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MOLLUSCAN POPULATIONS OF THE EDEN ESTUARY, FIFE, AND THE
USE OF NUMERICAL TAXONOMY METHODS TO DETERMINE THEIR
DISTRIBUTION PATTERNS.

By

ARGYRO ZENETOS

Graduate in Natural Sciences and Geography
University of Athens



A Thesis presented for the Degree of Master of Science to
the University of St. Andrews

April, 1980.

Th 9347

C E R T I F I C A T E .

I hereby certify that Argyro Zenetos has fulfilled the Conditions of the Ordinance No. 12 and Resolution of the University Court, 1974 No. 2, and that she is qualified to submit the accompanying thesis in application for the Degree of Master of Science.

Dr. A.R. MacGregor.

D E C L A R A T I O N .

I certify that the following thesis is my own composition, that is based on the results of research carried out by me and that it has not previously been presented in application for a Higher Degree.

Argyro Zenetos.

D E D I C A T I O N .

To my parents Marina and Georgios Zenetos for their financial support throughout this study.

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A B S T R A C T.

The aim of this study is twofold, firstly to recognize life and death assemblages among subfossils by using standard criteria and secondly to test the applicability of Numerical Taxonomy methods in defining biotopes and biofacies in Palaeoecology.

Among the criteria applied in distinguishing life and death assemblages, the following: dispersion of subfossils, faunal composition and diversity, population density, surface condition of shells and ratio of opposite valves, indicate that little postmortem transportation has taken place and that the subfossil assemblages represent accurately the life assemblages from which they were derived. Other criteria were either not applicable or when applied proved unreliable.

In examining biotopes and biofacies, several sets of data are combined in alternative techniques. For biofacies the most ecologically meaningful results are obtained by the correlation coefficient with numerical data or by the Matching coefficient with binary data. Most cluster methods produce similar results with the above coefficients. For biotopes analysis, both similarity coefficient and cluster method are critical to the resultant classification. The most successful distribution patterns are derived by use of the Matching coefficient and W.P.G.A. with binary data or Squared Euclidean Distance and Ward's method with standardized-by-species numerical data. It is suggested that the grain size of the substrate is the main factor determining the distribution of Mollusca in the Eden estuary, since the "textural facies" defined by Eastwood (1977) on the basis of the grain-size distribution in the Eden, are consistent with the biotopes delineated in this study.

S U M M A R Y.

The estuary of the river Eden was chosen for study from a palaeoecological standpoint because (a) its dead fauna was unexplored and (b) its sedimentology was already thoroughly investigated (Eastwood 1977).

The first step of this study was to explore quantitatively the distribution of molluscs throughout the area. Emphasis was given to the dead material but the living molluscs were kept for reference and comparison. An effort to distinguish life and death assemblages in the dead material was made, using the standard discrimination criteria described by Fagerstrom (1964). From these (1) dispersion of (sub)fossils, (2) faunal composition and diversity, (3) population density, (4) surface condition of shells and (5) ratio of opposite valves were applied successfully to the Eden dead molluscan populations and indicate that the majority of species (34 out of a total of 44 species), represent with fidelity the life assemblages from which they were derived. Knowledge of the 10 remaining species is such as to suggest that a degree of transportation does take place in the Eden estuary but it is not enough to obscure either the faunal composition or the relative abundances of species in the samples.

Having established that the molluscan dead populations (subfossil assemblages) reflect quite accurately the life assemblages from which they were derived, the next step was to determine biofacies and biotopes. The idea was to re-evaluate some commonly used Numerical Taxonomy methods and test the applicability of such methods on both living and dead populations as criteria for life and death assemblages discrimination.

The results for biofacies analysis showed that:

- (1) Lack of objective criteria to decide a priori which of the classificatory techniques is best, demands that different combinations of alternative techniques be used. From the resulting classifications that which makes more sense ecologically or leads to a more meaningful environmental interpretation can be considered more valid.
- (2) Empirically tested "best" techniques do not guarantee the best results with all types of data. Thus the Jaccard coefficient with W.P.G.A. is not the best selection in all cases, when biofacies are desired. In this biofacies analysis the Jaccard coefficient and its monotonic Czekanowski coefficient produced the least meaningful results ecologically, for all sets of data used.
- (3) The choice of similarity coefficient is critical to the resulting classifications. All sets of data were insensitive to clustering techniques but very sensitive to the similarity coefficients used.
- (4) Binary data contain enough information for the recognition of biofacies provided that the appropriate coefficient is used.
- (5) Unless a sample adequately represents the population of organisms at a station, the biofacies designated are of doubtful validity. Thus the data from the living Mollusca, being insufficient, do not allow any conclusions to be drawn and thereafter do not permit any comparisons between living and dead biofacies.
- (6) The best behaved combination for the Eden dead Mollusca is the Matching coefficient (and its monotonic Squared Euclidean Distance coefficient) based on binary data, and the correlation coefficient based on raw numerical data and clustered by

For biotopes analysis it was concluded that

- (1) The biotopes depend as much on the clustering method as on the similarity/dissimilarity measure used. For numerical data, the type of standardization (by sites or by species), is also critical to the resulting dendrogram.
- (2) Binary data contain enough information to give a clear picture of the area, but caution must prevail in the selection of the techniques to be used.
- (3) The best behaved combination for the Eden dead Mollusca biotopes are the Matching coefficient (and its monotonic Squared Euclidean Distance) based on binary data and clustered by W.P.G.A. and the Squared Euclidean Distance based on standardized-by-species numerical data and clustered by Ward's method.
- (4) Despite the inadequacy of the living Mollusca data, biotope patterns produced by living and subfossil Mollusca are similar, suggesting negligible postmortem transportation and burial of the fauna in its place of occurrence.

The biotopes of this study are consistent with Eastwood's (1977) "textural facies" patterns (based on the sediment size distribution), suggesting that the main factor determining the distribution of Mollusca in the Eden estuary is the grain size of the substrate.

