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Quantitative investigations of sand-bottom macrofauna along the Mediterranean north-west coast

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Abstract

Consideration of the range of quantitative data collected in a 4 year survey of macrobenthic fauna in sublittoral fine-sand on the north-west Mediterranean coast allows some far-reaching comments. As a diver-operated suction sampler was employed, density and biomass values obtained must be considered as the most accurate ones for such hard ground. The wide range of values observed from bay to bay and from year to year suggests different controlling factors. Among environmental factors, influence of exposure is clearly shown, and trophic conditions offered to filter and suspension feeders by the water column in controlling high biomass values is emphasized. Among biological factors, high growth and generation replacement rates for main species together with a high predation-rate explain changes and instability in fauna-assemblage structures of Mediterranean fine-sand macrofauna. Comparison of these biological data with those from north-west European shallow-sand associations reveals some important differences which suggest some restrictions to the parallel level-bottom community concept.

Introduction

Because of the sampling difficulty in sublittoral, fine, well-sorted sand in shallow waters, few quantitative data are available (McIntyre and Eleftheriou, 1968). Furthermore, the quantitative data available undervalue densities and more especially biomass, as they are obtained with grabs which are useless for taking deep, quantitative, samples in hard sand (Barnett and Hardy, 1967). In important tidal seas, beaches situated in the intertidal zone can be easily sampled during low tide with a shovel at a suitable depth to collect all the macrofauna (McIntyre, 1970). Unfortunately, in the Mediterranean Sea, the sandy bottoms corresponding to those of the intertidal beaches are subtidal; so, in order to compare the quantitative data reliably, it is necessary to use a more accurate bottom sampler.

Different types of diver-operated suction samplers have been described for shallow waters (Brett, 1964; Barnett and Hardy, 1967; Emig and Lienhart, 1967; Amouroux and Guille, in press), and it has been shown that these samplers, provide more suitable quantitative data than the classic grabs (Massé, 1967; Reys and Salvat, 1971; Amouroux and Guille, in press). Therefore, it is now possible to give an idea of real densities and biomass of sand macrofauna in infralittoral bottoms as defined by Peres and Picard (1964).

Since 1965, several stations on fine well-sorted sand bottoms have been sampled along the Provence coast (France). This paper presents the results of a 4 year survey, describes the range of quantitative data, and discusses the variations.

Material and methods

The area investigated (Fig. 1) stretches along 1° longitude (48 nautical miles); 5 bays have been examined. It is possible to divide the bays into three groups, according to water properties.

In the first group, the Camargue coast and Fos Gulf, the sampling stations are located near the mouth of a great river (Rhône) and exposed to eutrophic effects (Blanc et al., 1969; Blanc and Leveau, 1970). In the second group, Bandol and Verdon Bays, the bottom is washed by typical Mediterranean oligotrophic waters with a very low seston concentration (generally below 1 mg/l). Between these two groups, Prado Bay in the Marseille Gulf is washed by waters with a high organic-matter content due to sewage, which produces both a eutrophic effect and a pollution effect, so that some suspension-feeders indifferent to pollution (mainly polychaetes and *Phoronis*) occur in very large densities, while other species (mainly bivalves) have an abnormally short life cycle owing to pollution effects.

In the waters of the different bays, salinities near the bottom are generally fairly uniform about 38‰. Nevertheless, in Verdon Bay and near the Rhône mouth, dilution by surface fresh water may result in low salinity values from 35 to 36‰. The same phenomena occurs in Prado Bay for the upper water layer (0 to 1.5 m), near the shore.

Biological samples were taken at different stations ranging from 1.5 to 11 m depth. For each bay, a sampling station was chosen at 5 m depth; this was named the "reference station" as it represented the most typical macrofauna assemblage in fine sand.

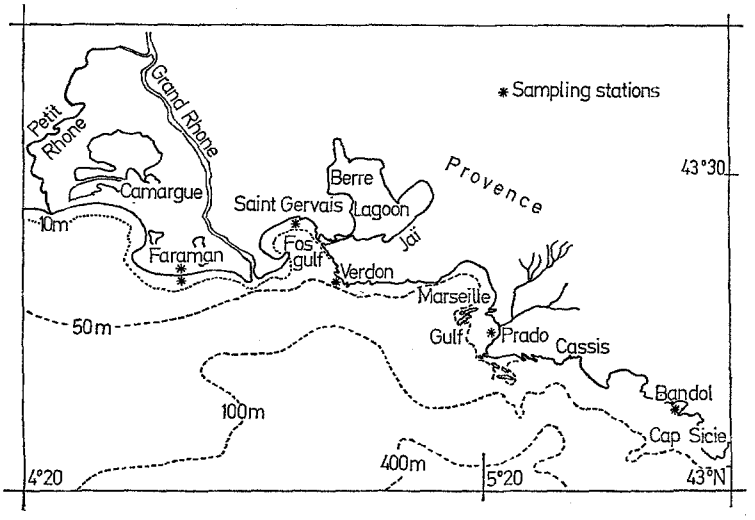

Fig. 1. Area investigated

Particle-size analyses were made of the sand which was, in all areas, well sorted. In the upper horizon, at a depth of 1.5 m, the median grain-diameter ranged from 120 to 220 μ. In the lower horizon (5 m deep and below), the median grain-diameter was smaller, from 103 to 125 μ.

The calcium-carbonate content varied greatly from bay to bay. Near the Rhône mouth it was low, about 24 to 27%. In Bandol and Prado Bays its average value was between 33 to 37%, while in the very small Verdon Bay it ranged from 70 to 73%.

