagoon mouth, this community was defined by sampling stations 6, 10 to 12 and 34. It corresponds to 4 % of the bottom surface, and it is characterized by *S. solida, N. cirrosa, S. papillocercus* and *A. tobianus*. Species richness and individual abundance are both low in this community due to coarse and moving sand sedimentation.

OII: intermediate assemblage, geographically inward of OI, located on slightly silty medium sand (mean = 1.32ø; median = 1.37ø; sorting coefficient = 0.99ø; mean silt percentage = 5.9 %). This assemblage comprises 11 % of the bottom surface and corresponds to the navigation channel, crossing the intertidal sand-bank along the northern margin of the lagoon. It was defined by sampling stations 1 to 5, 7, 8, 13, 14, 17, 18 and 20. Containing some species from both the marine and lagoon communities, this assemblage is also characterized by several species sampled only in this region, namely the polychaetes

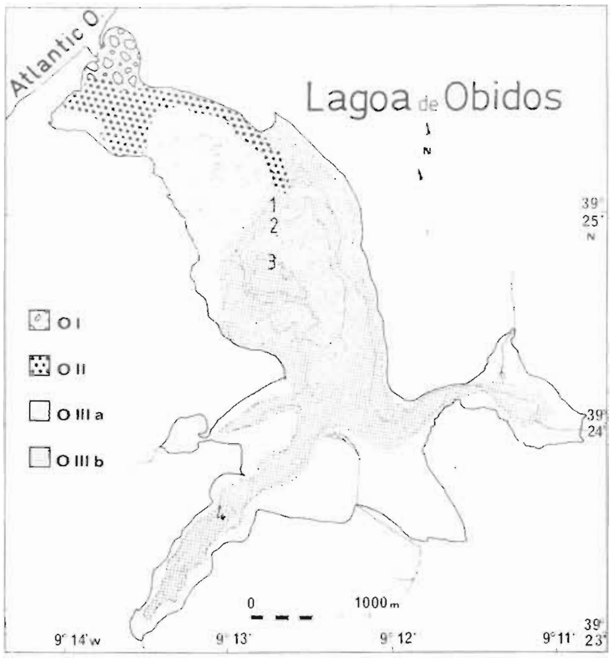

FIG. 8. — Spatial distribution of the macrozoobenthic communities in the lagoon of Obidos. OI = marine community of *Spisula solida-Nephtys cirrosa;* OII = ecotone area; OIII = lagoon community of *Abra ovata-Heteromastus filiformis* with OIIIa = sand-bank of *Pygospio elegans* and OIIIb = type lagoon community.

Cirriformia tentaculata, Sthenelais boa, Owenia fusiformis and *Phylo foetida,* and the molluscs *Nassarius reticulatus, Gibbula pennanti, G. umbilicalis* and *Venus striatula.*

This assemblage shows the highest values for species richness and intermediate values for total abundance. It may be considered an ecotone area in the sense described by ODUM (1971).

OIII: lagoon community, inward of OI and OII, mainly located on fine muds. This community corresponds to 85 % of the bottom surface and comprises both the intertidal sand-bank (sampling stations 15, 16 and 52 to 58, with mean = 1.54ø, median = 1.53ø, sorting coefficient = 0.77ø and mean silt content = 3.0 %), and the whole group of stations located in the center and innermost regions of the lagoon (sampling stations 19, 22 to 33 and 35 to 51, with mean and median > 4ø and mean silt content = 80 %).