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PART I.

CHAPTER 1.

I N T R O D U C T I O N.

The Eden estuary, though little studied in the past, over the last decade seems to have exerted some magic influence over students and researchers with various interests. Starting in 1875 the reports on the estuary of the river Eden are summarized below.

McIntosh (1875) while recording the marine Invertebrates and Fishes of St. Andrews referred to 7 Mollusca, 2 Arthropoda, 1 Coelenterata and 17 Protozoa species, found in the Eden estuary.

Wilson (1910) described the area and identified the fauna and flora found.

Brown (1938) gave detailed lists of the fauna of representative substrate areas throughout the estuary.

Perkins (1960) listed the littoral diatoms of the Eden and described their diurnal rhythm.

Chisholm (1971) described the stratigraphy of the Western margin of the Eden estuary.

Laverack and Blackler (1974) updated the floral and faunal lists for the Eden estuary and St. Andrews Bay.

Eastwood (1977) described the sedimentology, current patterns, temperature and salinity within the estuary.

Bell, Johnston and Cobb (1978) carried out an extensive survey of the Eden invertebrates and birds while Bell (1979) repeated the survey in determining the factors which influence the distribution of the Invertebrata fauna in the Eden estuary.

almost disappearing in the winter. Near L.W.M. (Low Water Mark) extensive mussel banks are covered with a dense growth of Fucus sp. Distribution of mussel banks can be seen in Figure 1.3. At the margins of the estuary, salt marshes are sparingly distributed, mainly in the Edenside Flat, a few in the Kincaple Flat. Cardium edule shell pavements and Arenicola marina casts complete the picture of the Eden estuary.

MORPHOLOGY

Several definitions have been given on the question what is an estuary? Prichard (1960) defines an estuary as "a semienclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage".

In examining the Eden estuary complex and trying to place it according to Prichard's (1967) two monothetic systems, it appears that a) Regarding the geomorphology, the Eden estuary corresponds more to "a drowned river valley" otherwise called "coastal plain estuary"; one in which "proceeding from the mouth towards the head, the salinity (defined either in terms of chlorinity or conductivity) usually decreases steadily" Prichard (in Lauff, 1967). b) Regarding the dominant physical processes the Eden estuary is a "tide dominated estuary" one in which "turbulence associated with the tidal currents results in mixing between the salt and fresh water, which in turn produces the density gradients associated with the non-tidal patterns" Prichard (in Lauff, 1967).

For average flow conditions, the mixing index (ratio of the volume of fresh water to the total volume of water entering the estuary during the period of flood tide) is 0.009

(Eastwood, 1977). This places the estuary in Prichard's (1955) Type C or "vertically homogeneous category". Under maximum flood conditions the estuary becomes a Type B or "partially mixed" body of water with a mixing index of 0.12. (Eastwood, 1977).

The Eden estuary is very wide and shallow and at low tide the whole area is exposed except for a narrow channel. The exposed area is covered by a variety of sediments ranging from coarse sand with a low silt content, to glutinous mud with a very high silt content. Numerous small drainage channels form dendritic patterns across the expanse of uncovered mud, mainly in the Kincaule Flat, (Fig. 1.2.).

Flood and ebb channels together with landforms such as the Coble Shore, the Out Head and Sanctuary Spit, are an important influence in the transport and deposition of sediments as indicated by the current flow patterns shown in Eastwood.

Eastwood (1977) studied the changes in coastal morphology between 1855 and 1975 and gave his conclusions as follows:

"Changes are considered on the basis of the movement of the line of HWMOST (High Water Mark Ordinary Spring Tides) as indicated on the various editions of the 1:10560 Ordnance Survey Maps (Fig. 1.4.). The distribution of sediment by coastal processes during the past 120 years has produced dramatic changes in the areal distribution of land and sea at the entrance to the Eden estuary.

The position of the Eden channel in the lower estuary has not remained stable. The Eden channel is now moving northwards and an average movement of 9 m a year has been calculated for the past 27 years".

SUBSTRATE

Chisholm (1971) describing the post-glacial transgression in N.E. Fife gives the succession of post-glacial sediments at an Eden estuary site, bordering the estuary on its Northern side, West of Coble House Point, and states:

"the sequence at the Eden estuary site is divided into two parts by an erosion surface. Below the erosion surface an upward sequence from the Sub-Carse Peat into clay with reedswamp vegetation represents the earliest phase of the transgression, (Flandrian marine transgression) during which a protected stretch of water or marsh developed at the expense of a wooded land surface. Above the erosion surface lies a bed of sand and this is overlain by the mottled silts which form the local "low raised beach" platform. The sand bed is continuous with the layer of sand which covers the whole area of Tentsmuir and which is a shoreline deposit. In the Atlantic period equivalent of the Eden estuary, however, as in the present estuary the beach sand will have merged laterally into channel sand. The bed of sand at the Eden estuary site is therefore interpreted simply as a "high energy" intertidal deposit which may have been formed on a beach, in a channel, or in an intermediate environment. Although its contact with the overlying silt is not exposed, the upper part of the sand contains silty lenses and patches, suggesting that the contact is gradational, and that the area became converted gradually into an intertidal mud flat, either by the growth of sand banks to seaward or by the lateral shifting of the Eden channel".