The sand was generally very clean, with a low organic content. The total organic-carbon content, expressed as a percentage of dried sediment, fluctuated from 0.2 to 1%, the total nitrogen content from 0.01 to 0.03%.

The sampling technique with a diver-operated, quantitative suction sampler has been described in full by Massé (1970a), with special emphasis on the careful handling underwater, necessary to obtain valuable quantitative data.

Owing to high air-temperatures, it is necessary to use a 10 or 15% solution of commercial formalin buffered with borax to preserve the macrofauna and residue retained in the sample bag of the suction sampler. Sorting of the animals from the residue is performed after a second careful laboratory sieving on a 0.7 mm mesh in a water bowl to reduce the sample size. As has been discussed several times (Holme, 1953; Reish, 1959; Sanders, 1960; Thorson, 1966), the sieving technique has a very important effect on density values, which increase rapidly as mesh-size decreases. Although benthos scientists are not in full agreement upon what constitutes a standard mesh size (Holme and McIntyre, 1971), many use a 1 mm mesh (Ziegelmeier, 1963, 1970; Guille, 1969; Stripp, 1969; Pearson, 1970; and others).

Some differences arise also depending upon whether the diameter of a round-holed mesh is considered, or, if a square mesh is used, whether the side or the diagonal of the mesh aperture is considered. The 0.7 mm mesh used in this study has a square aperture, with a 1 mm diagonal as in Jones (1969).

In expressing biomass values, the greatest difficulty for comparison purposes lies in the fact that several weights may be considered: fresh, wet, dry, or ash-free weight. It seems better to express the biomass data in dry weight of organic matter, i.e., without shell, skeleton, or gut contents. The ash-free weight has not been evaluated because we must keep in mind that formalin preservation is responsible for organic-matter loss (Holme, 1964; Reys and Salvat, 1971) and that sampling and sieving techniques which fragment many animals (bivalve siphon-tips, polychaete palps, ophiuroid arm-tips, etc.), are also responsible for an organic-matter loss which may affect the ash weight of soft tissues and inorganic remains.

The fauna assemblage

The detailed species lists for each station, as well as density and biomass values, have been published in several papers (Massé, 1970b, 1971a, b, c). In the present paper, only the most abundant species collected during the 4 year survey are mentioned, together with the mean density values throughout the period.

From Picard's descriptive and qualitative study (1965), the fine sand bottom fauna in shallow waters may be divided into two different biocoenosis from the parallel level-bottom community point-of-view. Also in my quantitative survey in the sublittoral fine-sand belt, the two horizons have been recognized, the mutual limit of which depends mainly on exposure. Some species living generally in the upper sand-

Table 1. *Most abundant species and mean number of individuals/m² for upper horizon in Prado Bay*

Rank	Species	Density
1	*Spio decoratus*	2770
2	*Corbula (Lentidium) mediterranea*	1099
3	*Cumopsis longipes*	1097
4	*Donax semistriatus*	367
5	*Atylus* sp.	194
6	*Tellina tenuis*	102
7	*Glycera convoluta*	56
8	*Magelona papillicornis*	24
9	*Drilonereis filum*	17
10	*Venus gallina*	16

bottom horizon are found deeper under extreme exposure conditions; on the other hand, some species living generally in the deeper horizon have invaded very shallow sand under sheltered exposure conditions.

Upper horizon

The fauna assemblage corresponds to "fine sand biocoenosis in very shallow waters" (Peres, 1967). Table 1 presents details of the most abundant species ranking from 1 to 10 according to mean density-values, these being especially high in Prado Bay, generally low in the open sea (Table 7).

Deep horizon

The fauna assemblage corresponds to "fine well sorted sand biocoenosis" (Peres, 1967). Tables 2 to 6 present different aspects of the main species-stock from bay to bay at different depths. Comparison of these Tables with those of McIntyre and Eleftheriou (1968), reveals important similarities, which make it possible to refer the superficial and deep horizons of Mediterranean sublittoral sand to the boreal shallow sand and boreal off-shore sand associations, respectively, as defined by Jones (1950).

Fauna structure

Upper horizon (Fig. 2)

Three sampling stations were located in the Marseille Gulf; stations varied in degree of exposure: Station A, exposed; Station B, more moderate exposure; Station C, sheltered. As sampling times in such shallow waters of necessity must correspond with good weather conditions, we noticed an increase of crustacean fauna with degree of exposure. In bad weather, this motile fauna migrates deeper. On the other hand, an increase in polychaete and mollusc numbers and weights occurs with moderate exposure, and total density and biomass values increased under sheltered conditions. At each station, the mollusc biomass is very important, as exposure conditions are not ex-

Table 2. *Most abundant species and mean number of individuals/m² in deeper horizon, Prado Bay (Stations 1 and 2)*

Rank	Species	Density	Species	Density
Station 1 (−5 m)			Station 2 (−5 m)	
1	*Phoronis psammophila*	4905	*Phoronis psammophila*	4080
2	*Spio decoratus*	2346	*Spio decoratus*	972
3	*Clymene oerstedi*	431	*Clymene oerstedi*	263
4	*Owenia fusiformis*	267	*Owenia fusiformis*	177
5	*Ampelisca brevicornis*	339	*Magelona papillicornis*	174
6	*Magelona papillicornis*	262	*Ampelisca brevicornis*	159
7	*Nephthys hombergi*	124	*Nephthys hombergi*	102
8	Paraonidae[a]	(109)	Paraonidae[a]	(80)
9	*Atylus* sp.	73	*Glycera convoluta*	50
10	*Pseudocuma longicornis*	72	*Donax venustus*	49
11	*Cumopsis longipes*	72	*Venus gallina*	49
12	*Venus gallina*	63	*Pseudocuma longicornis*	42
13	*Donax venustus*	61	*Iphinoe douniae*	39
14	*Sigalion mathildae*	51	*Atylus* sp.	34
15	*Iphinoe douniae*	49	*Sigalion mathildae*	30
16	*Prionospio caspersi*	47	*Perioculodes longimanus*	25
17	*Pariambus typicus*	42	*Cumopsis longipes*	21
18	*Perioculodes longimanus*	29	*Pariambus typicus*	19
19	*Glycera convoluta*	28	*Tellina fabula*	18
20	*Tellina fabula*	25	*Dosinia lupinus*	17
21	*Spisula subtruncata*	24	*Eteone syphonodonta*	15
22	*Loripes lacteus demaresti*	14	*Loripes lacteus demaresti*	15
23	*Dosinia lupinus*	9	*Spisula subtruncata*	13