The lagoon community is characterized by a large number of species frequently reported from lagoon systems, namely the molluscs *A. ovata* and *H. ventrosa,* the annelids *H. filiformis, C. capitata, N. diversicolor, P. ciliata, P. antennata, M. fuliginosa* and *T. benedeni,* the arthropods *C. insidiosum, G. insensibilis, M. gryllotalpa, S. hookeri* and Chironomids, and the phoronid *P. psammophila.*

The lagoon community has no particular subdivisions. However, the intertidal sand-bank is characterized by the polychaete *Pygospio elegans,* collected only in this region. The assemblages Bb_1, Bb_2 and Bb_3 established within the group Bb show only different species richness and individual abundance with an impoverishment gradient from Bb_1 to Bb_2 and to Bb_3. This gradient is established from outwards (Bb_1) to inwards (Bb_3) and corresponds to an increasing silt content of the surface sediments. The mean silt content of subgroups, Bb_1, Bb_2 and Bb_3 is respectively 30 %, 83 % and 99 %.

Table IV presents the total number of individuals and species of each of the assemblages, together with species sampled only once in each of the regions.

This coenotic model for the lagoon of Obidos suggests that the major factor determining the composition and distribution pattern of macrozoobenthos is related to a hydrosedimentological gradient acting along the longitudinal axis of the lagoon. This gradient could be expressed as a decreasing hydrodynamic energy level as distance from the lagoon entrance increases, resulting in an increase in the sedimentary silt content in the inner areas and in higher annual amplitudes of physico-chemical parameters in the innermost regions.

TABLE IV. — Distribution of the number of species and individuals in each of the communities. N, number of sampling stations; S, number of species; F1, number of species sampled once; s, mean number of species per sampling station; T, number of individuals per sampling station; t, mean number of individuals per samplig station; A, bottom percentage area.

Communities	*N*	*S*	*F1*	*s*	*T*	*t*	*A*
Marine	5	26	12	10	261	52	4 %
Lagoon	40	84	23	19	62067	1552	85 %
sand-bank	9	54	15	21	18629	2070	
mud-bottom	31	72	17	18	43438	1401	
Bb1	4	59	24	34	22780	5695	
Bb2	17	51	16	17	15446	909	
Bb3	10	37	10	14	5212	521	
Ecotone	12	97	23	37	5829	486	11 %
Total	57	119	21	22	68157	1196	100 %

DISCUSSION

According to the NICHOLS & ALLEN (1978) classification of lagoon systems, based on the relative importance of wave action, tidal currents and fluvial inputs, the lagoon of Obidos may be considered a semi-enclosed system, comparable namely to the lagoon of Albufeira, western coast of Portugal (QUINTINO & RODRIGUES, 1986) and the lagoon of Moulay-bou-Salham, atlantic coast of Morocco (BIDET *et al.*, 1977). In this type of lagoon system the major hydrodynamic agents are the waves and tidal currents, tending to establish a shallow and narrow entrance channel subject to episodic sand obstructions. Muds predominate in the inner areas and sandy sediments are distributed only near the entrance area.

The bio-sedimentological gradients identified suggest a coenotic model consisting of sucessive inward zones related to the incursion of coastal waters through the entrance channel. Thus, surface sediments and benthic communities are both distributed along the longitudinal axis of the lagoon, without showing particular transverse components. This distribution is represented by an outer marine community settled on clean coarse unstable sand, in contrast to an inner lagoon community settled on fine muds, connected by an ecotone area settled on more diverse surface sediments.

The faunal composition of the lagoon of Obidos can be related to the Atlantic and Mediterranean fauna of coastal or lagoon systems (MUUS, 1967; RASMUSSEN, 1973; GUELORGET & PERTHUISOT, 1983). In this analysis, the outer marine community corresponds to a similar community described by RETIÈRE (1979) in Rance Maritime and by GENTIL (1982) in the outer part of Aber Wrac'k, both settled on unstable medium to coarse sands due to strong hydrodynamic action. The inner lagoon community is typical of coastal Atlantic and Mediterranean lagoons and is related to the *biocenose lagunaire euryhaline et eurytherme* (LEE) (PÉRÈS & PICARD, 1964; BELLAN, 1964) and to the *Cardium edule - Scrobicularia plana* variety of the *Macoma balthica* community in THORSON'S (1957) system.