Eastwood (1977) carried out an extensive analysis of the sediments and with the application of cluster analysis (Wishart, 1970) to the raw weight percentage data obtained by

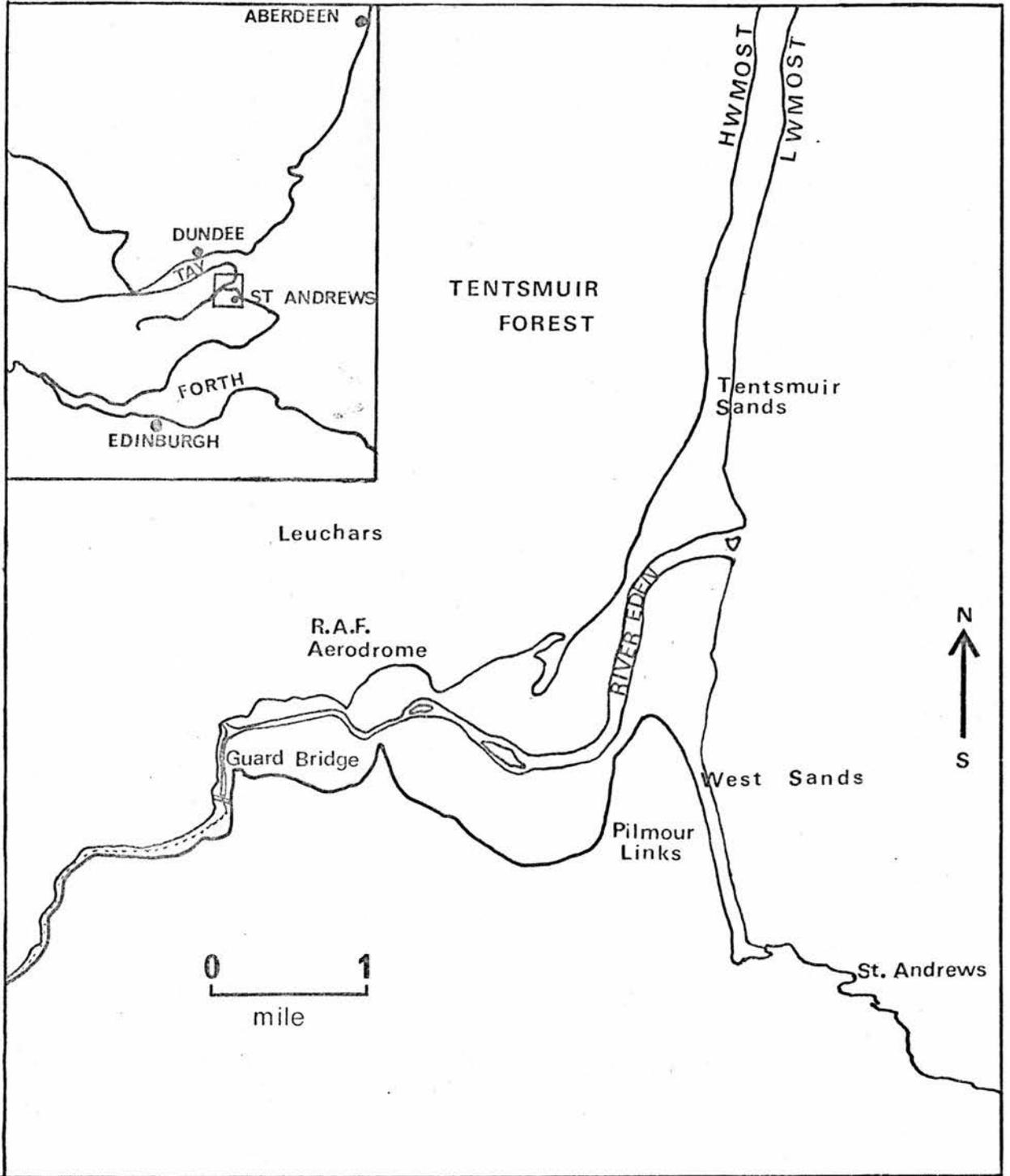
sieve and pipette analysis, he defined "Textural Facies" (groups of sediments with distinct textural attributes). In the intertidal flat sediments he distinguished four such Textural Facies (Fig. 1.5). The sediments of Textural Facies I are typically fine sands with varying proportions of medium sand. They are transported and deposited in a high energy environment dominated by tidal currents. Wave action is subordinate but important in certain areas. In Textural Facies II the sediments are typically very well sorted fine sands containing very minor amounts of medium sand but significant amounts of very fine sand. They are also transported and deposited in a high energy environment dominated by wave action. Textural Facies III sediments occur in the low-energy marginal areas of the middle estuary and are fine sands with an admixture of very fine sand, silt and clay. Deposition of very fine sand and silt and clay from waning flood-tidal currents is believed to be of importance, as is the trapping of suspended sediment by mats of filamentous algae. An abundant mobile in-fauna has the effect of producing a texturally homogeneous sediment. The sediments of Textural Facies IV are the finest in the estuary and occur in areas adjacent to the Eden channel. Deposition is strongly influenced by factors other than hydrodynamic ones and the role of the mussel Mytilus edulis, in extracting particulate matter from suspension and depositing it in the form of pseudo-faecal pellets is considered of major importance.

TABLE 1.1.

Average rainfall in the Eden catchment (1916-1950) and the monthly averages of rainfall run-off and mean river flow for 1974. (after Eastwood, 1977).

	1916-1950		1974	
	Aver. rain mm	Arcal rain mm	Run-off mm	Mean flow cumecs
January	85	89	38	4.37
February	57	50	35	4.45
March	54	88	39	4.47
April	49	19	17	1.99
May	66	50	15	1.70
June	55	45	11	1.34
July	82	52	8	0.91
August	82	47	7	0.81
September	73	85	9	1.08
October	86	40	9	1.03
November	80	106	38	4.47
December	70	88	48	5.54

Average rainfall figures supplied by the Meteorological Office and the remainder by the Tay River Purification Board.



Map 1.1 Location of the study area.