[a] Mainly *Aricidea catherinae*.

Table 3. *Most abundant species and mean number of individuals/m² in Bandol Bay*

Rank	Species	Density	Species	Density	Species	Density
Station 1 (−5 m)			Station 2 (−8 m)		Station 3 (−11 m)	
1	*Bathyporeia guilliamsoniana*	153	*Ampelisca brevicornis*	237	*Chone* cf. *filicaudata*	233
2	*Lumbriconereis impatiens*	139	*Bathyporeia guilliamsoniana*	95	*Ampelisca brevicornis*	199
3	*Phoronis psammophila*	129	*Tellina fabula*	65	*Urothoe grimaldi*	90
4	*Ampelisca brevicornis*	111	*Chone* cf. *filicaudata*	63	*Tellina fabula*	88
5	*Urothoe grimaldi*	47	*Venus gallina*	62	*Bathyporeia guilliamsoniana*	70
6	*Venus gallina*	32	*Lumbriconereis impatiens*	57	*Venus gallina*	58
7	*Scoloplos armiger*	31	*Magelona papillicornis*	38	*Paradoneis armata*	56
8	*Chone* cf. *filicaudata*	23	*Urothoe grimaldi*	38	*Lumbriconereis impatiens*	54
9	*Magelona papillicornis*	21	*Perioculodes longimanus*	35	*Sigalion mathildae*	46
10	*Sigalion mathildae*	21	*Sigalion mathildae*	28	*Perioculodes longimanus*	42
11	*Perioculodes longimanus*	19	*Phoronis psammophila*	25	*Apseudes latreilli (mediterraneus)*	37
12	*Paradoneis armata*	19	*Paradoneis armata*	19	*Magelona papillicornis*	31

treme, even at Station A. Although mollusc biomass increases steadily from Station A to Station C, in diagrammatic representations the decrease in mollusc weight, as a percentage of the total biomass, from

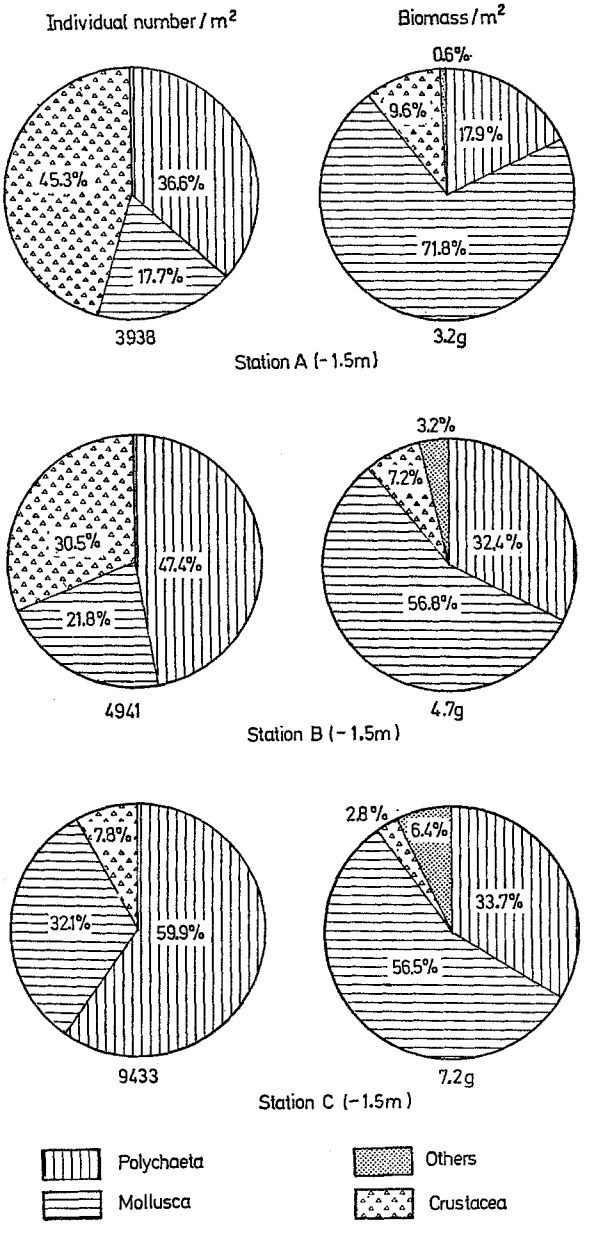

Fig. 2. Main group stocks as percentage of density and biomass values for the 3 stations of upper horizon, Prado Bay

Station A to Station C is correlated with an important polychaete-biomass increase.

