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THE BENTHIC FAUNA OF DIFFERENT SOFT SUBSTRATA IN THE PAGASSITIKOS GULF (GREECE)

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ABSTRACT

The macrozoobenthos data of the Greek gulf of Pagassitikos were exhaustively analysed with a view to depicting accurately the biocoenose of the entire range of soft substrata. These were assigned a coarseness index, or "sand equivalent", **s′**, estimated from the percentages of sand and silt. Each species observed in the region displayed a relationship between its abundance species observed in the region displayed a relationship between its abundance and **s′**. All such equations were grouped into six types, having as chief representatives, in increasing order of preference for mud, *Notomastus latericeus, Onchnesoma steenstrupii, Tharyx dorsobranchialis, Thyasira flexuosa, Tauberia gracilis* and *Callianassa stebbingi.* A mathematical technique permitted the identification of the type to which a species belonged, even in the common instance of scanty data. It thus became possible to determine in the most reliable manner the structure of the benthic communities as a function of the coarseness of their habitat. The method, enabling most accurate comparisons of distant areas, should help assessing the effects of other parameters.

INTRODUCTION

For a long time, it has been observed that the nature of the substrate (rock, sand, silt, mud), together with various characteristics of the water, greatly influences the macrozoobenthos communities. Considerable work was carried out on the subject, in particular by Petersen (1913), Davis (1923), Beanland (1940), Holme (1949), Thorson (1966), Driscoll (1967, 1975), McIntyre and Eleftheriou (1968), Longbottom (1970), Bloom *et al* (1972), Driscoll and Brandon (1973), Rhoads (1974). In the instance of particular species, it was reported (Wilson, 1955; Sanders, 1958; Longhurst, 1958; Ursin, 1960; Buchanan, 1963) that the sediment texture seemed to have little effect.

To help establish numerical relationships between the grain size of the substrate and the number of macrozoobenthos species, **g,** and individuals, **i,** in a sample of area **d** m^2, Satsmadjis (1982) calculated an index of coarseness, or "sand equivalent", **s′**, from the equation:

$$s' = s + t / (0.2\ s + 5) \qquad (1),$$

where **s** represents the percentage of sand and **t** that of silt. This formula enabled Bogdanos and Satsmadjis (1985) to arrive at accurate estimates of **g** and **i** as a function of **s′** in the Pagassitikos Gulf, on the eastern coast of Greece. This permitted, indirectly, to determine the independent action of depth.

The present work deals with the effect of the above index of coarseness on the abundance of the most common species found in the embayment (Fig. 1). It thus makes possible the determination of the exact composition of the biocoenoses as a function of **s′**. This in turn aids towards measuring the separate action of other factors.

METHODOLOGY

Sediment sampling

The material was drawn from a total of 39 locations, situated in the Bay of Volos, the main body of the Pagassitikos Gulf (especially off the Angistri Promontory) and the Volos, Trikeri and Oreos Channels (see Fig. 1 and Fig.

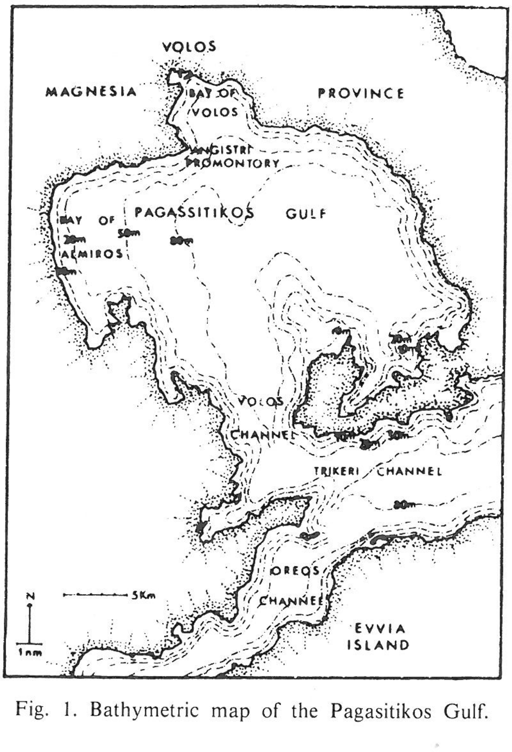

Fig. 1. Bathymetric map of the Pagasitikos Gulf.

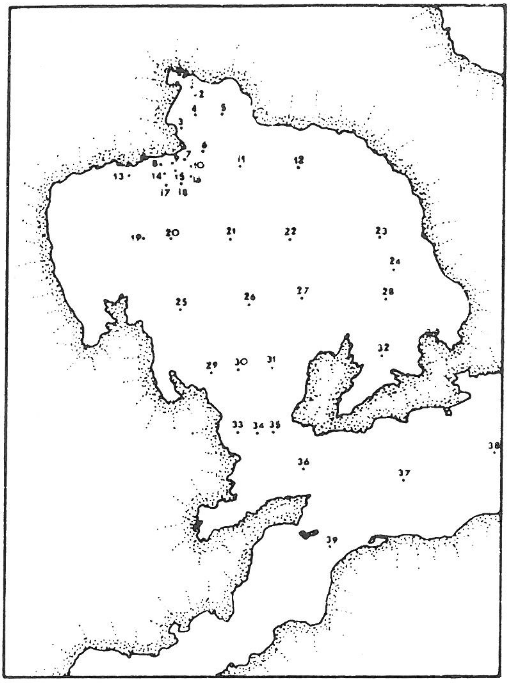

Fig. 2. Sampling locations in the Pagasitikos Gulf.

2). A Van-Veen grab was employed; it had an area of 0.18 m^2 on the first cruise and 0.1 m^2 on the next ones. The sampling took place on six occasions (August, November 1975, February, May, August and December 1976), six times from 20 points (2, 4, 5, 6, 7, 8, 11, 12, 16, 17, 20, 21, 22, 25, 26, 27, 33, 35, 36, 37), five times from 8 (9, 10, 13, 14, 15, 18, 38, 39), four times from 7 (1, 3, 19, 23, 28, 30, 34), three times from station 32 and twice from 3 sites (24, 29, 31), bringing the total to 197 samples.

Macrozoobentos separation and taxonomy

Immediately upon emptying the Van-Veen sampler, about fifty grammes of sediment was set aside for the determination of the grain size composition and stored in deep freeze. The rest was exposed to a strong current of sea water over a large 1-mm metal sieve superposed on a 0.5-mm one. The residues were gathered in a plastic jar of one litre and sufficient quantities of 5% formaldehyde and 0.2% Rose Bengal solution in water were poured to cover the material. On returning from the cruise, the samples were freed from this liquid and any mud left by washing with tap water on a 0.5-mm sieve. They were then preserved in 75% alcohol until viewed through the microscope.

Species identification was achieved with the help of the works cited by Bogdanos and Satsmadjis (1983).

Grain size determination

The composition of the sediment sample in sand, silt and clay was ascertained by the method described by Buchanan (1971) as modified by Satsmadjis and Voutsinou-Taliadouri (1985).

The results of the analyses appear in Table I.

TABLE I Stations positions, depths and sediment characteristics.

Station	Latitude north	Longitude east	Depth metres	Sand %	Sediment Silt %	Clay %	Sand Equiv.	Org. C. %
35	39°05.4′	023°02.1′	77	79.4	86	12.0	79.8	0.13
36	39°03.8′	023°03.9′	72	73.4	12.0	14.5	74.0	0.24
11	39°17.1′	023°00.0′	62	67.2	20.1	12.7	68.3	0.46
4	39°19.1′	022°57.7′	37	62.3	26.8	11.0	63.8	0.40
39	39°00.0′	023°05.1′	65	59.9	9.2	30.9	60.4	0.77
5	39°19.2′	022°59.3′	42	48.9	38.8	12.3	51.5	0.50
3	39°18.7′	022°56.6′	20	37.1	42.9	20.0	40.6	0.56
2	39°20.0′	022°57.8′	31	34.0	49.3	16.7	38.2	0.85
6	39°17.8′	022°57.9′	60	33.7	44.8	21.5	37.5	0.63
34	39°05.4′	023°01.4′	81	31.1	30.1	38.7	33.8	0.67
1	39°20.6′	022°57.4′	17	26.7	46.5	26.8	31.2	0.71
13	39°16.6′	022°53.8′	55	26.5	44.0	29.5	30.8	0.68
19	39°14.0′	022°54.9′	56	22.6	48.2	29.2	27.7	0.59
7	39°17.5′	022°57.0′	58	20.3	50.7	28.9	25.9	0.78
10	39°17.0′	022°57.2′	72	18.5	49.3	32.2	24.2	0.90
12	39°17.1′	023°03.4′	90	15.8	39.2	45.0	20.6	0.77
29	39°08.0′	022°58.4′	74	9.9	58.3	31.8	18.3	0.71
8	39°17.1′	022°54.4′	60	7.7	55.9	36.4	16.2	0.82
38	39°04.4′	023°15.0′	85	6.4	51.3	42.3	14.6	0.68
31	39°08.0′	023°01.9′	83	6.2	48.8	45.0	14.0	0.63
18	39°16.4′	022°56.7′	75	4.4	55.8	39.7	13.9	0.78
17	39°16.3′	022°55.8′	70	4.3	55.6	40.1	13.8	0.78
15	39°16.9′	022°56.4′	70	2.3	59.5	38.3	13.2	0.82
37	39°03.2′	023°09.7′	85	4.5	49.3	46.2	12.9	0.71
9	39°17.2′	022°56.2′	64	1.2	60.3	38.5	12.7	0.80
25	39°11.0′	022°56.4′	66	3.5	52.6	43.9	12.7	0.77
28	39°11.3′	023°08.5′	92	2.5	54.0	43.5	12.3	1.02
16	39°16.6′	022°57.2′	75	2.2	54.1	43.7	12.1	0.85
14	39°16.7′	022°55.8′	66	1.6	55.1	43.3	12.0	0.84
24	39°14.2′	023°09.0′	97	1.1	55.2	43.8	11.7	1.10
20	39°14.1′	022°52.4′	76	3.0	48.0	49.0	11.6	0.79
23	39°14.3′	023°08.2′	96	3.5	44.9	51.6	11.4	0.98
33	39°05.4′	023°00.0′	80	2.2	48.4	49.4	11.1	0.76
32	39°08.7′	023°08.0′	87	1.2	48.3	50.5	10.4	0.98
27	39°11.4′	023°03.2′	88	1.4	41.3	57.3	9.2	0.87
26	39°11.0′	023°00.4′	86	1.2	41.9	58.0	9.2	0.85
30	39°08.0′	023°00.0′	80	1.4	41.0	57.6	9.2	0.65
21	39°14.1′	023°00.0′	90	1.5	36.9	61.6	8.5	0.90
20	39°14.2′	023°03.2′	97	0.9	35.3	63.7	7.7	0.71