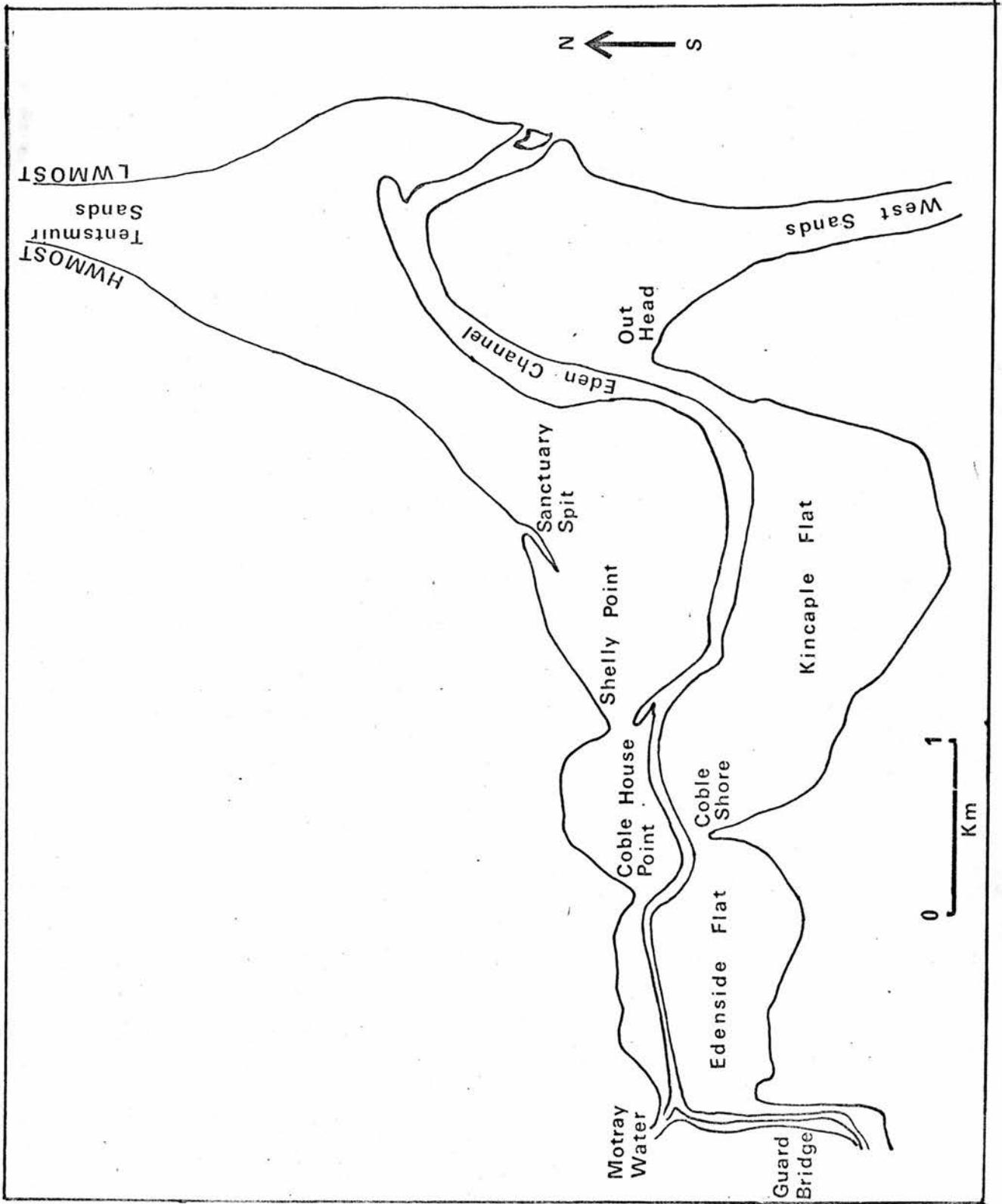


Fig.1.1 The geographical features of the Eden estuary.



Fig. 1.2. Aerial photograph (infra-red) showing the drainage pattern in the Kincaid Flat.

Fig. 1.3. Aerial photograph (infra-red) showing the locations of mussel banks as white patches bordering the channel and some of its tributaries in the Eden estuary.