These data may be compared with McIntyre's observations (1970) on the north-west Scottish coast,

Table 4. *Most abundant species and mean number of individuals/m² in Verdon Bay*

Rank	Species	Density	Species	Density
Station 1 (5 m)			Station 2 (9 m)	
1	*Atylus* sp.	330	*Spisula subtruncata*	428
2	*Magelona papillicornis*	150	*Paradoneis armata*	202
3	*Venus gallina*	86	*Magelona papillicornis*	184
4	*Siphonoecetes sabatieri*	48	*Ampelisca brevicornis*	134
5	*Ampelisca brevicornis*	48	*Venus gallina*	118
6	*Paradoneis armata*	47	*Bathyporeia guilliamsoniana*	55
7	*Bathyporeia* sp.	39	*Perioculodes longimanus*	54
8	*Nephthys* sp.	36	*Iphinoe armata*	53
9	*Perioculodes longimanus*	28	*Atylus* sp.	52
10	*Hippomedon massiliense*	27	*Nephthys* sp.	45
11	*Glycera* sp.	26	*Tellina fabula*	38
12	*Spisula subtruncata*	25	*Lumbriconereis impatiens*	36

Table 5. *Most abundant species and mean number of individuals/m² in Fos Gulf (reference station 5 m deep)*

Rank	Species	Density
1	*Venus gallina*	205
2	*Urothoe grimaldi*	116
3	*Lumbriconereis impatiens*	69
4	*Ampelisca brevicornis*	68
5	*Sigalion mathildae*	55
6	*Magelona papillicornis*	43
7	*Bathyporeia guilliamsoniana*	29
8	*Spisula subtruncata*	22
9	*Nephthys hombergi*	22
10	*Clymene* sp.	17
11	*Acrocnida brachiata*	16
12	*Glycera convoluta*	15
13	*Diogenes pugilator*	14

and are of general interest (Southward, 1953); they illustrate exposure influence as an environmental factor on quantitative sand-bottom macrofauna distribution in shallow waters.

Deep horizon (Figs 3—7)

In Prado Bay (Marseille Gulf), the special conditions previously mentioned involve an interesting phenomenon. An important pollution effect, especially at Station 2, greatly limits the mollusc-population development, and most species have a very short life cycle (Massè, 1971a). On the other hand, some pollution-resistant species such as *Phoronis psammophila* and *Spio decoratus* find good trophic conditions and are overwhelmingly dominant, so that most of the fauna components such as crustaceans and molluscs, although present in good average densities, are represented by small percentage values in diagrams (Fig. 3).

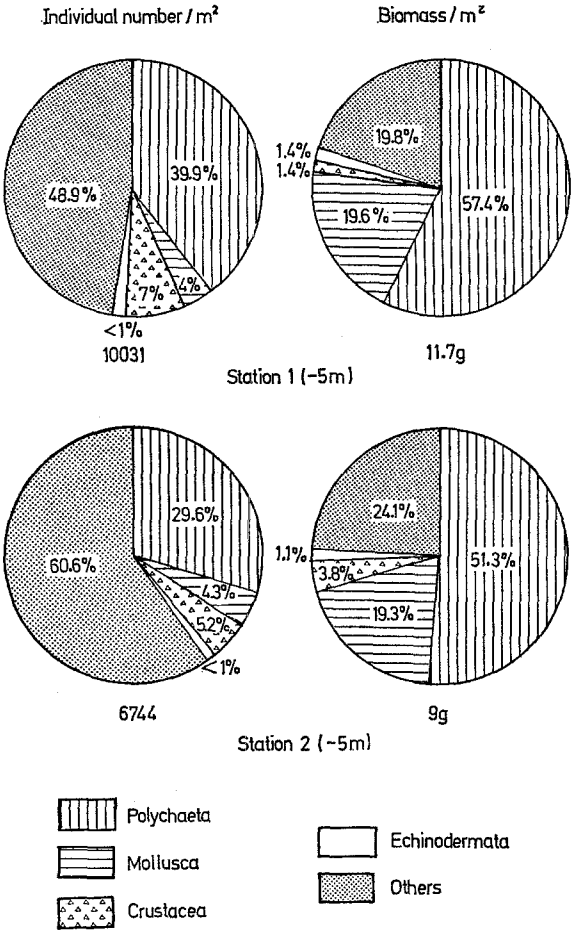

Fig. 3. Main group stocks as percentage of density and biomass values for the 2 stations in deep horizon, Prado Bay

With the exception of the crustaceans, which seem as important and sometimes more numerous in the upper than in the deeper horizon, every group espe-

Table 6. *Most abundant species and mean number of individuals/m² along Camargue coast (Faraman Lighthouse meridian)*

Rank	Species	Density	Species	Density	Species	Density
Station 1 (—5 m)			Station 2 (—6 m)		Station 3 (—7 m)	
1	*Urothoe pulchella*	260	*Magelona papillicornis*	675	*Magelona papillicornis*	1217
2	*Magelona papillicornis*	189	*Urothoe grimaldi*	134	*Owenia fusiformis*	620
3	*Spisula subtruncata*	163	*Bathyporeia guilliamsoniana*	117	*Bathyporeia guilliamsoniana*	165
4	*Urothoe grimaldi*	157	*Lumbrinereis impatiens*	103	*Lumbrinereis impatiens*	138
5	*Tellina tenuis*	103	*Urothoe pulchella*	87	*Urothoe grimaldi*	121
6	*Ampelisca brevicornis*	88	*Owenia fusiformis*	82	*Urothoe pulchella*	107
7	*Lumbrinereis impatiens*	84	*Spisula subtruncata*	69	*Acrocnida brachiata*	84
8	*Bathyporeia guilliamsoniana*	72	*Tellina tenuis*	67	*Nephthys hombergi*	60
9	*Donax* sp.[a]	68	*Donax* sp.	60	*Donax* sp.	57
10	*Nephthys hombergi*	39	*Nephthys hombergi*	54	*Paradoneis armata*	56

[a] Mainly *Donax semistriatus* at Stations 1 and 2, mainly *D. venustus* at Station 3.

cially polychaetes and molluscs shows an increase in numbers of species and individuals as the water deepens.