Establishment of standard abundance function

The institution of the relationship between the abundance, or number of individuals per square meter of sea floor, **j,** of a given species and the index of coarseness, **s′**, of the sediment presents great difficulties. These originate from the practical necessity of examining samples quite small, say $0.1m^2$, while surface irregularities, such as hollows or projections, may exert great infuence on the fauna. Furthermore, various natural events (recruitment, predation, landing of organic matter, current) could induce major changes in the benthic assemblages at a specified place. In consequence, to improve the reliability, the sampling locations were appointed to subgroups, the number of which was made as large as six, in order to permit the drawing of fairly complex curves. Since depth, **h,** lowers the abundance in the Pagassitikos Gulf, it was taken into consideration, using the correction factor (2.20-0.0166 h) propounded by Bogdanos and Satsmadjis (1985).

The subgroups, in order of increasing fineness, comprised respectively 7,7,7,7,6 and 5 stations. They had mean "sand equivalent", **s′**, values of 62.9, 32.2, 17.4, 12.8, 11.4 and 8.8. Their average depths, **h,** were 54, 51, 77, 75, 84 and 88 m. The sums of the real areas of the samples were 4.38, 3.82, 3.50, 4.28, 2.92, 3.20 m^2 (total 22.10 m^2). After multiplying by the term (2.20-0.0166 h) to adjust for the depth of each station, these figures became 5.66, 5.20, 3.25, 4.19, 2,51, 2.34 m^2 (total $23.15m^2$). They correspond to a depth of 72 m, since this value makes the correcting factor equal to one. The more accurate correction, based on the overall abundance, **i,** versus **h** non linear function was not applied because of the doubt as to the exact shape of the curve upon which it relied. The ratio of the total number of individuals, **J,** of a particular species in a subgroup to the amended sample area of the latter represents the species abundance, **j,** for the average index of coarseness, **s′**, of the subgroup. The plotting of the six **j, s′** coordinates enables the subjective drawing of a smooth curve, depicting **j** as a function of **s′** at a depth of 72 m. For another depth, **j** must be multiplied by the term (2.20-0.0166h), which affords a sufficient, though only approximate correction.

An equation arrived at in this manner presents great reliability in the instance of the first few dominant species. However, for the majority of them, for which **j** is relatively small, it would be more or less conjectural. A way of avoiding this drawback consists of expressing **j** as the percentage ratio, **q,** of its maximal value. This renders the functions comparable and, therefore, assignable to one of several models, the number of which was limited to six, owing to the scarcity of data in the case of most species. Each standard was defined by averaging similar curves given by dominant species.

Determination of the standard abundance function of a species.

The reliable selection of the model abundance function best fitting a particular species requires that the total number of individuals of that species observed in the sample exceeds 20. This results from the shape of the curve depending on six points, each of which, to have any meaning, should be based on an actual number of individuals of at least 4 on the average. The samples taken from the Pagassitikos Gulf, with a total surface of 22.10 m^2, contained 353 species. Of these, 45 had at least 50 individuals each, 76 25, 117 12 and 150 6. In consequence, the abundance function of just around one fifth of the species could be determined with sufficient confidence. For that reason, the number of **j, s′** sets of figures on which to base the choice of the fitting curve was reduced from 6 to 3. To that end, the subgroups of stations $\mathbf{A_1}$, $\mathbf{A_2}$, $\mathbf{B_1}$, $\mathbf{B_2}$, $\mathbf{C_1}$ and $\mathbf{C_2}$ were made into the groups **A, B** and **C.** For each type of function **a, b, c, d, e, f** and group, a certain percentage of the total abundance **z′** was estimated as shown in Table II and explained in the annex.

TABLE II Percentage **q** of the maximum of the species abundance in the subgroups of stations and percentage of the total of the abundance of a species in a subgroup, $z = 100\ q/\Sigma q$ and group, **z′**.

Type of function	Parameter	Sand Equivalent Group **A**		Group **B**		Group **C**		Total
		A1 62.9	**A2** 32.2	**B1** 17.4	**B2** 12.8	**C1** 11.4	**C2** 8.8	
	q	97	73	3	2	1	0	176
a	**z**	55.1	41.5	1.7	1.1	0.6	0.0	100
	z′	—	96.6	—	2.8	—	0.6	100
	q	97	59	22	11	7	0.0	196
b	**z**	49.5	30.1	11.2	5.6	3.6	0.0	100
	z′	—	79.6	—	16.8	—	3.6	100
	q	96	90	63	48	42	17	356
	z	27.0	25.3	17.7	13.5	11.8	4.8	100
c	**z′**	—	52.3	—	31.2	—	16.6	100
	q	52	99	92	73	65	29	410
d	**z**	12.7	24.1	22.4	17.8	15.9	7.1	100
	z′	—	36.8	—	40.2	—	23.0	100
	q	48	40	100	95	87	62	432
e	**z**	11.1	9.3	23.1	22.0	20.1	14.4	100
	z′	—	20.4	—	45.1	—	34.5	100
	q	20	16	35	57	72	100	300
f	**z**	6.7	5.3	11.7	19.0	24.0	33.3	100
	z′	—	12.0	—	30.7	—	57.3	100

The values **q** of the standard functions can be converted into actual abundances, **j,** simply by multiplying then by the «abundance coefficient», **K.** The latter depends on the actual abundances, **ja, jb** and **jc** in the groups of stations **A,B** and **C** and the sum, Σq, of the "relative abundances" of the relevant type, quoted in Table II. It is given by the equation:

$$K = 2(ja + jb + jc)/\Sigma q \qquad (2).$$

To facilitate the calculations, Table III provides, for each of the six patterns, the "relative abundance", **q,** corresponding to twenty values of **s′**, chosen because of their practical interest.

TABLE III Species relative abundance and number in sample of species and individuals as a percentage of the maximum.

Sand Equiv.	Species relative abundance						Number in sample as a percentage of the maximum	
s′	Type **a**	Type **b**	Type **c**	Type **d**	Type **e**	Type **f**	Species **g′**	Indiv. **i′**
7	0	0	5	8	22	95	25.2	18.8
8	0	0	12	14	46	99	27.3	21.8
9	0	2	20	26	62	100	29.4	24.7
10	1	4	30	42	73	98	31.4	27.5
12	1	8	43	66	88	72	35.4	32.4
14	2	12	52	80	96	52	39.3	37.1
16	2	17	59	89	99	40	43.0	41.5
18	5	23	65	95	99	33	46.6	45.7
20	11	28	70	97	98	28	50.2	49.7
22	22	34	74	99	92	25	53.6	53.6
24	36	39	77	100	82	21	56.8	57.3
26	47	44	82	100	70	19	60.0	60.8
28	57	49	85	99	57	17	63.0	64.2
30	65	54	87	99	46	16	65.9	67.4
35	78	65	93	96	38	15	72.7	74.3
40	85	75	97	90	37	15	78.7	80.0
50	92	90	100	75	41	16	88.5	89.3
60	96	96	98	57	47	20	95.3	95.8
70	98	98	94	45	51	24	99.1	99.3
80	100	100	87	40	54	26	100.0	100.0

Increase in the number of species with the area.

The number of individuals, **i,** rises linearly with the sampling area, **d,** but, obviously, the number of species, **g,** does not. The direct establishment of the relation between **g** and **d** presents great difficulty and hazard. It requires a diver very carefully taking by hand contiguous samples of exactly 0.1 m^2 and repeating this operation at several places with sediments of various textures. Ideally, for the needs of this study, the depth should be 72 m. Furthermore, since randon effects make **g** fluctuate widely at a particular location, the investigation would involve a large number of samples. In consequence, of necessity, the growth in the number of species with the sample size can be estimated only approximately using the available data.