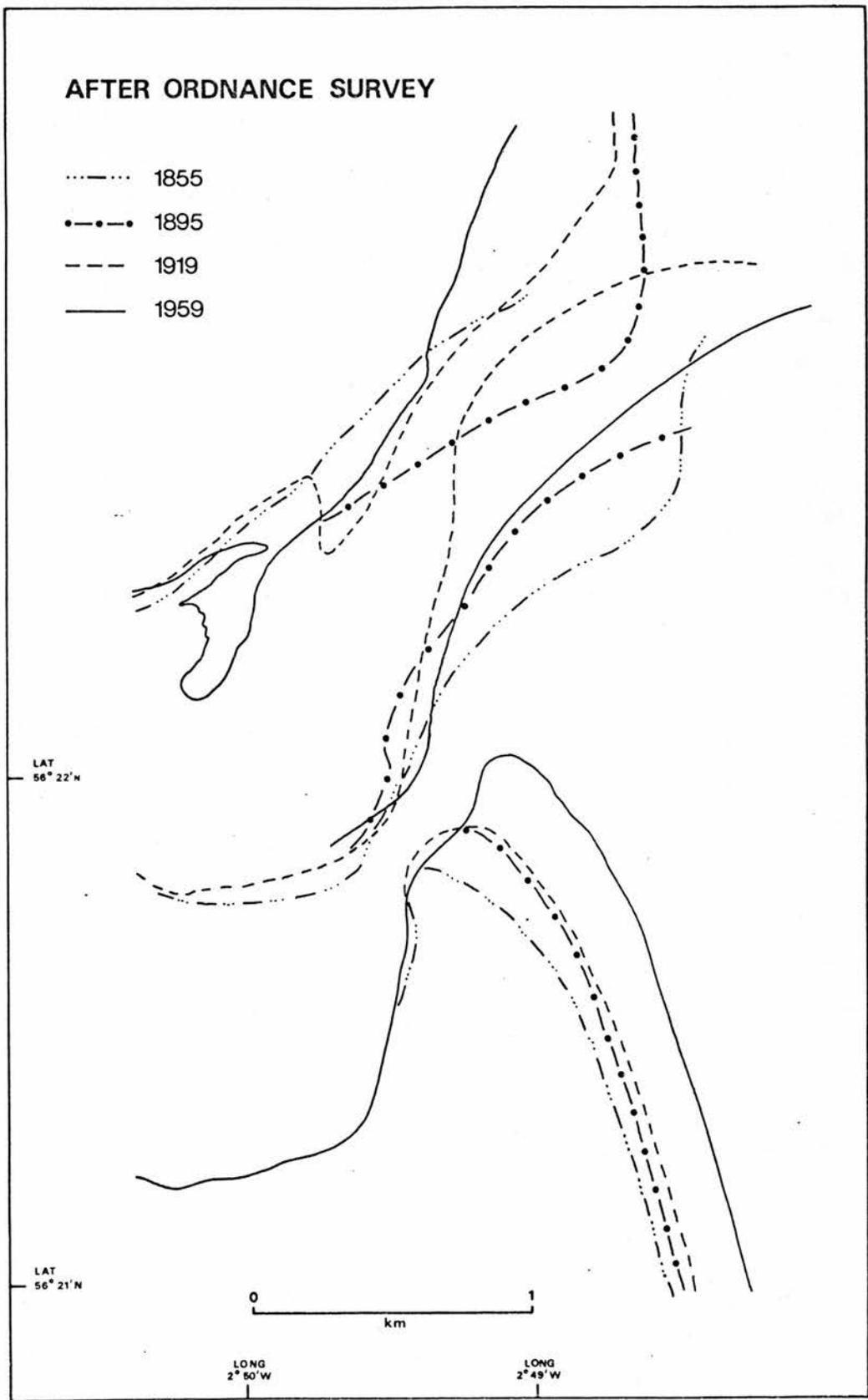


Fig.1.4 Change in H.W.M.O.S.T. and main channel between 1855 and 1959 (after Eastwood, 1977)

TEXTURAL FACIES

- I = Fine sand with some medium sand
- II = Well sorted fine sand.
- III = Fine with some very fine sand silt and clay
- IV = Very fine sand silt and clay.

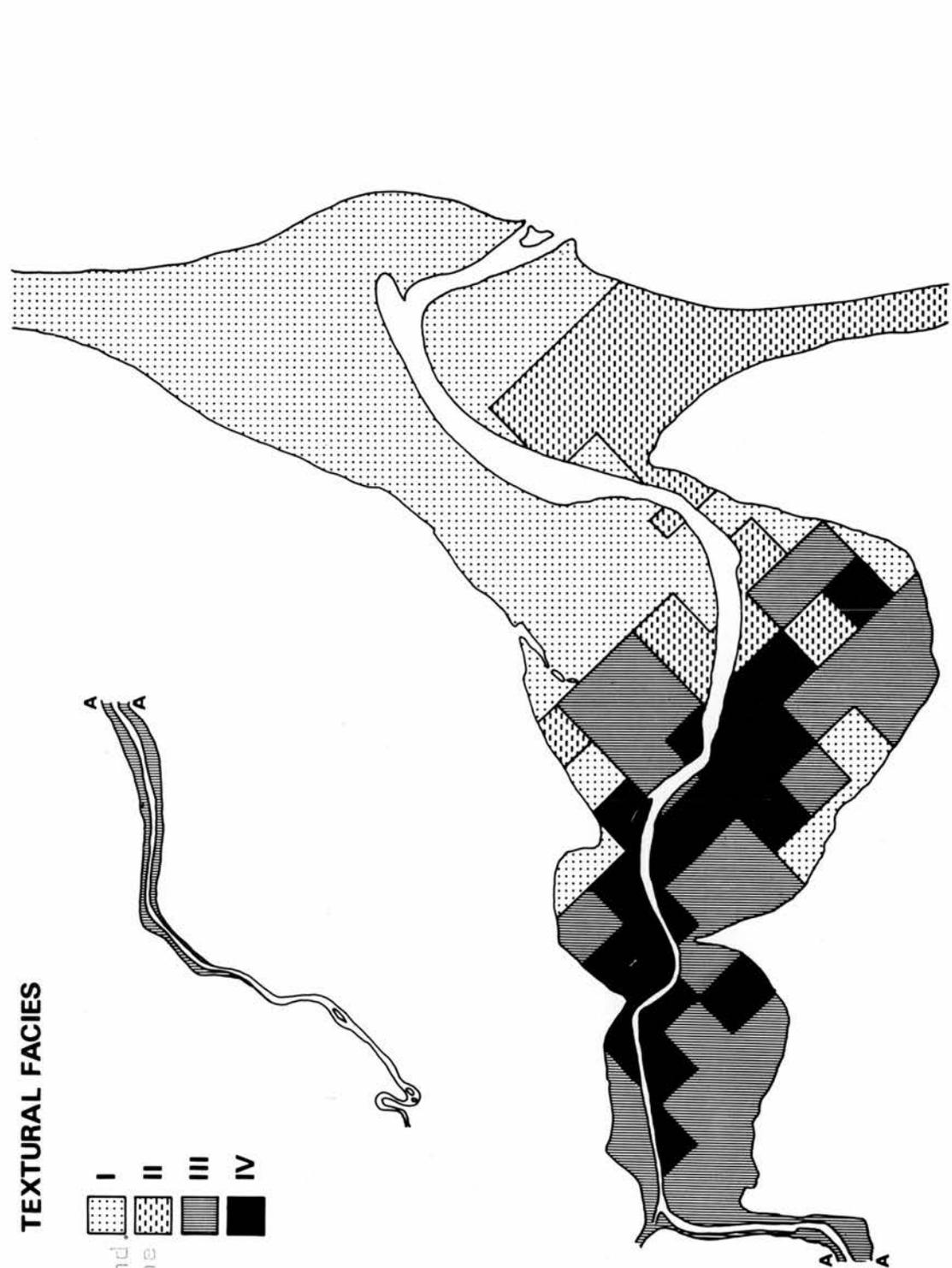
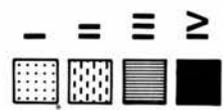


Fig. 1.5. Areal distribution of the four intertidal flat "textural facies" as described in page 6 (after Eastwood, 1977).