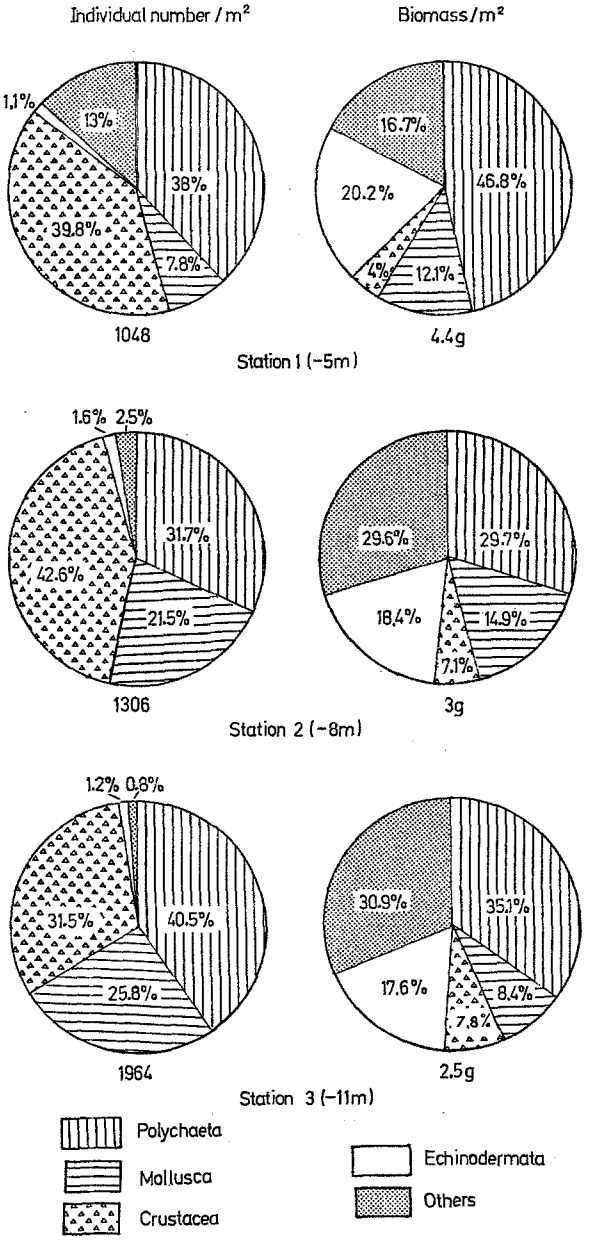

Fig. 4. Main group stocks as percentage of density and biomass values for the 3 stations in Bandol Bay

Macrofauna composition appears to vary from bay to bay owing to different water properties. In oligotrophic conditions (Bandol and Verdon Bays; Figs. 4 and 5) scarcity of molluscs and polychaetes emphasize the crustacean-stock importance (mainly amphipods),