To that end, let us call $g' = g/go$ and $d' = d/do$, in which **g** and **go** are the number of species in samples of respective areas **d** and do = 0.1 m^2 when the substrate has the same sand equivalent, **s'**. Since **s'** does not appear substantially to affect the equation giving **g'** as a function of **d'** and as **go** can be calculated from **s'** ($go = f_1(s')$), the relation between **g'** and **d'** enables finding **g** from **d** whatever the coarseness of the sediment: $g = go \cdot g' = f_1(s')g'$ and $d = do \cdot d' = 0.1\ d'$. The samples collected from stations belonging to the same group during the six cruises indicate that an area of 1 m^2 contains on the average 4.0 times as many species as a 0.1 m^2 one: $g' = 4.0$ for $d' = 10$. But samples taken on the same day from sites very close to one another and of similar **s'** point to $g' = 3.3$ for $d' = 10$. Hence, we may reasonably assume that a 1 m^2 sample holds around 2.5 times as many species as a 0.1 m^2 sample drawn from the same exact point.

RESULTS AND DISCUSSION

Types of abundance function

The graphs selected as models to depict the percentage ratio, **q,** of the abundance to the maximal one as a function of the "sand equivalent", **s',** appear in Figures 3, 4 and 5. It may happen that a particular species fails to reveal any trend at all, because of extraordinary coincidences or extreme scarcity of data. However, generally, the real equations either closely follow the patterns or intermediate ones.

Type **a** (Fig. 3) concerns organisms exhibiting the strongest liking for large grains. It comprises the following species, listed by order of decreasing abundance: *Notomastus latericeus, Paralacydonia paradoxa, Lumbriconereis gracilis, Lumbriconereis latreilli, Eunice vittata, Magelona papilicornis, Tharyx marioni, Chrysopetalum debile, Cirratulus cirratus, Mystides limbata, Chone duneri* and *Laonice cirrata.* Type **b** (Fig. 3) differs from type **a** only in that it reflects more tolerance of the macrozoobenthos to muddy surroundings and, conversely, not as much dependence upon the presence of sand. This causes **q**

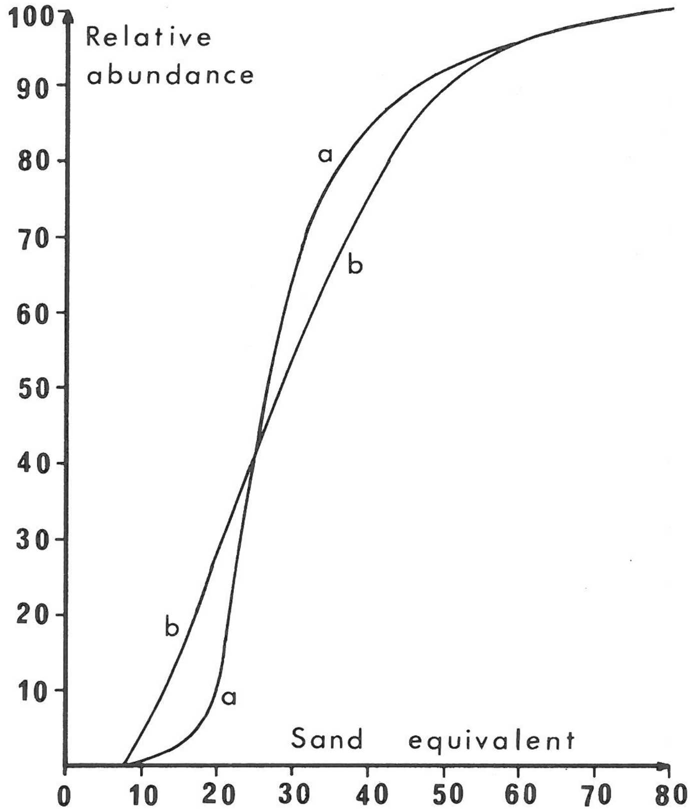

Fig. 3 Relative abundance function types **a** and **b**.

to rise up to 80 for values of **s′** between 8 and 45. The chief representatives of type **b** are: *Onchnesoma steenstrupii, Cirratulus sp., Aricidea fragilis mediterranea, Ammotrypane aulogaster, Asyhis biceps, Harmothoe lunulata, Amphiura filiformis, Clymene santanderensis, Stylarioides plumosa* and *Cirratulidae.*

Type **c** (Fig. 4) illustrates fauna growing on a faily wide range of substrata, but especially the coarse ones. It includes *Tharyx dorsobrancialis, Glycera convoluta, Ampelisca diadema, Hyalinoecia bilineata, Mellina palmata, Labidoplax digitata, Processidae, Chaetozone setosa, Aricidea fauveli, Spiophanes bombyx, Pilargis falcata, Myriochelle heeri.* Type **d** (Fig. 4) reflects even greater ubiquity than type **c,** though with a definite adaptation to silt and clay. It fits *Thyasira flexuosa, Prionospio ehlersi, Terebelides stroemi, Nephthys hombergii, Nephtys hystricis, Podarke pallida, Leanira yhleni, Ancistrosyllis robusta, Prionospio malmgreni.*

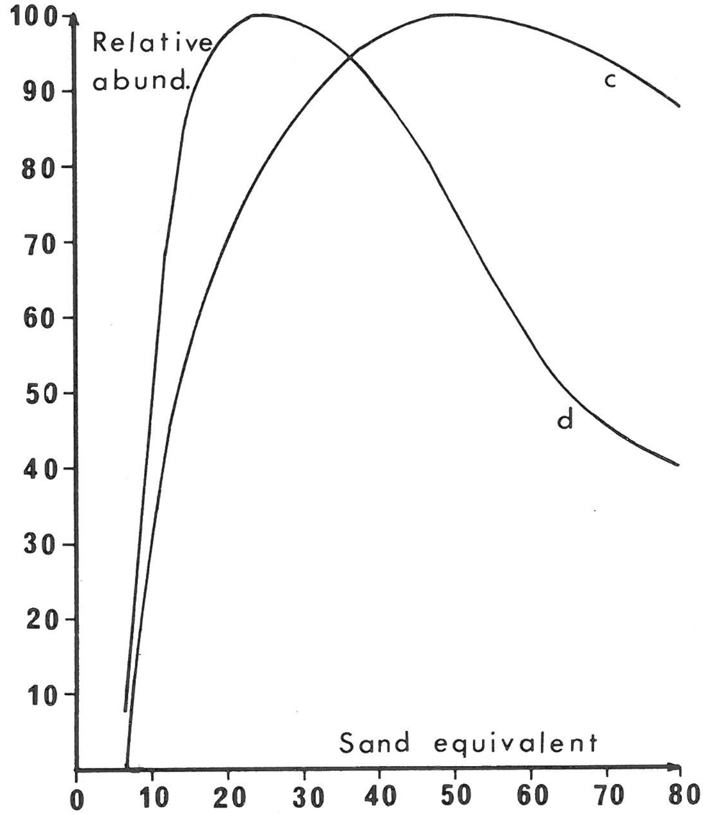

Fig. 4. Relative abundance function types **c** and **d.**

Type **e** (Fig 5) possesses a remarkable feature, clearly educed from the data, a trough occurring when s′ = 40. This intimates that the organisms, although exhibiting their greatest density on rather fine sediments (s′ = 17), would grow better on coarser ones were it not for enhanced competition or predation there by species less suited for conditions prevailing on muddy bottoms. Type **e** embraces *Tauberia gracilis, Lumbrioconereis impatiens, Apseudes latreilli, Harpinia Della-Valei, Sternaspis scutata, Marphysa bellii, Poecilochaetus serpens, Chrysallida sp.* Type **f** manifests perfect adaptation to clayey substrata. Like type **e,** it shows a minimum for **s′**=40, but much broader. It has very few representatives: *Callianassa stebbingi, Vibilidae, Lysianassa longicornis.*

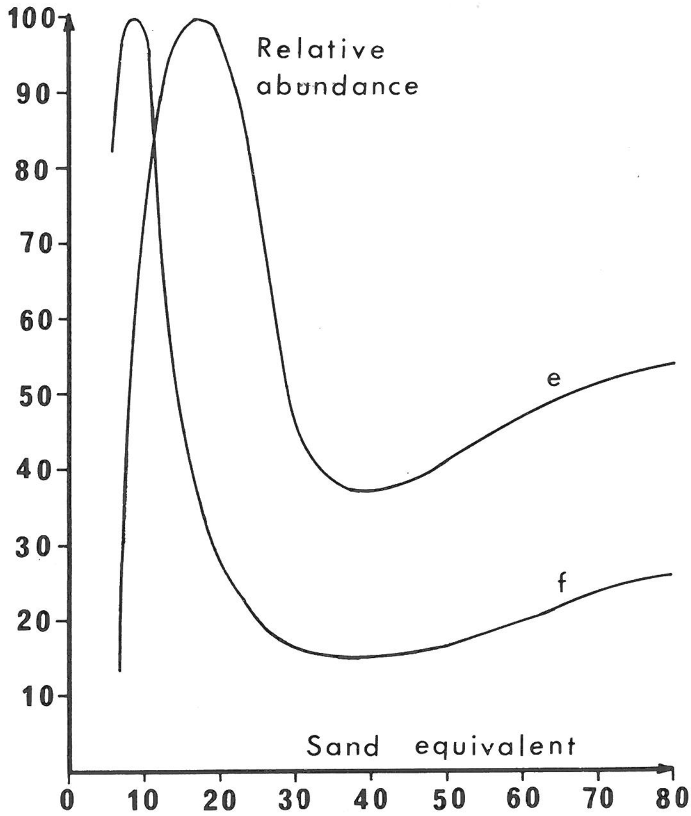

Fig. 5. Relative abundance function types **e** and **f.**

Differences between model and actual abundance functions

The procedure described in the annex for the determination of the type of relative abundance function suiting best a species proved very reliable. The six most abundant species, each of which gathers a total of 308 to 871 individuals in the 197 studied grab samples, often fit the model curves remarkably well. This is demonstrated by the considerable fall in the value of **E** (the sum of the three squares of the differences between true and ideal relative abundance figures) when dealing with the appropriate type. In the instance of *Notomastus latericeus* (type **a**), E=**3.6,** 494, 2979, 5409, 8631 and 10929; for *Onchnesoma steenstrupii* (type **b**), E=491, **0.08,** 1120, 2754 5255 and 7626; for *Tharyx dorsobranchialis* (type **c**), E=2041, 546, **105,** 850, 2438 and 4452; for *Thyasira flexuosa* (type **d**), E=5979, 3045, 563, **123,** 611 and 2628; for