This scheme for the distribution and composition of soft bottoms and benthic communities in the lagoon of Obidos is similar to the one described in the lagoon of Albufeira, Portugal (QUINTINO *et al.*, 1987) and to the general model proposed by GUELORGET & PERTHUISOT (1983) for the perimediterranean lagoon systems. The major difference may be considered to be the initial inwards species enrichment. This may reflect the stronger wave action and tidal currents in the entrance channels of Atlantic laggons.

The inner lagoon community, occupying 85 % of the total bottom surface, has a species composition which also reflects an organic enrichment of sediments (*M. fuliginosa, H. filiformis, P. ciliata, T. benedeni, P. psammophila, C. gibba*, etc.) (PEARSON & ROSENBERG, 1978). Recorded densities higher than 10,000 ind. m^{-2} (unpubl. data), could, in a situation of temporary oxygen depletion, induce mass mortality in this community, as observed in the lagoon of Albufeira, during a period when the communication with the ocean was obstructed (QUINTINO & RODRIGUES, 1985). In order to study the dynamics of these benthic populations a quantitative survey was held from October 1984 to December 1986.

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REFERENCES

AMANIEU, M., GUELORGET, O. & MICHEL, P. 1977. Richesse et diversité de la macrofaune benthique d'une lagune littorale Mediterranéenne. *Vie Milieu*, 27 (1B): 85-109.

AMANIEU, M., GUELORGET, O. & MICHEL, P. 1979. Evolution structurale des peuplements de la macrofaune benthique des étangs palavasiens. *Vie Milieu*, 28-29 (4AB): 513-547.

BENZECRI, J. P. *et al.* 1973. *L'analyse des donnèes. 1: La taxinomie, 2: L'analyse des Correspondances*. Dunod. Paris.

BIDET, J.-C., CARRUESCO, C. & GENSOUS, B. 1977. Un milieu sédimentaire actuel: la lagune de Moulay-bou-Salham (côte atlantique marrocaine). *Bull. Inst. Géol. Bassin d'Aquitaine*, 22: 189-230.

CABIOCH, L. 1968. Contribution à la connaissance des peuplements benthiques de la Manche Occidentale. *Cah. Biol. Mar.*, (5) (suppl.): 493-720.

CALDEIRA, M., HENRIQUES, M. & DUARTE, F. 1986. Caracterização fisico-quimica da lagoa de Obidos. *In: Contribuição para a caracterização ecológica da lagoa de Obidos*. 15-83. Report LNETI, Dezembro 1986.

CHARDY, P., GLÉMAREC, M. & LAUREC, A. 1976a. Application of inertia methods to benthic marine ecology: pratical implication of the basic options. *Estuarine Coastal Mar. Sci.*, 4: 179-205.

CHARDY, P., DESBRUYÈRES, D. & LAUREC, A. 1976b. Bionomie benthique du plateau continental de l'Archipel des Iles Kerguelen - macrofaune 4. Analyse multivariable des taxocenoses annelidiennes du Golfe du Morbihan. *CNFRA*, 39: 97-105.

CREVEL, L. 1983. *Contribution à l'étude de la dynamique sédimentaire dans la partie nord-orientale de la Baie de Seine*. Thèse 3ème cycle. Univ. Paris-Sud (Orsay).

DOEGLAS, D. J. 1968. Grain-size indices, classification and environment. *Sedimentology*, 10: 83-100.

FOLK, R. L. & WARD, W. C. 1957. Brazos River bar, a study in the significance of grain-size parameters. *J. Sediment. Petrol.*, 27: 3-27.

GENTIL, F. 1982. Description du benthos de l'Aber Wrac'k (Nord Bretagne) et impact à court terme des hydrocarbures de l'"Amoco Cadiz". *107ème Congrès National des Sociétés Savantes, Brest, 1982, Sciences. II*: 111-125.

GUELORGET, O. & PERTHUISOT, J.-P. 1983. Le domaine paralique. Expressions geologiques, biologiques et économiques du confinement. *Trav. Lab. Geol. E. N. S., Paris*, 16: 1-136.