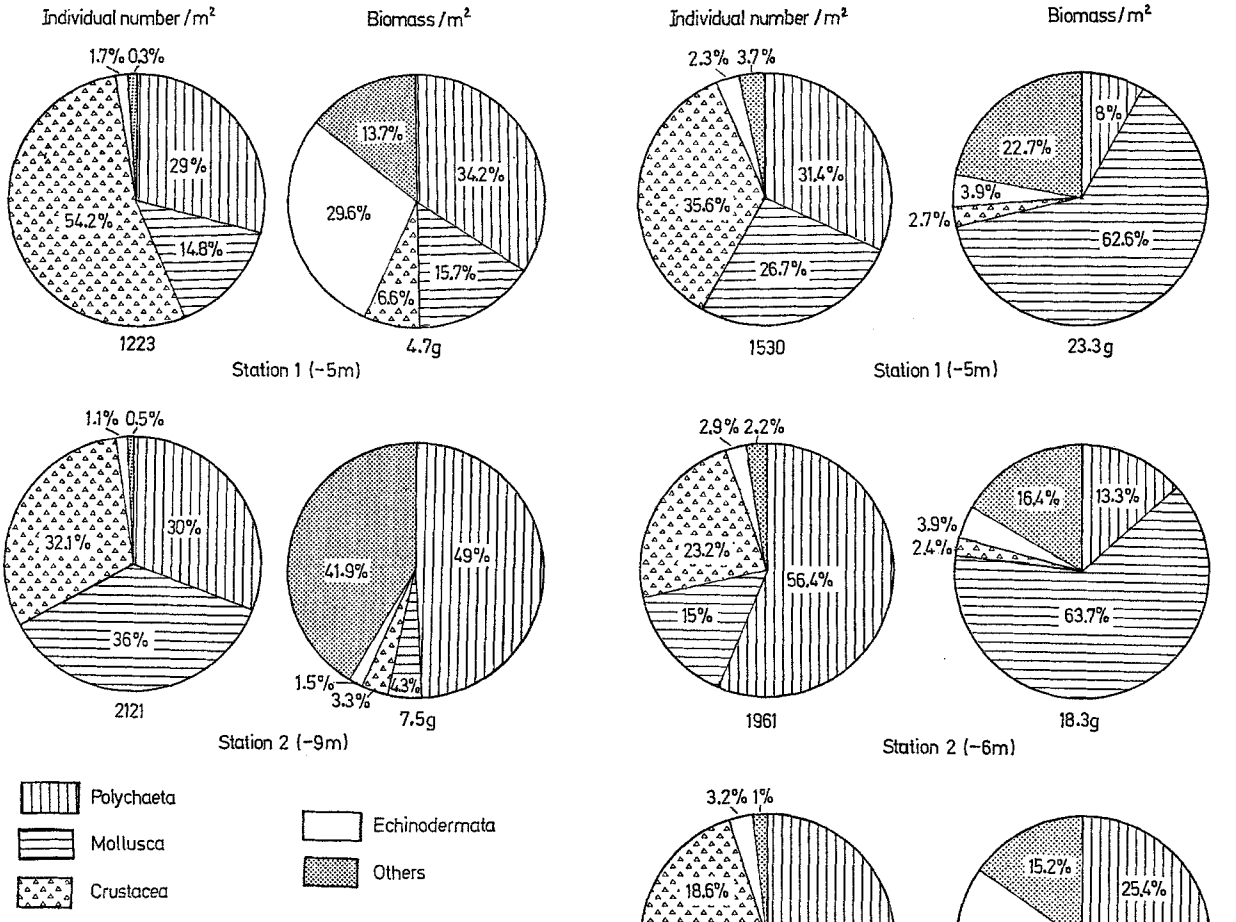

Fig. 5. Main group stocks as percentage of density and biomass values for the 2 stations in Verdon Bay

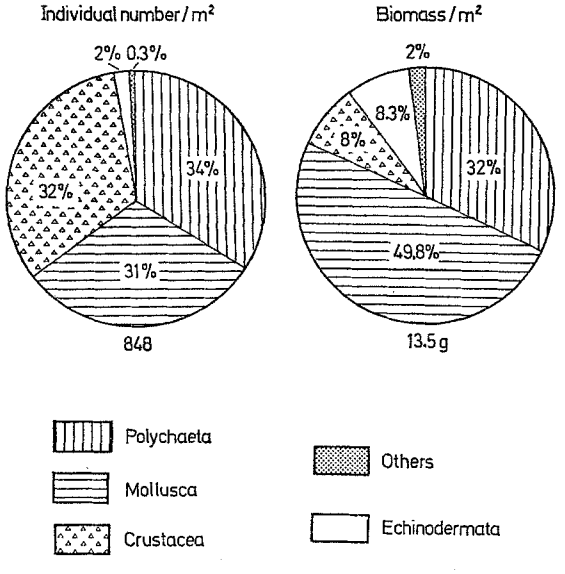

Fig. 6. Main group stocks as percentage of density and biomass values in the Fos Gulf (5 m depth)

Fig. 7. Main group stocks as percentage of density and biomass values for the 3 stations along Camargue coast

although crude densities are not particularly high (about 600 individuals/m²).

In eutrophic conditions (Fos Gulf and the Camargue coast; Figs 6 and 7), the importance of molluscs and polychaetes reduce, in diagrams, the crustacean-stock importance (about 470 individuals/m²). The average density and biomass values are high under such conditions.

Considering the echinoderm fauna, we must note a balance between the echinoderm-biomass importance and the mollusc abundance. This balance has been studied in detail in Bandol Bay for the *Astropecten* sea-star population effect on meiobenthic molluscs (MASSÉ, 1970b; see also CHRISTENSEN, 1970), in Verdon Bay for the *Echinocardium cordatum* population (MASSÉ, 1971b) and on the Camargue coast for the *Ophiura texturata* population (MASSÉ, 1971c).

Quantitative data

Average values of densities and biomass for the 4 year survey appear in Table 7; the three main groups of bottom, according to water properties, as referred to above, have been separated. Comparison of these data reveals an important range of densities and biomass for almost identical grades of bottom deposit (fine, well-sorted sand) and for a restricted area comprising 1° longitude (48 nautical miles).

Table 7. *Mean density and biomass values during 4 year survey in the different bays. Density: number of individuals/m²; biomass: dry weight/m²*

Water column			Oligotrophic conditions		Prado Bay		Eutrophic conditions	
Quantitative data			Density	Biomass (g)	Density	Biomass (g)	Density	Biomass (g)
Depth	Upper horizon	1.5 m	428	1.8	6104	5	55445[a]	157.2[a]
	Deep horizon	5 m	1135	4.6	8387	10.4	1189	18.4
		7—11 m	2042	3.6	—	—	3227	10.1

[a] These two values come from a study on fine-sand macrofauna in a marine lagoon (MASSÉ, 1971d).

Considering that these are mean values, we can postulate that the various density and biomass values available for equivalent level-bottom communities on a world scale would be included in the range observed in this study, in so far as the different data can be compared.

From a general point of view, the results of this quantitative survey require some comments:

(1) In the open sea, density and biomass values for the upper horizon of sand bottom are lower than for the deep horizons.

(2) In the deep horizons, as regards densities, an increase of values occurs as the water deepens, due to an increase in settlement success, so that the abundance of young individuals do not induce increased biomass.

(3) On the contrary, as regards biomass, in the deep horizons of sand bottom there is a decrease of biomass values with depth. The highest biomass occurs in a narrow belt of ground between 5 to 6 m depth, where the largest specimens of fine-sand macrofauna species are living.

Table 7 clearly illustrates the influence of the water column on the shallow-water fine-sand macrofauna biomass. In the Mediterranean Sea, where waters have a generally poor production rate, and so exhibit oligotrophic conditions, the eutrophic effect due to estuarine or sub-estuarine conditions is especially important.