Tauberia gracilis (type **e**), E=8988, 5524, 1707, 565, **30** and 518; for *Callianassa stebbingi* (type **f**), E=10993, 7439, 3075,1667,621 and **13.**

Relatively uncommon species (total of 31 to 41 individuals in the 197 samples) still appear to follow closely enough one of the six patterns. Thus, in the case of *Cossura coasta* (type **a**), E=**20,** 711, 3524, 6139, 9560 and 11970; for *Pectinaria koreni* (type **b**), E=952, **99,** 834, 2229, 4589 and 7297; for *Iphinoe serrata* (type **c**), E=2183, 670, **79,** 752, 2194 and 3879; for *Nucula turgida* (type **d**), E=4685, 2228, 190, **36,** 643 and 2050; for *Callianassa sp.* (type **e**), E=15100, 10132, 4831, 2746, **1749** and 3942; for *Vibilidae* (type **f**), E=15218, 11866, 7014, 5421, 3711 and **1075.**

Effect of the substratum on the biocoenoses

Fig. 6 illustrates the powerful influence of the texture of the sediment on the benthic assemblages. In particular, it indicates that, when the "sand

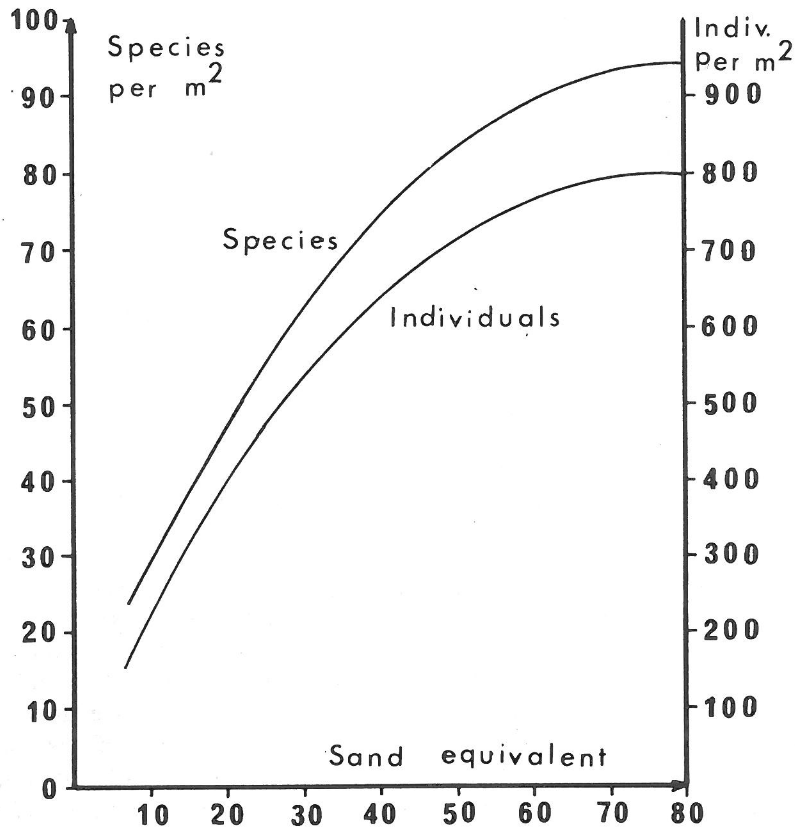

Fig. 6 Number of species and individuals in a 1 m^2 sample as the function of the "sand equivalent" of the substratum.

equivalent", **s'**, increases from 7 to 80, the number of species, **g**, and the number of individuals, **i**, per square metre rise up from, respectively, 24 and 150 to 94 and 798.

Table III dispays this subordination in a manner independent from the sample size, by expressing **g** and **i** as percentages, **g'** and **i'**, of their maximal values, occurring when s'=80. It reveals that **s'** affects **g** and **i** nearly to the same extent, reducing them by half when dropping from 80 to 20 and to a quarter as it diminishes to 7 for **g** and 9 for **i**. The actual values of **g** and **i** are found by multiphying **g'** and **i'** by a factor of, respectively 0.3756 and 0.798 for d=0.1 m^2 and 0.936 and 7.98 for d=1m^2, assuming a depth of 72 m.

Table IV catalogues the first most common 112 species by order of decreasing mean abundance in all the collected samples. It provides the type,

TABLE IV Species abundance on different substrata

Species	Code N°	Type	Abund. Coeff.	Sand Equivalent 7	10	14	20	35	80
Onchnesoma steenstrupii	001	b	0.88	0.0	3.5	10.6	24.6	57.2	88.0
Tharyx dorsobranchialis	002	c	0.45	2.2	13.5	23.4	31.5	41.8	39.2
Tauberia gracilis	003	e	0.37	8.1	27.0	35.5	35.9	14.1	20.0
Callianassa stebbingi	004	f	0.50	47.5	49.0	26.0	14.0	7.5	13.0
Thyasira flexuosa	005	d	0.274	2.2	10.7	21.9	26.6	26.3	11.0
Notomastus latericeus	006	a	0.33	0.0	0.3	0.7	3.6	25.7	33.0
Clycera convoluta	007	c	0.188	0.9	5.6	9.8	13.2	17.5	16.4
Ampelisca diadema	008	c	0.194	1.0	5.8	10.1	13.6	18.0	16.9
Paralacydonia paradoxa	009	a	0.273	0.0	0.3	0.5	3.0	21.3	27.3
Lumbriconereis gracilis	010	a	0.254	0.0	0.3	0.5	2.8	19.8	25.4
Lumbriconereis latreilli	011	a	0.232	0.0	0.2	0.5	2.6	18.1	23.2
Lumbriconereis impatiens	012	e	0130	2.9	9.5	12.5	12.6	4.9	7.0
Apseudes latreilli	013	e	0114	2.5	8.3	10.9	11.1	4.3	6.2
Prionospio ehlersi	014	d	0.102	0.8	4.0	8.2	9.9	9.8	4.1
Eunice vittata	015	a	0.147	0.0	0.1	0.3	1.6	11.5	14.7
Harpinia Della-Valei	016	e	0.086	1.9	6.3	8.3	8.3	3.3	4.6
Terebelides stroemi	017	d	0.078	0.6	3.0	6.2	7.6	7.5	3.1
Hyalinoecia bilineata	018	c	0.069	0.3	2.1	3.6	4.8	6.4	6.0
Sternaspis scutata	019	e	0.067	1.5	4.9	6.4	6.5	2.5	3.6
Cirratulus sp.	020	b	0.108	0.0	0.4	1.3	3.0	7.0	10.8
Aricidea fragilis mediterranea	021	b	0.102	0.0	0.4	1.2	2.9	6.6	10.2
Magelona papilicornis	022	a	0.106	0.0	0.1	0.2	1.2	8.3	10.6
Melinna palmata	023	c	0.064	0.32	1.9	3.3	4.5	6.0	5.6
Labidoplax sp.	024	c	0.055	0.3	1.7	2.9	3.8	5.1	4.8
Nephthys hombergii	025	d	0.058	0.5	2.3	4.6	5.6	5.6	2.3
Amotrypane aulogaster	026	b	0.098	0.0	0.4	1.2	2.7	6.4	9.8
Tharyx marioni	027	a	0.092	0.0	0.1	0.2	1.0	7.2	9.2
Nephtys hystricis	028	d	0.051	0.4	2.0	4.1	4.9	4.9	2.0