CHAPTER 2.
DATA COLLECTION.

SAMPLING METHODS

Forty eight sites were sampled in the intertidal flats of the Eden estuary. Their locations follow a sampling plan coarser than Eastwood's based on the Ordnance Survey National Grid. The sampling sites were located at 400 m intervals in N-S transects with an E-W spacing of 400 m (unlike Eastwood's 200 m) (Fig. 2.1.). No samples were taken from the channel bed. Site C 4 was located in an inaccessible area due to yielding mud and was therefore sampled 200 m North of C 3. Sites G 4 and J 4 were both situated in the channel and so G 4 was omitted while J 4 was sampled 100 m Eastwards of the grid point.

Because of spatial heterogeneity it is too much to believe that areas represented by single samples can be considered adequately sampled, and therefore two samples were collected from each site, 1 m apart. This approach is in agreement with Buzas' (1969) statement that "sampling theory indicates that an efficient estimate of density or proportions, including the dichotomous presence-absence, requires more than one biologic sample in any sampling area".

A tin box, open on one side, 17.5 cm x 11 cm, was inserted 20 cm deep into the sediment and dug out with a spade. The depth of 20 cm was considered sufficient since most of the molluscan species live in the upper 20 cm of sediment. However adults of large species such as Mya arenaria live deeper than 20 cm and so the samples are biased with respect to the larger individuals of these species. The material was then emptied into a bucket to be carried to the laboratory. In this way no internal structures were preserved and all

information on the depth of the existing living and dead fauna was lost.

Sampling took place between June 9th, 1978 and August 22nd, 1978 at low tide. The sites were marked with metal rods 1 m high (50 cm in the sediment), so that they can be recognized in a future survey.

Repeated sampling throughout the year would most likely reveal more living species as well as the seasonal variations of the existing living populations. Such variations were demonstrated by Brown (1938). However it is doubtful that repeated sampling would alter the relative abundance of the dead faunal species in a given site. Although this study is concerned, among others, with the relationship between the living and subfossil populations (dead material), and this would change with more information about the living populations, a second sampling was not feasible because of the limited time of this study and thus the inadequacy of living populations to represent the area of sampling is considered whenever ecological interpretations are attempted.

PREPARATION OF THE LABORATORY.

In the laboratory the material was passed, wet, through a set of 3 sieves 2 mm, 1 mm, 0.5 mm where the analogous parts (>2 mm, 1-2 mm, 0.5-1 mm) were retained after sieving. The <0.5 mm part was discarded. Sieving time varied according to the type of sediments, from half an hour, for samples of medium fine sand, so two hours for samples of very fine sand with silt and clay fractions. The >2 mm part often contained small stones which are widely distributed through the estuary.

At this stage annelids and molluscs visible to the naked eye were removed from the samples. The annelids were kept in special bottles with 40% solution of formalin and sent to the Gatty Marine Laboratory for future identification. The molluscs were identified and kept in 40% formalin solution as reference material. Other living organisms such as Corophium volutator, Carcinus maenas etc. were not separated.

The remaining parts - consisting of dead molluscs, living and dead arthropods, Echinocardium fragments, pseudo-faecal pellets, and often small stones or even coarse sand (0.5-1 mm part) - were dried for 24 hours in the oven at 90°C and afterwards weighed and stored in plastic bags. So each sample was split into three plastic bags containing the >2 mm part, the 1-2 mm part, and the 0.5-1 mm part.

SORTING OUT THE SAMPLES.

On account of the difficulty of identifying the very small fragments involved no attempt was made to sort the 0.5-1.0 mm fraction of the samples. In determining whether it was essential to separate the 1-2 mm part, both 1-2 m and >2 mm parts were sorted out and identified for 2 random samples. The results showed clearly that the proportions of molluscan species (expressed either as terms of biomass = dry weight per m², or number of shells per m²) remained stable in the two parts of each sample. Assuming that the same holds true for all samples, as Dr. A.C. Gordon suggested (personal communication), it is sufficient to separate the >2mm part and be confident that the results are representative of the whole sample.

Nevertheless the results are biased with regard a) to the ≤ 2 mm living molluscs (latest spatfall) which failed to appear in the examined fraction b) to the molluscan species whose micro-architecture, organic matrix and surface area per unit weight are, as demonstrated by Driscoll (1967), of considerable importance in shell durability when valves are subjected to abrasion by surf.

Both whole and broken shells, as far as they could be identified using a x 20 lens, were sorted and identified. Shell structure, ornamentation, size, dentition, adductor scars etc. aided in the identification of the small fragments. Still it was not possible to identify them all and so categories like "unidentified bivalves" and "unidentified gastropods" appear in every sample. Besides gastropods and bivalves, fragments of Echinocardium cordatum and plates of Balanus crenatus were distinguished. The rest were put under the heading of "remaining part". A typical sheet of data (Table 2.1) includes dry weight for each species, genus or composite group plus number of valves for bivalves and number of specimens for gastropods, in the two samples of each site. To prevent multiple counting a shell fragment was counted only if it included the umbo in the case of a bivalve or the base of the columella in the case of a gastropod. In order to reach a number of specimens for the bivalves the tallied number of valves was divided by two and rounded upwards. This is an arbitrary conversion used in the past by workers such as Johnson (1965), Warne (1969), Turner and Perkins (1972) and Peterson (1976).

Identification was feasible to species level for most shells but not all. For Anomia, Pecten, Dosinia, Venerupis,

Thracia and Patella that were scarce and broken, identification was possible only to generic level. Another problem that arose was the distinction of Spisula and Mactra. Whole big shells are easily separated but not tiny broken shells. Both genera were therefore put under the heading "Spisula-Mactra". The same holds true for Solen and Ensis where not a single whole valve was found. Thus "Solen-Ensis" includes all broken shells that belong to either genus.