These data confirm SOUTHWARD's view (1953), whereby he explains faunal paucity of some Isle-of-Man beaches by scarcity of fresh water, and agree with MCINTYRE and ELEFTHERIOU's view (1968) that the water overlying the sand must supply most of the organic matter required by the benthic fauna. Furthermore, experimental proof of the effect of eutrophic conditions in the water column on sand benthic-macrofauna has been given by TREVALLION and ANSELL (1967). This direct relationship between eutrophic conditions in the water column and high biomass values of sand-bottom macrofauna is bound up with the fact that the bulk of the biomass in a sand deposit comprises filter and suspension feeders (bivalves, polychaetes, etc.).

Discussion

Distribution

The well-sorted sand biotope off the Provence coast (north-western part of the Mediterranean Sea) is characterized by its little spread with depth increase. Generally, two factors control clean, fine-sand extension. The first is the existence of a sea-grass bed in every area with clear water, and good light-penetration. The second is the rapid increase of fine deposits with depth near river mouths with turbid fresh-water outflow. These two phenomena can be related to tidal-current absence, which allows silt and clay sedimentation and sea-grass implantation at about 10 m depth, i.e., a depth greater than where direct swell action is important.

Quantitative and dynamic aspects

As already indicated, the fine-sand macrofauna studied here is characterized by a wide range of density and biomass values. Using a diver-operated suction sampler, sampling variability for replicate samples may not be sufficient to explain such a range of

values, as shown previously in a methodical comparative study (Massé, 1970a).

From detailed quantitative faunal lists of the macrobenthic species given in Massé (1970b, 1971a, b, c) three major groups of changes can explain the variations in data.

Firstly, short-term changes, correlated, for example with good or bad hydrodynamic or trophic conditions, affect mainly motile macrofauna. This kind of macrofauna is able to move rather quickly and, sometimes, results in high population densities. We can include, in this group, peracarid and eucarid bentho-planktonic crustaceans, Nassidae (molluscs), small demersal fishes, etc.; this fauna is directly affected by exposure, as shown by Lagardere (1966), and McIntyre (1970). As these density variations concern mainly small crustaceans, they have no important effect on biomass values.

Secondly, seasonal changes, generally correlated with reproductive and recruitment processes, generally affect bivalve molluscs at different seasons for each species, and amphipods (such as *Ampelisca brevicornis*) during summertime. Generally, settlement of young bivalves or polychaetes results in an important increase in population density values, but a fairly high mortality rate involves a rapid decrease in densities and, therefore, no effect on biomass values results. This has also been reported by Stripp (1969).

Thirdly, long-term changes, correlated with successful recruitment of a species until now not abundant, are irregular and unforeseeable. The best example in this study is that of *Spisula subtruncata* (Massé, 1971c); for this species many examples may be found in the bibliography (Davis, 1923, 1925; Hagmeier, 1930; Ziegelmeier, 1963, 1970; etc.); these changes are, however, true for numerous other species such as *Echinocardium cordatum*, Massé, 1971a), *Venus gallina* (Ansell, 1961), and various polychaetes (Ziegelmeier, 1970; Peer, 1970). As regards this kind of change, both density and biomass values are affected. The successful settlement of a population provides an increase in biomass during the fast growth-rate period and a decrease when the mortality is more important than the growth-weight increment.

This dynamic aspect of variations of quantitative data and changes in fundamental fauna-assemblage, which occur, as previously mentioned, from bay to bay in the restricted biogeographical area surveyed, requires some comment:

(1) Most data available in the specialised literature on this subject are obtained from a few samples generally collected at the same time or season, so that no range of variation can be calculated; the comparison is, therefore, meaningless from a general point of view, more especially in shallow waters; the sampling gear efficiency is also not always known.

(2) On the basis of this 4 year survey, performed on one sort of sediment in a very restricted shallow belt of ground, the wide range of values obtained include the quantitative data available in literature for this kind of ground. Therefore, any comparison of "richness" of ground between two far-distant geographical areas cannot be done in this way.

3. From the point of view of "parallel level-bottom communities" as developed by Thorson (1957), it seems hazardous to attempt to characterize a community type by a mean biomass-value, because of changes through seasons, years, and from bay to bay in one area.

Macrofauna structure

Comparison with macrofauna community-structure is, in this study, restricted to the same temperate West European biogeographical district; this allows a meaningful comparison, as component species are similar, and data available more abundant.

As mentioned above, the upper horizon of Mediterranean well-sorted sand may be compared to Jones' boreal shallow-sand association as described by McIntyre and Eleftheriou (1968). In such a community, and particularly in sheltered beaches, where a sand-macrofauna community reaches its fullest development, bivalves comprise the bulk of the biomass, and *Tellina tenuis* is dominant. Considering the *T. tenuis* population structure in Scottish waters (McIntyre, 1970), 5 to 8 year-classes are found from beach to beach. This means that such a community will be very stable, even if there is some failure in recruitment from year to year. The bulk of the biomass is made up by *T. tenuis*, a long-lived species, in Scottish waters. Similar observations may be made on the Atlantic French coast (Salvat, 1967; Faure, 1969).

On the north-west Mediterranean coast, as described in detail by Massé (1971a), bivalves comprise the bulk of the biomass: *Corbula* (*Lentidium*) *mediterranea*, *Donax semistriatus*, and *Tellina tenuis*. These bivalves have a mean life cycle of 1 year; only a few have a 2 year span. This shortness in life cycles involves important fluctuations in population structure, stock, and biomass, owing to the recruitment process (Thorson, 1946, 1966).