Species	Code N°	Type	Abund. Coeff.	Sand Equivalent 7	10	14	20	35	80
Procecidae un.sp.	029	c	0.056	0.3	1.7	2.9	3.9	5.2	4.9
Marphysa bellii	030	e	0.048	1.1	3.5	4.6	4.7	1.8	2.6
Chrysopetalum debile	031	a	0.077	0.0	0.1	0.2	0.8	6.0	7.7
Asychis biceps	032	b	0.069	0.0	0.3	0.8	1.9	4.5	6.9
Podarke pallida	033	d	0.047	0.4	1.8	3.8	4.6	4.5	1.9
Choetozone setosa	034	c	0.043	0.2	1.3	2.2	3.0	4.0	3.7
Aricidea fauveli	035	c	0.041	0.2	1.2	2.1	2.9	3.8	3.6
Harmothoe lunulata	036	b	0.066	0.0	0.3	0.8	1.8	4.3	6.6
Leanira yhleni	037	d	0.038	0.3	1.5	3.0	3.7	3.6	1.5
Amphiura filiformis	038	b	0.059	0.0	0.2	0.7	1.7	3.8	5.9
Clymene santanderensis	0.39	b	0.060	0.0	0.2	0.7	1.7	3.9	6.0
Ancistrosyllis robusta	040	d	0.036	0.3	1.4	2.9	3.5	3.5	1.4
Poecilochaetus serpens	041	e	0.038	0.8	2.8	3.6	3.7	1.4	2.1
Cirratulus cirratus	042	a	0.057	0.0	0.1	0.1	0.6	4.4	5.7
Spiophanes bombyx	043	c	0.035	0.2	1.0	1.8	2.4	3.3	3.0
Chrysallida sp.	044	e	0.030	0.7	2.2	2.9	2.9	1.1	1.6
Mystides limbata	045	a	0.053	0.0	0.1	0.1	0.6	4.1	5.3
Prionospio malmgrenii	046	d	0.031	0.2	1.2	2.5	3.0	3.0	1.2
Pilargis falcata	047	c	0.032	0.2	1.0	1.7	2.2	3.0	2.8
Stylarioides plumosa	048	b	0.046	0.0	0.2	0.6	1.3	3.0	4.6
Cirratulidae un. sp.	049	b	0.046	0.0	0.2	0.6	1.3	3.0	4.6
Chone collaris	050	a	0.049	0.0	0.0	0.1	0.5	3.8	4.9
Laonice cirrata	051	a	0.046	0.0	0.0	0.1	0.5	3.6	4.6
Myriochelle heeri	052	c	0.024	0.1	0.7	1.2	1.7	2.2	2.1
Cossura coasta	053	a	0.043	0.0	0.0	0.1	0.5	3.4	4.3
Chone dunneri	054	a	0.042	0.0	0.0	0.1	0.5	3.3	4.2
Paraonidae un. sp.	055	c	0.027	0.1	0.8	1.4	1.9	2.5	2.3
Paguroidea un. sp.	056	a	0.044	0.0	0.0	0.1	0.5	3.4	4.4
Aspidosiphon muelleri	057	a	0.043	0.0	0.0	0.1	0.5	3.4	4.3
Vibilidae un. sp.	058	f	0.047	4.5	4.6	2.4	1.3	0.7	1.2
Psamobia sp.	059	a	0.041	0.0	0.0	0.1	0.5	3.2	4.1
Venus cassina	060	a	0.041	0.0	0.0	0.1	0.5	3.2	4.1
Nucula turgida	061	d	0.022	0.2	0.9	1.8	2.1	2.1	0.9
Neosabellides oceanica	062	b	0.036	0.0	0.1	0.4	1.0	2.3	3.6
Syllis cornuta	063	a	0.038	0.0	0.0	0.1	0.4	3.0	3.8
Hyalinoecia brementi	064	b	0.037	0.0	0.1	0.4	1.0	2.4	3.7
Iphinoe serrata	065	c	0.021	0.1	0.6	1.1	1.5	2.0	1.8
Metaphoxus sp.	066	b	0.028	0.0	0.1	0.3	0.8	1.8	2.8
Pectinaria horeni	067	b	0.029	0.0	0.1	0.3	0.8	1.9	2.9
Cultellus pellucidus	068	b	0.029	0.0	0.1	0.3	0.8	1.9	2.9
Callianassa sp.	069	e	0.020	0.4	1.5	1.9	1.9	0.8	1.1
Dodecaceria concharum	070	a	0.030	0.0	0.0	0.1	0.3	2.3	3.0
Nematonereis unicornis	071	a	0.029	0.0	0.0	0.1	0.3	2.3	2.9
Lysianassa longicornis	072	f	0.027	2.6	2.6	1.4	0.8	0.4	0.7
Sphaerosyllis ovigera	073	a	0.026	0.0	0.0	0.1	0.3	2.0	2.6
Labidoplax digitata	074	c	0.015	0.1	0.4	0.8	1.0	1.4	1.3
Ampharetidae un. sp.	075	b	0.026	0.0	0.1	0.3	0.7	1.7	2.6
Physcosoma granulatum	076	b	0.024	0.0	0.1	0.3	0.7	1.6	2.4

Species	Code N°	Type	Abund. Coeff.	Sand Equivalent 7	10	14	20	35	80
Glycera lapidum	077	a	0.024	0.0	0.0	0.0	0.3	1.9	2.4
Notomastus sp.	078	d	0.012	0.1	0.5	1.0	1.2	1.2	0.5
Sphaerosyllis bulbosa	079	a	0.023	0.0	0.0	0.0	0.3	1.8	2.3
Goneplax rhomboides	080	e	0.012	0.3	0.9	1.2	1.2	0.5	0.6
Leucothoe spinicarpa	081	c	0.014	0.1	0.4	0.7	1.0	1.3	1.2
Aricidea curviseta	082	a	0.023	0.0	0.0	0.0	0.3	1.8	2.3
Clymene oerstedii	083	a	0.023	0.0	0.0	0.0	0.3	1.8	2.3
Clymene collaris	084	e	0.013	0.3	0.9	1.2	1.3	0.5	0.7
Mysidacea un.sp.	085	d	0.012	0.1	0.5	1.0	1.2	1.2	0.5
Aricidea suesica simplex	086	b	0.020	0.0	0.1	0.2	0.6	1.3	2.0
Cucumaria tergestina	087	b	0.020	0.0	0.1	0.2	0.6	1.3	2.0
Anobothrus gracilis	088	c	0.012	0.1	0.4	0.6	0.8	1.1	1.0
Elisia sp.	0.89	b	0.020	0.0	0.1	0.2	0.6	1.3	2.0
Upogebia littoralis	090	d	0.012	0.1	0.5	1.0	1.2	1.2	0.5
Brissus unicolor	091	d	0.011	0.1	0.4	0.9	1.1	1.1	0.4
Leiochone clypeata	092	a	0.018	0.0	0.0	0.0	0.2	1.4	1.8
Phtisica marina	093	a	0.018	0.0	0.0	0.0	0.2	1.4	1.8
Corbulla gibba	094	a	0.018	0.0	0.0	0.0	0.2	1.4	1.8
Thyone fusus	095	b	0.016	0.0	0.1	0.2	0.4	1.0	1.6
Goniada maculata	096	a	0.017	0.0	0.0	0.0	0.2	1.3	1.7
Cardium sp	097	a	0.016	0.0	0.0	0.0	0.2	1.2	1.6
Leptochellia savignii	098	a	0.015	0.0	0.0	0.0	0.2	1.2	1.5
Monoculodes gibbosus	099	a	0.016	0.0	0.0	0.0	0.2	1.2	1.6
Amaea trilobata	100	c	0.009	0.0	0.3	0.5	0.6	0.8	0.8
Scaphander lignarius	101	c	0.009	0.0	0.3	0.5	0.6	0.8	0.8
Clymene santanderensis	102	b	0.014	0.0	0.1	0.2	0.4	0.9	1.4
Pista cristata	103	a	0.014	0.0	0.0	0.0	0.2	1.1	1.4
Scalibregma inflatum	104	c	0.009	0.0	0.3	0.5	0.6	0.8	0.8
Maldanidae un. sp.	105	c	0.009	0.0	0.3	0.5	0.6	0.8	0.8
Galathea sp.	106	a	0.015	0.0	0.0	0.0	0.2	1.2	1.5
Echinocyamus pussilus	107	a	0.013	0.0	0.0	0.0	0.1	1.0	1.3
Clymene robusta	108	a	0.013	0.0	0.0	0.0	0.1	1.0	1.3
Aonides paucibranchiata	109	e	0.007	0.2	0.5	0.7	0.7	0.3	0.4
Cirrophorus branchiatus	110	a	0.012	0.0	0.0	0.0	0.1	0.9	1.2
Jasmineira caudata	111	a	0.013	0.0	0.0	0.0	0.1	1.0	1.3
Gammarus olivii	112	a	0.012	0.0	0.0	0.0	0.1	0.9	1.2

a,b,c,d,e or **f,** of each species, its "abundance coefficient" **K,** code number (based on the rank) and number of individuals per m^2, **j,** for $s'=7$, 10, 14, 20, 35 and 80, estimated from **K** and the relative abundances, **q,** shown in Table III. Its interest lies in its permitting reliable comparisons with the fauna of the other parts of the Mediterranean and holding all the data necessary for further study. However, though theoretically ideal for describing biocoenoses, it fails to underline the dramatic changes taking place when the substratum becomes finer.

Dealing with samples of fixed area, **d,** has the advantage of creating two fundamental characteristics, the number of species, **g**, and the total number of individuals, **i.** Citing the species by order of abundance for each selected index of coarseness improves further the presentation of the macrozoobenthos composition, which, obviously, depends on **d.** A very large value of **d** tends to bring confusion, while a small one affords an inadequate picture. By making **d** relatively great, $1m^2$, a neat and detailed enough view of the fauna is elicited. Thus, Table V, in which the species are designated by the same code number as in Table IV, shows that, when **s′** goes up from 7 to 80, the number of species quadruples, while the mean species abundance, i/g has a moderate only increase, from 6.2 to 8.5 individuals per species. Furthermore, on the qualitative side, *Callianassa stebbingi* (code number 004) and *Tauberia gracilis* (003), which contribute 65% of all individuals in the finest sediment, represent barely 5% of those in the coarsest one, where they rank respectively 11^{th} and 7^{th}. Conversely, of the first two dominant species in the sandy habitat, *Onchnesoma steenstrupii* (001) and *Tharyx dorsobranchialis* (002), the former

TABLE V Biocenoses of various soft substrata in 1 m^2 samples.