Site E 5

1st Sample

2nd Sample

	dry wt. in g.	No. of valves	No. of spec.	dry wt. in g.	No. of valves	No. of spec.
<i>Macoma balthica</i>	2.07	14	7	3.88	30	15
<i>Scrobicularia plana</i>	0.47	5	3	0.46	5	3
<i>Cardium edule</i>	53.80	46	23	19.24	30	15
<i>Mya arenaria</i>	2.25	5	3	0.63	2	1
<i>Mytilus edulis</i>	152.00	48	24	183.24	80	40
<u>Unidentified bivalves</u>	0.28			0.22		
<i>Hydrobia ulvae</i>	0.10	-	12	0.74	-	95
<i>Potamopyrgus jenkinsi</i>	-	-	-	0.10	-	12
<i>Littorina saxatilis</i>	0.55	-	7	0.91	-	24
<i>Littorina littorea</i>	1.60	-	1	3.34	-	2
<i>Littorina littoralis</i>	0.51	-	4	2.50	-	14
<u>Unidentified gastropods</u>	1.43		-	2.00		
Balanoidea	0.03			-		
Remaining part >2mm	1.51			0.57		
1-2 mm part	15.60			15.52		
0.5-1 mm part	7.42			9.03		

TABLE 2.1. Typical sheet of data.

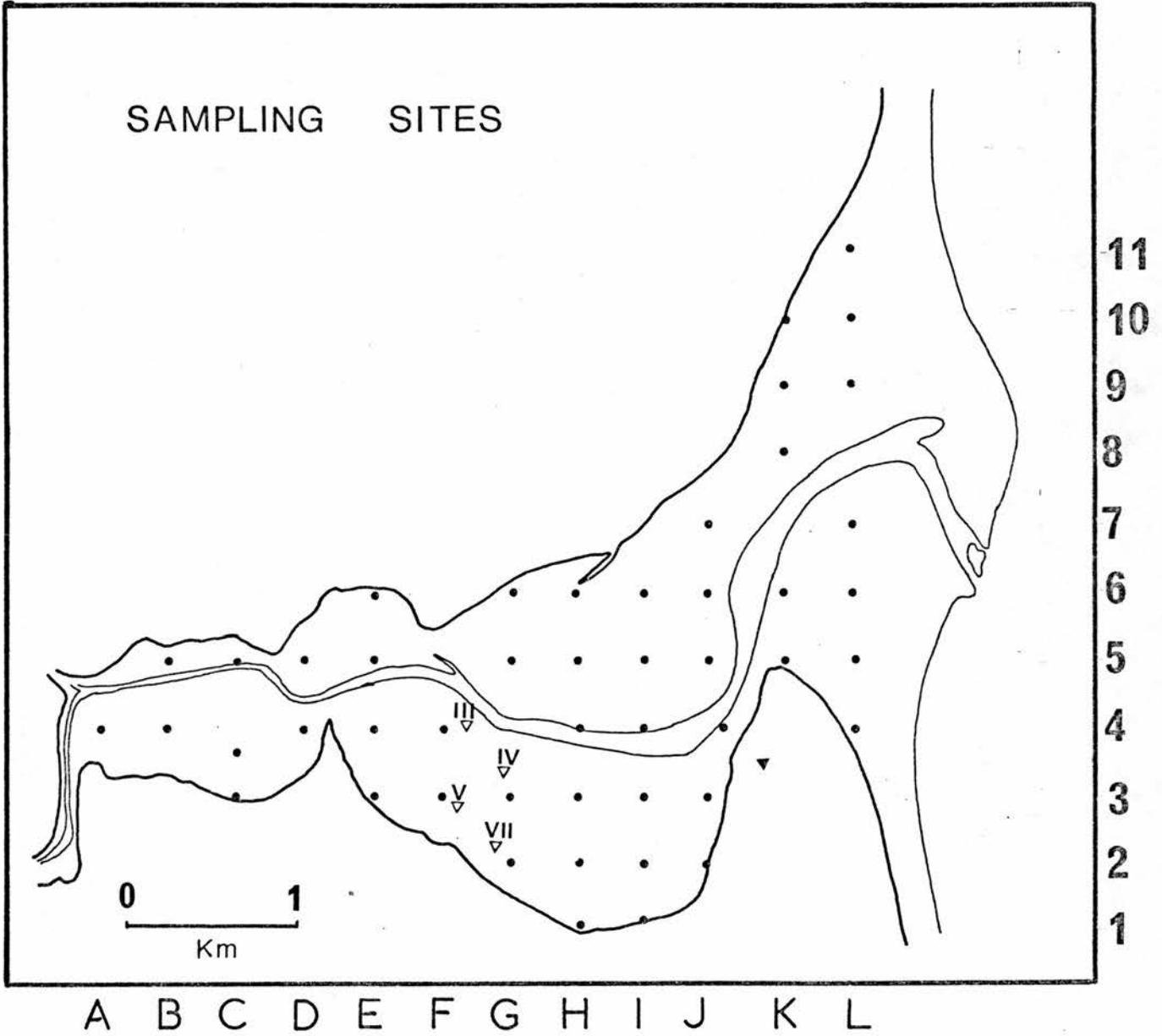


Fig. 2.1 Location of the sampling sites (dots) Triangles III, IV, V and VII are Brown's (1938) stations.

CHAPTER 3.

MACROFAUNA CONSTITUENTS AND THEIR DISTRIBUTION.

GENERALITIES.

Comparing the Eden estuarine fauna with that of St. Andrews Bay it can be seen that the estuarine fauna is poor in number of species, though some of its species are excluded from the St. Andrews Bay fauna. This is partly due to the inability of many marine species to withstand dilute media and of many fresh water species to inhabit more saline media. Between the two extremes, a brackish-water fauna comprising a few characteristic species exist, and may achieve high densities.