The same phenomenon occurs for the species living in the deep horizon of fine, well-sorted sand. This deep horizon is equivalent to Jones' boreal off-shore sand association as described by McIntyre and Eleftheriou (1968) and to Petersen's *Venus gallina* community. This community is made up of the following species: *Venus gallina*, *Tellina fabula*, *Spisula subtruncata*, *Magelona papillicornis*, *Spio*, *Nephthys*, *Owenia*, *Echinocardium cordatum*, *Acrocnida brachiata*, etc. The different data, from north-European coasts, available on the life cycles of the species just mentioned (Ansell, 1961; Buchanan, 1966; and others) compared with data from the Provence coast (see for comparisons Massé, 1972) show that the life cycle of most

species is shorter in the latter area, where the life span exceeds very rarely 2 years, with a mean term of 1 year (MASSÉ, 1971a, b). In the same way, considering the main invertebrate predators such as *Astropecten* sea stars and naticid gastropod drillers (MASSÉ, 1970b, 1971a) and comparing, respectively, CHRISTENSEN's data (1970) on *Astropecten irregularis*, and ANSELL (1960), and GREEN's data (1968) on naticid drillers, we can emphasize that the predation rates found in north-Mediterranean Sea are higher.

Such different life spans and generation-replacement rates for the same species at the two extreme limits of their biogeographical distribution range stress the difficulty in comparing communities and in appreciating the true signification of quantitative data, especially for different biogeographical districts such as boreal and tropical districts. This indicates the poor interest of rough quantitative data for a whole community in shallow waters. We must bear in mind that quantitative data such as densities and biomass result from complex factors including environmental and trophic conditions, species interaction, reproduction and recruitment processes.

Production

Production data is of more value but, unfortunately, such data are almost non-existent for marine bottom-macrofauna. Furthermore, production computations vary from one paper to another (JENSEN, 1919; SANDERS, 1956; MASSÉ, 1968; PENZIAS, 1969; BIRKETT, 1970; PEER, 1970; TREVALLION, 1971; etc.), depending upon whether production is considered in a general energy-flow context or only as somatic-growth increment for successive short intervals; whether or not production bound up with mortality is included; and whether or not spawning and regeneration of tissues are included. In most cases, data are available only for the most conspicuous and abundant species of a community. More often, in the absence of true quantitative production data, abstract considerations on productivity efficiency are predicted from mean growth-rates, generation-replacement rates, and biomass values. In this way, in north-west Mediterranean benthic fine-sand communities in shallow waters which are generally composed of short-lived animals with high growth-rates, a high production rate may be expected. Indeed, the fast generation-replacement of animals in the Mediterranean Sea populations is well illustrated by the low mean size of most Mediterranean individuals, compared with those living on the north European coast. Besides, the high growth-rate of most Mediterranean animals is bound up with the fact that they are in their first year of life. Biomass values being of the same order of magnitude in north boreal and Mediterranean communities, the production rate must be higher in the latter, as both growth-rate and generation-replacement rate are slower in the former.

The above assumption is supported by comparison of TREVALLION's production data (1971), on a boreal population, with my own production data on Mediterranean populations. In order to compare these production data, we must consider that my "production" corresponds roughly to the sum of TREVALLION's somatic growth/m^2 and yield/m^2. In the north-west Mediterranean Sea, production data on a *Spisula subtruncata* population (MASSÉ, 1968), and a *Venus gallina* population (MASSÉ, 1971b) are 10 g/m^2/year and 20 g/m^2/year dry weight, respectively, whereas, on the Scottish coast, production data on a *Tellina tenuis* population (TREVALLION, 1971) are below 2 g/m^2 dry weight for the best year.

The same ascertainment may be made with PEER's data (1970) on a *Pectinaria hyperborea* population on the north-west Atlantic coast for which production may be evaluated between 5 and 15 g/m^2/year wet weight.

Both examples given above for Mediterranean populations require some comments, as generally *Spisula* populations are considered to be high-production populations, *Venus* populations to be low-production (THORSON, 1957). The *Spisula* population studied was located at the extreme limit of this species distribution range (5 m depth) and severe hydrodynamic conditions involve protection against most of the common predators (MASSÉ, 1971c) so that, unlike normal Mediterranean grounds, the population was composed of old, slow-growing, individuals. The production rate would have been higher during the first year of life. On the other hand, the *Venus gallina* population is composed of young fast-growing animals, as usual in fine-sand Mediterranean grounds.

This indicates that, as regards production-rate, we must bear in mind that latitude, topographic localization which controls environmental factors, and population structure are not dissociable. From the "parallel level-bottom community" point of view, the shallow fine-sand bottom communities (*Tellina* and *Venus* community) cannot be characterized by a production rate independently from the three previously mentioned factors. This conflicts with THORSON's conception (1956, p. 695) on temperature adaptation and equivalence of marine parallel level-bottom communities, and reduces the general application of such a concept. Therefore, it seems more accurate to consider the level-bottom communities in the sense developed by MUUS (1967) of rough descriptive units helpful for marine biologists of different regions.

Summary

1. The use of a diver-operated suction sampler allows us to obtain a good idea of macrofauna density and biomass values in sublittoral fine sand.

2. The 4 year survey specifies the range of quantitative data which forms the subject of this paper and points out the main variation causes.

3. Influences of exposure and trophic conditions in the water column on biomass values are clearly shown.

4. The short life-cycle of most species explains changes and instability in fauna assemblage, as the replacement of generations involves a hazardous pelagic larval stage.

5. Being composed mainly of young, fast-growing individuals, the populations living in Mediterranean fine-sand bottoms have high production rates.

6. Comparison between north-west European shallow fine-sand communities and equivalent Mediterranean communities allows some restriction to the "parallel level-bottom community" concept.

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