	Sand equivalent											
	7		10		14		20		35		80	
	g 24	i 150	g 29	i 219	g 37	i 296	g 47	i 397	g 68	i 593	g 94	i 798
Rank	Spec. code	N° ind.	Spec. code	N° ind	Spec. code	N° ind.	Spec. code	N° ind.	Spec. code	N° ind.	Spec. code	N° ind.
1	004	84	004	58	003	41	003	45	001	67	001	112
2	003	14	003	32	004	30	002	39	002	49	002	50
3	058	8	002	16	002	27	005	33	005	31	006	42
4	012	5	005	12	005	26	001	31	006	30	009	35
5	072	4	012	11	012	15	004	17	009	25	010	32
6	013	4	013	10	013	13	008	17	010	23	011	30
7	002	4	016	7	001	12	007	17	011	21	003	25
8	005	4	008	7	008	12	012	16	008	21	008	21
9	016	3	007	7	007	11	013	14	007	20	007	21
10	019	3	019	6	016	10	014	12	003	16	015	19
11	030	2	058	5	014	10	016	10	015	14	004	16
12	008	2	014	5	019	8	017	9	014	12	005	14
13	007	2	001	4	017	7	019	8	022	10	020	14
14	014	1	030	4	025	5	025	7	004	9	022	13
15	041	1	017	4	030	5	028	6	017	9	021	13
16	044	1	041	3	028	5	018	6	027	8	026	12
17	017	1	072	3	033	4	030	6	020	8	027	12
18	025	1	025	3	018	4	033	6	021	8	031	10
19	028	1	044	3	041	4	023	6	018	8	012	9
20	033	1	018	2	023	4	029	5	026	8	032	9
21	069	1	028	2	037	4	024	5	023	7	036	8
22	023	1	023	2	024	3	037	5	031	7	013	8
23	018	1	033	2	029	3	041	5	025	7	018	8

Rank	Sand equivalent 7, g 24, Spec. code	7, i 150, N° ind.	10, g 29, Spec. code	10, i 219, N° ind	14, g 37, Spec. code	14, i 296, N° ind.	20, g 47, Spec. code	20, i 397, N° ind.	35, g 68, Spec. code	35, i 593, N° ind.	80, g 94, Spec. code	80, i 798, N° ind.
24	024	1	024	2	040	3	006	4	029	6	039	8
25			029	2	044	3	040	4	024	6	038	7
26			037	2	046	3	009	4	012	6	042	7
27			069	2	058	3	020	4	028	6	023	7
28			040	2	034	3	034	4	032	5	045	7
29			034	1	035	3	046	4	033	5	029	6
30					069	2	021	4	042	5	050	6

TABLE V (continued)

Rank	Sand equivalent 14, Spec. code	14, N° ind.	20, Spec. code	20, N° ind.	35, Spec. code	35, N° ind.	80, Spec. code	80, N° ind.
31	043	2	035	4	013	5	024	6
32	061	2	044	4	036	5	016	6
33	047	2	010	3	045	5	048	6
34	055	2	026	3	034	5	049	6
35	072	2	011	3	039	5	051	6
36	020	2	043	3	035	4	056	6
37	021	1	047	3	038	4	053	5
38			061	3	050	4	057	5
39			032	2	037	4	054	5
40			055	2	051	4	014	5
41			069	2	040	4	059	5
42			036	2	053	4	060	5
43			038	2	056	4	063	5
44			039	2	057	4	034	5
45			052	2	016	4	064	5
46			015	2	043	4	019	4
47			065	2	054	4	035	4
48					059	4	062	4
49					060	4	017	4
50					046	4	043	4
51					047	4	070	4
52					048	4	067	4
53					049	4	068	4
54					063	4	071	4
55					019	3	047	4
56					055	3	066	4
57					064	3	030	3
58					062	3	073	3
59					070	3	075	3
60					071	3	076	3
61					052	3	077	3

Rank	Sand equivalent 35, Spec. code	35, N° ind.	80, Spec. code	80, N° ind.
62	061	2	025	3
63	065	2	055	3
64	073	2	079	3
65	067	2	082	3
66	068	2	083	3
67	077	2	041	3
68	030	2	052	3
69			028	3
70			086	3
71			087	3
72			089	3
73			033	2
74			065	2
75			092	2
76			093	2
77			094	2
78			096	2
79			044	2
80			095	2
81			097	2
82			099	2
83			037	2
84			098	2
85			106	2
86			040	2
87			102	2
88			103	2
89			074	2
90			107	2
91			108	2
92			111	2
93			046	2
94			058	2

is altogether absent and the latter holds the 7^{th} position in the substratum with $s'=7$. Hence, a natural environment unfavorable to life affects deeply the benthic communities, reducing drastically the number of both species and individuals, as well as changing the order of abundance of the species.

Dominance function

As emphasized in the previous section, when dealing with samples of constant area, **d**, a large rise in the index of coarseness, **s'**, on the average, just per-

TABLE VI. Cumulative percentage distribution of the ranked species abundance, $1 m^2$ samples.

Cumul. Percent species	Cumulative percentage individuals for sand equivalent of								
	7,		10	14	20	35	80	Mean 10 – 80	
	Actual	Function						Actual	Function
4	53.3	55.9	29.0	18.8	19.8	23.4	28.7	23.9	25.0
8	64.6	64.7	43.5	32.8	35.4	35.7	42.3	37.9	37.9
10	67.5	67.7	47.8	39.3	40.4	40.8	47.1	43.1	42.7
12	70.1	70.1	51.1	44.2	44.3	45.5	51.0	47.2	46.9
16	73.4	74.0	57.1	51.1	52.2	53.2	57.3	54.2	53.8
20	76.2	77.1	62.6	57.1	58.9	58.1	62.5	59.8	59.5
24	78.7	79.7	66.6	62.8	63.9	62.1	66.3	64.3	64.2
28	81.2	81.8	70.3	67.8	67.8	65.7	69.6	68.2	68.2
30	82.5	82.8	72.2	70.2	69.4	67.4	71.4	70.1	70.0
32	83.8	83.7	73.9	72.2	70.9	69.0	72.9	71.8	71.7
36	86.0	85.4	76.8	75.6	73.6	72.0	75.7	74.7	74.8
40	87.9	86.9	79.5	78.1	76.5	74.7	78.3	77.4	77.6
44	89.4	88.3	81.8	80.5	78.9	77.0	80.7	79.8	80.1
48	90.7	89.5	83.8	82.5	81.3	79.3	83.1	82.0	82.3
50	91.3	90.1	84.9	83.4	82.4	80.4	84.0	83.0	83.4
52	92.0	90.7	85.9	84.4	83.3	81.5	85.0	84.0	84.4
56	93.0	91.7	87.5	86.4	85.2	83.3	86.8	85.8	86.3
60	93.6	92.7	89.2	88.0	87.1	85.2	88.6	87.6	88.0
64	94.3	93.6	90.7	89.6	89.0	87.1	90.1	89.3	89.6
68	94.9	94.5	91.9	91.0	90.9	88.9	91.5	90.8	91.1
70	95.2	94.9	92.5	91.8	91.6	89.8	92.1	91.6	91.8
72	95.5	95.3	93.1	92.5	92.3	90.7	92.9	92.3	92.5
76	96.2	96.1	94.1	94.0	93.8	92.6	94.3	93.8	93.8
80	96.8	96.8	95.2	95.3	95.2	94.2	95.3	95.0	95.0
84	97.4	97.5	96.2	96.4	96.2	95.7	96.2	96.1	96.1
88	98.1	98.2	97.3	97.3	97.2	97.0	97.2	97.2	97.2
90	98.4	98.5	97.8	97.8	97.7	97.7	97.6	97.7	97.7
92	98.7	98.8	98.3	98.3	98.1	98.2	98.1	98.2	98.2
96	99.3	99.4	99.3	99.4	99.1	99.0	99.0	99.2	99.1
100	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

ceptibly enhances the number of individuals of each species, despite the huge increase in the total number of individuals, **i.** This peculiar finding makes worthwhile ascertaining whether or not **s′** influences the ratios of the abundances, **j,** of the species, especially the dominant ones, to one another. This requires studying the "dominance functions", or relationship between the cumulative percentage of individuals, $w=100\Sigma_1^n j/i$, and the cumulative percentage of species, $p=100\ n/g$, where **n** is the rank of the last species used to calculate **w** and **p,** while $\Sigma_1^n j/i$ is the sum of the ratio j/i for the first **n** species, in a sample of **g** species and **i** individuals.

TABLE VIIa Cumulative percentage distribution of the ranked species abundance. Assemblages of 25 species.