JAMBU, M. 1978. *Classification automatique pour l'analyse des données. 1 - méthodes et algorithmes* . Dunod. Paris.

JAMBU, M. & LEBEAUX, M.-O. 1978. *Classification automatique pour l'analyse des données. 2 - Logiciels*. Dunod. Paris.

LARSONNEUR, C. 1977. La cartographie des dépots meubles sur le plateau continental français: méthode mise au point et utilisée en Manche. *J. Rech. Oceanogr.*, II (2): 33-39.

LEBART, L., MORINEAU, A. & TABARD, N. 1977. *Technique de la description statistique. Mèthodes et logiciels pour l'analyse des grands tableaux*. Dunod. Paris.

MALMGREN, B., OVIATT, C., GERBER, R. & JEFFRIES, H. P. 1978. Correspondence analysis: applications to biological oceanographic data. *Estuarine Coastal Mar. Sci.*, 6: 429-437.

MORGANS, J. F. C. 1956. Notes on the analysis of shallow-water soft substrata. *J. Anim. Ecol.*, 25: 367-387.

MUUS, J. L. 1967. The fauna of danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow beaches of the mesohaline zone. *Medd. Dan-Fisk Havunders. Gelser.*, 5 (1): 1-316.

NICHOLS, M. & ALLEN, G. P. 1978. Sedimentary processes in lagoons. *Seminar on present and future research in coastal lagoons.* UNESCO, Div. Mar. Sci., Beaufort, NC.

ODUM, E. P., 1971. *Fundamentals of Ecology.* Saunders. Philadelphia.

PEARSON, T. & ROSENBERG, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.*, 16: 229-311.

PLANTE, R., FRONTIER, S., LE LOEUFF, P. & REYS, J.-P. 1983. Stratégies d'échantillonnage et fluctuations naturelles dans des écosystèmes benthiques. Deux exemples en milieu tropical. *Oceanol. Acta (sp. vol.) Proceedings 17th European Marine Biology Simposium, Brest, 27th September-1st October.* 153-157.

QUINTINO, V. & RODRIGUES, A. M. 1985. Estudo da macrofauna bentónica da lagoa de Albufeira, costa oeste de Portugal: sedimentologia, estrutura de povamentos e stress ambiental provocado pelo fecho da lagoa em Janeiro/Fevereiro de 1985. *In: Caracterização ecológica e potencialidades de utilização da lagoa de Albufeira*: 156-265. Repport LNETI, Dezembro 1985.

QUINTINO, V. & RODRIGUES, A. M. 1986. Cartografia dos sedimentos superficiais da lagoa de Albufeira. *Rec. Hidricos*, 7 (1): 87-100.

QUINTINO, V., RODRIGUES, A. M., GENTIL, F. & PENEDA, M. C. 1987. Macrozoobenthic community structure in the lagoon of Albufeira, western coast of Portugal. *J. Exp. Mar. Biol. Ecol.*, 106: 229-241.

RASMUSSEN, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia*, 11: 1-507.

RETIÈRE, C. 1979. *Contribution à la connaissance des peuplements benthiques du golfe Normanno-Breton.* Thèse d'état. Univ. Rennes.

RODRIGUES, A. M. & QUINTINO, V. 1986. Macrofauna bentónica da ria de Alvor, costa sul de Portugal: sedimentologia, estrutura e distribuição de povoamentos. *In: Caracterização ecológica da ria de Alvor*: 88-188. Repport LNETI. Julho 1986.

THORSON, G. 1957. Bottom communities (sublitoral or shallow shelf). *In: Treatise on marine ecology and paleoecology* (J. W. Hedgepeth, ed.) *Mem. Geol. Soc. Amer.*, 67: 461-534.

TRASK, P. D. 1930. Mechanical analysis of sediments by centrifuge. *Econ. Geol.*, 25: 581-599.