Cumul. percent. species	Cumulative percentage individuals for sand equivalent of 7	10 Actual	10 Function	14	20	35	80	Mean 14 – 80 Actual	Mean 14 – 80 Function
4	56.1	27.4	29.0	15.2	13.5	15.6	20.4	16.2	15.1
8	65.6	42.5	41.5	26.4	25.2	27.0	29.6	27.0	26.7
10	68.3	46.2	46.1	31.4	30.2	30.6	33.4	31.4	31.5
12	71.0	50.0	50.0	36.4	35.1	34.2	37.2	35.7	35.7
16	74.4	55.7	56.5	46.1	44.4	41.2	43.6	43.8	43.1
20	77.4	60.8	61.7	51.7	49.5	47.0	49.5	49.4	49.2
24	80.4	65.8	66.1	56.5	54.7	52.3	54.9	54.6	54.8
28	83.0	68.9	69.8	61.0	59.8	57.2	59.5	59.4	59.6
30	84.3	70.6	71.5	63.2	62.2	59.6	61.4	61.6	61.7
32	85.6	72.2	73.1	65.4	64.6	62.1	63.3	63.8	63.8
36	87.8	75.5	76.0	69.5	68.8	66.7	67.2	68.0	67.6
40	89.6	78.3	78.6	73.2	72.4	70.5	70.6	71.7	71.0
44	90.9	80.7	80.9	77.0	75.4	73.7	73.5	74.9	74.1
48	92.1	83.0	83.0	79.9	78.1	76.5	76.1	77.6	76.9
50	92.6	84.0	84.0	81.2	79.3	77.6	77.4	78.9	78.3
52	93.2	84.9	85.0	82.5	80.5	78.8	78.6	80.1	79.5
56	94.1	86.8	86.7	84.4	82.6	80.9	81.0	82.2	82.0
60	95.0	88.7	88.4	86.2	84.4	83.0	83.4	84.2	84.2
64	95.9	90.1	89.9	88.1	86.2	84.9	85.6	86.2	86.3
68	96.6	91.5	91.3	89.6	88.0	86.7	87.8	88.0	88.2
70	96.9	92.2	92.0	90.4	88.9	87.6	88.7	88.9	89.1
72	97.2	92.9	92.7	91.1	89.8	88.6	89.6	89.8	90.0
76	97.6	94.3	93.9	92.6	91.6	90.5	91.2	91.5	91.7
80	98.1	95.3	95.1	94.1	93.1	92.3	92.9	93.1	93.3
84	98.6	96.2	96.2	95.5	94.6	94.0	94.3	94.6	94.8
88	98.9	97.2	97.2	96.7	96.1	95.6	95.8	96.0	96.2
90	99.1	97.7	97.7	97.3	96.9	96.4	96.6	96.8	96.9
92	99.3	98.1	98.2	97.8	97.6	97.2	97.3	97.5	97.6
96	99.6	99.1	99.1	98.9	98.8	98.6	98.7	98.8	98.8
100	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table VI presents the results of such computations using the data in Table V, except in the case of $s'=7$, needing, for improved accuracy, the species abundance values quoted in Table IV. To facilitate comparisons, **w** was estimated again for the displayed round values of **p** through simple interpolation. As can be seen, the means of the figures for $s'=10$, 14, 20, 35 and 80, the discrepancies of which appear of no statistical importance, agree closely whith the in logarithms second degree equation, represented graphically in Fig. 7 ("37-94 species"): $\log w = -0.1534(\log p)^2 + 0.8296 \log p + 0.9546$ (3), the coefficients of which have been deduced from the three p-w coordinates 8-37.9, 28-68.2, 100-100. The function for $s'=7$: $\log w = -0.0274 (\log p)^2 + 0.2519 \log p + 1.06058$ (4), based on the p-w coordinates 12-70.1, 36-85.4 and 100-100, also fits very well the data. Clearly, in spite of the violent changes occurring in samples of fixed dimensions when **s'** rises from 10 to 80, the dominant species that represent a certain fraction of all the species contribute about the same percentage of individuals whatever **s'**.

Tables VIIa, VIIb, and VIIc concern the dominance functions in the case of the most abundant species numbering only respectively 25, 10 and 5. Along with Table VI, they demonstrate that **w** tends to fall for a certain value of **p** as the number of species becomes smaller. Fig. 7, where the graphs marked 25, 10 and 5 species refer to mean values for **s'** in the range 14-80, illustrates the observation. The curves for $s'=7$ and 10, which were not drawn to avoid confusion, would have presented steeper initial slopes. Variations in the total number of individuals have less effect on the functions, since they correspond to much smaller changes in the number of species.

The weak relationship between the habitat and the equations, together with their dependence upon the number of species throw a serious doubt on the validity of a rich assortment of "dominance diversity" indices. Let us apply one of them, Shannon's, to the present data. $I_S = - \Sigma i/I \cdot \log_2 i/I$ (5), where **I** is the total number of individuals in the assemblage and **i** that of each species. The data in Table V, referring to an area, **d,** of $1m^2$, give the following results: $s'=7$, $I_S = 2.74$; $s'=10$, $I_S = 3.95$; $s'=14$, $I_S = 4.54$; $s'=20$, $I_S = 4.88$; $s'=35$, $I_S = 5.41$; $s'=80$, $I_S = 5.64$. Samples 10 times smaller ($d=0.1m^2$), with 2.5 fewer species, yield much lower figures: $s'=7$, $I_S = 2.04$; $s'=10$, $I_S = 3.05$; $s'=14$, $I_S = 3.63$; $s'=20$, $I_S = 3.91$; $s'=35$, $I_S = 4.34$; $s'=80$, $I_S = 4.66$. Thus, a 2.5 times reduction in the number of species causes $\mathbf{I_s}$ to drop by one unit, so that $\mathbf{I_s}$ for $s'=80$ and $d=0.1m^2$ becomes about the same as $\mathbf{I_S}$ for $s'=14$ and $d=1m^2$, in spite of enormous biocoenose differences.

Sanders (1968) also found "dominance diversity" indices unsatisfactory. He preferred counting the number of species observed in a given number of individuals. Here, for $s'=7$, 10, 14, 20, 35 and 80, areas of, respectively, 1.00, 0.68, 0.51, 038, 0.25 and $0.19m^2$ yield all 150 individuals and, respectively, 24, 26, 29, 33, 40 and 49 species. Conversely, areas of, respectively, 1.00, 0.57, 0.31, 0.174, 0.079 and $0.050m^2$ contain all 24 species and, respectively, 150, 125, 92, 69, 47 and 40 individuals. Hence, "species diversity", especially when based on assemblages with a fixed number of species, has sufficient reliablility. However, its calculation presupposes knôwing the relation between the number of species and the sample area, which can be at best approximate, since no direct practical way of establishing it exists. The diversity indices are legacies of an epoch when the use of instruments such as dredge and sled excluded quantitative sampling and compelled scientists to wander along devious, complicated and uncertain routes in an effort to gain some indispensable knowledge about the species richness of a habitat. In contrast, grab sampling affords a concrete and sensitive procedure for measuring the biocoenose diversity, quite simply by referring to the number of species in a sample of fixed size.

TABLE VIIb Cumulative percentage distribution of the ranked species abundance. Assemblages of 10 species.

Cumul. percent species	Cumulative percentage individuals for sand equivalent ob									
	7		10		14	20	35	80	Mean 14 – 80	
	Actual	Function	Actual	Function					Actual	Function
10	63.2	64.0	34.9	37.0	20.8	18.7	22.1	28.9	22.6	22.7
20	73.7	72.6	54.2	52.5	36.0	34.9	38.3	41.9	37.8	38.0
30	79.7	78.5	63.9	63.2	49.7	48.5	48.5	52.7	49.8	49.9
40	83.5	83.0	71.1	71.3	62.9	61.4	58.4	61.8	61.1	59.9
50	86.5	86.8	77.7	78.0	70.6	68.5	66.7	70.0	69.0	68.5
60	89.5	90.0	83.7	83.6	77.2	75.5	74.3	77.8	76.2	76.1
70	92.5	92.9	88.0	88.5	83.2	82.6	81.2	84.2	82.8	82.9
80	95.5	95.5	92.2	92.8	89.3	89.2	88.1	89.7	89.1	89.1
90	97.7	97.8	96.4	96.6	94.9	95.0	94.7	95.1	94.9	94.8
100	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

TABLE VIIc Cumulative percentage distibution of the ranked species abundance. Assemblages of 5 species.

Cumul. percent species	Cumulative percentage individuals for sand equivalent of									
	7		10		14	20	35	80	Mean 14 – 80	
	Actual	Function	Actual	Function					Actual	Function
20	73.0	73.0	45.0	46.5	29.5	27.3	33.2	41.3	32.8	31.0
40	85.2	85.2	69.8	67.5	51.1	50.9	57.4	59.8	54.8	55.0
60	92.2	92.0	82.2	81.5	70.5	70.9	72.8	75.3	72.4	73.3
80	96.5	96.6	91.5	91.8	89.2	89.7	87.6	88.2	88.7	87.9
100	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Sequence of ranked species abundance

Tables VI and VII, as well as Fig. 7, indicate that, for a particular value of the "sand equivalent", **s'**, the slope at the start of the "dominance function" grows steeper as the number of species, **g**, waxes larger. This occurs because the dominant species go on contributing nearly the same proportion of individuals as before, while their number becomes a much smaller percentage of the total, **g.** Owing to this strong dependence on **g**, the "dominance function" would appear of limited interest. However, as seen in the previous section, when dealing with samples of constant areas, $d=1m^2$, a change in **g** due to a difference in **s'** within a fairly wide range (10-80) does not affect it appreciably. The knowledge of equation (3) enables calculating in this case the abundances, **j**, of all the species listed by order of decreasing values of **j.**

Let $\mathbf{j_n}$ be the abundance of the species of rank **n** and f (p) the cumulative percentage of individuals, **w**, corresponding to the cumulative percentage of species, **p**, in (3). We have:

$$j_n = i/100[f[(100/g)\cdot n] - f[(100/g)(n-1)]] \qquad (5),$$

where **i** is the total number of individuals in the sample. The values of **j** thus estimated agree closely with the actual ones: they differ from them by an average of just 11% in the instance of the first 20 species.

To facilitate the comparison of species dominance, we make $g = 10$ and $i=100$ in (5). The latter becomes:

$$j_n = f(10n) - f[10(n-1)] \qquad (5a),$$

where f(p) represents an equation computed from the data in the same manner as (3) and (4). Also, we convert abundances, which have little meaning in themselves, into characteristic ratios of abundances j_n/j_{10}. The first term, j_1/j_{10}, of such a series of "standard abundances" can be viewed as a "dominance factor", increasing with the degree of dominance. For a particular substratum coarseness, the initial slope of f (p) diminishes with the sample area, **d**, and so do the ratios j_n/j_{10}. However, each of them, when taken to a certain power, the same for all the terms of the series, very nearly gives the original one. This finding suggests the existence of "homologous" dominance functions typical of a specified habitat.

Comparison of regions

The present work has demonstrated that the coarseness of the substratum, expressed as "sand equivalent", **s'**, affects the macrozoobenthos of the Pagassitikos Gulf considerably more than any other factor. It has such a powerful action that the fauna of two sites in the area may differ more from each other than the average of the embayment from a distant part of the Mediterranean. The major reason for it seems the dependence of the dissolved oxygen content upon **s′**. Undoubtedly, fine particles, besides hampering the motion of epifauna, retard the exchange of gases, while their presence testifies to the lack of strong currents of oxygen rich water. Also, as a rule, they contain more organic carbon, the bacterial decomposition of which consumes oxygen. Furthermore, Voutsinou-Taliadouri and Satsmadjis (1982) have established that the level in sediments of metals, possibly deleterious as a whole, rises as the grains become smaller. Whatever the explanation, benthic comparisons of regions, to have any meaning, must concern substrata of the same texture.

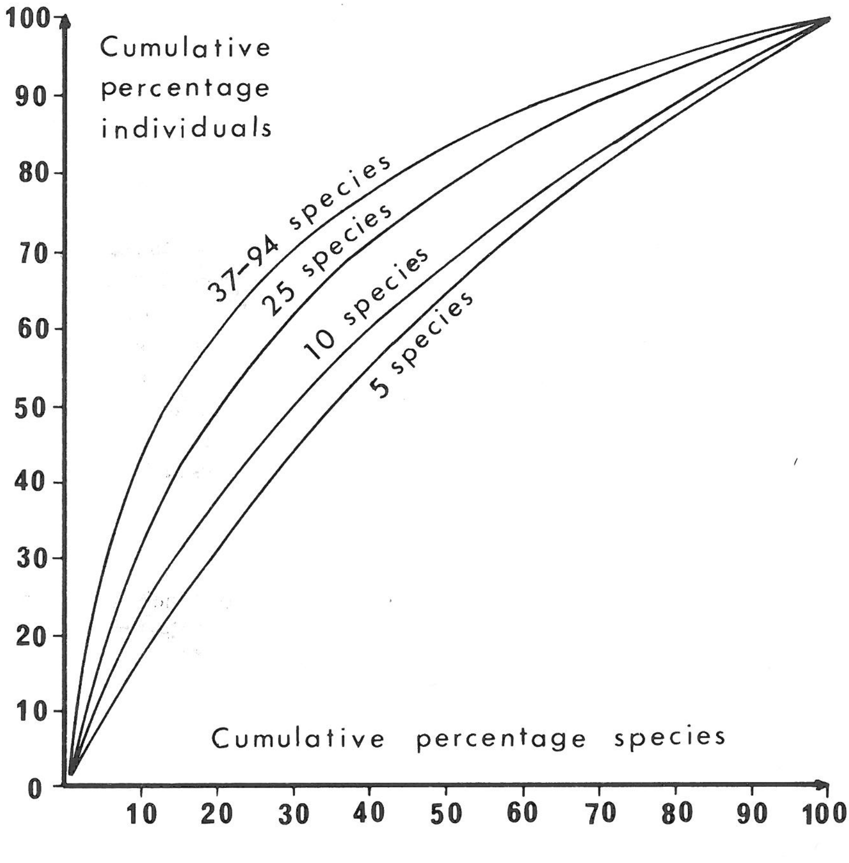

Fig. 7. Influence of the total number of species on the dominance function.

Depth, **h,** though closely correlated with **s′,** acts independently from it, presumably by affecting the amount of oxygen available. In the Pagassitikos Gulf, where it reaches a maximum of just 100m, it has been found, as mentioned earlier, to affect the number of individuals, **i,** by a factor of (2.20 – 0.0166 h). This means that a sample from a depth of 50m with s′=10 contains as many individuals as one with s′ =14 drawn from 72m. In the absence of sufficient evidence to the contrary, we may assume that the assemblage has more or less the composition shown in Table V for s′=14. However, samples taken at depths of several hundred meters could reveal that **h** does not inhibit the growth of species in exactly the same fashion as does the value of **s′** when reduced.

Food, as indispensable as oxygen to animal life, should induce benthic enrichment. Paradoxically, stations with high levels of organic matter in the sediment and of dissolved inorganic nutrients in the water above it exhibit smaller abundance. This happens because, in general, they relate to fine material or great depth. But a rise in inorganic nutrients from one cruise to another does tend to result in enchanced **g** and **i** figures. As in the case of depth, the Pagassitikos Gulf data do not suffice to ascertain whether or not the composition of assemblages in contact with water richer in nutrients corresponds to that of coarser substratum with the same **g** and **i.**

Temperature must affect benthos. However, below a certain depth, it hardly varies throughout the year and in the whole of the Mediterranean. On the contrary, shallow waters undergo wide temperature fluctuations, as well as powerful stirring. Other factors that would alter the composition of the assemblages are: turbidity, strong currents, lower and unsteady salinity due to the vicinity of a large river, the geological history of the area, the casual introduction of new species etc. Their influence could be estimated by comparing regions with dissimilar biocoenoses after taking into account the coarseness of the sediment.

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ANNEX

Determination of the standard abundance function of a particular species

The models of abundance function were established by using the values of the percentage, **q,** of the maximum abundance for the mean "sand equivalents" s'_1, s'_2, s'_3, s'_4, s'_5 and s'_6, i.e. 62.9, 32.2, 17.4, 12.8, 11.4, and 8.8, of the substrata of the subgroups of stations A_1, A_2, B_1, B_2, C_1 and C_2. To these values of **s′** and for each type of function, **a, b, c, d, e** and **f,** correspond the relative abundances q_1, q_2, q_3, q_4, q_5 and q_6, estimated from the Figures 1, 2 and 3. As done in Table II, these enable calculating first

$$\Sigma_q = q_1 + q_2 + q_3 + q_4 + q_5 + q_6,$$

then $z = 100q/\Sigma_q$ for each subgroup and, finally,

$$z' = 100(q_n + q_{n+1})/\Sigma_q,$$

where $n = 1$ for group **A,** $n = 3$ for **B** and $n = 5$ for **C.**

Calling q'_a, q'_b and q'_c the relative abundances of the groups **A, B** and **C** for a specified type of function and z'_a, z'_b and z'_c the corresponding **z′** values, we have:

$$q'_a = 1/2(q_1 + q_2), \quad q'_b = 1/2(q_3 + q_4) \quad \text{and} \quad q'_c = 1/2(q_5 + q_6).$$

Consequently:

$$z'_a = (q_1 + q_2)/(q_1 + q_2 + q_3 + q_4 + q_5 + q_6) = 2q'_a/(2q'_a + 2q'_b + 2q'_c),$$
$$z'_a = q'_a/(q'_a + q'_b + q'_c) = q'_a/\Sigma q'.$$

In the same manner:

$$z'_b = q'_b/\Sigma q', \quad \text{and} \quad z'_c = q'_c/\Sigma q'.$$

Furthermore, since the ratio, **K′,** of the relative abundance, **q,** to the species abundance, **j,** is constant in a given standard function, we also have:

$$z'_a = K'j_a/(K'j_a + K'j_b + K'j_c) = j_a/(j_a + j_b + j_c),$$
$$z'_a = j_a/\Sigma j$$

Similarly:

$$z'_b = j_b/\Sigma j \quad \text{and} \quad z'_c = j_c/\Sigma j.$$

Hence, to each pattern of relative abundance function correspond three characteristic **z′** figures, namely z'_a, z'_b, z_c. These are merely the group species abundances, j_a, j_b and j_c, expressed as percentages of their sum $(j_a + j_b + j_c)$. They vary considerably, as shown in Table II, from $z'_a = 96.6$, $z'_b = 2.8$ and $z'_c = 0.6$ for type **a** to $z'_a = 12.0$, $z'_b = 30.7$ and $z'_c = 57.3$ for type **f,** at the other end of the scale. The computation of actual **z′**, symbolized by **z″**, requires finding the observed abundances, **j′**. Let us call J_A, J_B and J_C the sum of all the individuals found in the samples belonging to the respective group of stations **A, B** and **C.** Since the corresponding total areas, corrected for depth, are 10.86, 7.44 and 4.85 m^2, we have:

$j'_a = J_A/10.86$, $j'_b = J_B/7.44$ and $j'_c = J_C/4.85$.

Consequently:

$$z''_a = 100\, j'_a/(j'_a + j'_b + j'_c),$$
$$z''_b = 100\, j'_b/(j'_a + j'_b + j'_c),$$
$$z''_c = 100\, j'_c/(j'_a + j'_b + j'_c).$$

The values of z''_a, z''_b and z''_c must now be compared with those of each of the six types, **a**, **b**, **c**, **d**, **e** and **f,** of relative abundance function.
This is achieved by adding the squares of the differences $(z''-z')$.

$E = (z'_a - z''_a)^2 + (z'_b - z''_b)^2 + (z'_c - z''_c)^2.$

As shown in Table II, for type **a,** $z'_a = 96.6$, $z'_b = 2.8$ and $z'_c = 0.6$ for type **b**, $z'_a = 79.6$, $z'_b = 16.8$ and $z'_c = 3.6$ etc. The type of the species is that for which **E** is smallest.