The living molluscs from the Eden estuary are compared with those of the Tay and Forth estuaries to assess the richness of the fauna. The living and dead molluscs from the Eden estuary are compared with the fauna recorded for St. Andrews Bay. Paradoxically 5 marine species, e.g. Ostrea edulis, Crassostrea sp., Hiatella arctica, Barnea candida and Tritonalia aciculata identified in Eden are not mentioned at all in St. Andrews fauna.

The emphasis of this study is given to molluscs but field observations of other estuarine organisms in high densities make it necessary to refer to them whether they are estuarine annelids e.g. Arenicola marina, Nereis diversicolor or amphipods e.g. Corophium volutator or crabs e.g. Carcinus maenas or fishes e.g. Gasterosteus aculeatus or even barnacles e.g. Balanus crenatus. Some space is also devoted to the macroflora.

Finally the distribution of the living and dead Mollusca is given separately for each species and an attempt at interpretation is made having in mind environmental factors which

control the distribution of animal species in estuaries:

- a) salinity b) substrate c) degree of shelter (or exposure)
- d) temperature e) food sources f) current velocity g) oxygen concentration h) predators i) pollution.

LIVING MOLLUSCA RECORDED IN EDEN.

Several surveys since 1875 have recorded 21 species of Molluscs (10 bivalves, 11 gastropods) living in the Eden estuary.

Among the bivalves, Cardium edule and Mytilus edulis are found by all investigators. Macoma balthica and the gastropod Hydrobia ulvae though not mentioned by Wilson (1910) are recorded as abundant by other workers as true estuarine animals. Mya arenaria and Scrobicularia plana noted as abundant in some samples during this study were not recorded by Bell (1978).

Littorina is abundant in the estuary on stones and seaweeds with different species occupying different zones. The species recorded in the Eden are Littorina littorea, L. littoralis (Brown's L. obtusata) and L. saxatilis (Brown's L. rudis.) Retusa obtusa and R. alba (Brown's Cylichna obtusa) have also been noted in the Eden.

Of all the surveys summarized in Table 3.1 the most detailed seems to be Brown's (1938) carried out in a few representative sites throughout a year. The rest are either occasional or cover an extensive area but sampled once, thus recording a limited number of species.

LIVING MOLLUSCA OF THE EDEN-TAY-FORTH ESTUARIES.

From comparisons of the Mollusca reported as living in the three neighbouring estuaries (Table 3.2), it appears that either the Tay and Eden are inhabited by richer faunas in number of species or that the Firth of Forth fauna has not yet been thoroughly investigated. It is difficult to believe that the bigger Firth of Forth estuary is inhabited by only 8 species of molluscs, but the Eden by 21 species.

The sources of information about the Eden fauna are mentioned previously. The Tay estuary fauna is recorded by Alexander et al. (1935) and by Khayrallah and Jones (1975). McLusky and Bryant (1979) in their survey of the invertebrate fauna of the Forth estuary, from 100 stations, mention only Macoma, Cardium, Mya, Mytilus, Hydrobia and Retusa. Read (1977) recorded as well Tellina tenuis and Tellina fabula.

Scrobicularia plana, a clearly estuarine animal, is noted by McIntosh (1875) as being common in the mouth of the Tay estuary in muddy sand, but not mentioned in the Firth of Forth faunal lists. Mya truncata, Lutraria lutraria, Donax vittatus and Solen sp. are absent from the Tay estuary fauna lists. On the other hand Venus striatula, Hiatella galliana, Hiatella arctica, Spisula solida, Modiolus modiolus and Modiolus barbatus, present in the Tay, do not appear in the Eden estuary records.

Among the gastropods Retusa obtusa, Retusa alba, Aporrhais pes-pelecani, Chiton marginatus and Limopontia capitata, are not recorded in Tay and vice versa Patella vulgata, Acmaea testudinalis, Potamopyrgus jenkinsi, Gibbula cneraria and Orchidoris fusca are not recorded as living in the Eden.

No conclusions can be drawn regarding the Forth estuary molluscs. The number of species recorded is small and this is thought to be a feature of insufficient sampling. The Eden and Tay estuaries seem to be inhabited by similar faunas (Table 3.2). The differences in the Mollusca lists may be attributed to different sampling methods, by different workers, at different sites, possibly at different seasons of the year.

DEAD MOLLUSCA FOUND (Table 3.3).

Thirty bivalve species and fourteen gastropod ones were found in states varying from whole articulated valves buried in the living position e.g. Mya arenaria to completely fragmented valves where identification was hard and estimation of number of valves not possible because the umbo was not preserved e.g. Barnea candida.

Comparison of the list of dead mollusca with that of living mollusca recorded in Eden-Tay-Forth estuaries, shows that fourteen out of thirty bivalve species and eleven out of fourteen gastropod species are known to live in the three estuaries. Reference to the St. Andrews Bay fauna, reveals that only 6 out of the 30 bivalve species and 1 out of the 14 gastropod ones have hitherto been identified in the Eden, while many of the others are recorded as abundant between tide marks e.g. Littorina sp., Patella, etc. or common in sandy grounds e.g. Thracia, Solen-Ensis, Tellina tenuis etc.

Hiatella arctica and Potamopyrgus jenkinsi have not previously been found in the Eden or even around St. Andrews Bay by earlier workers but have been noted in the Tay by

Alexander et al. (1935), Ostrea edulis and Crassostrea angulata have also not been recorded in the Eden or around St. Andrews Bay, although they both penetrate estuaries and are certainly distributed in the North Sea (Campbell, 1976). For Crassostrea though it is not strange that it has not been found, since until the middle of the nineteenth century it was confined to the Mediterranean (Perkins, 1974) and most of the surveys around St. Andrews took place before Crassostrea invaded the North Sea.

Barnea candida and Tritonalia aciculata are the only Mollusca left which are not recorded alive in St. Andrews Bay or the surrounding estuaries and for which not much information is available.

OTHER ORGANISMS

A. Flora.

Algal mats are extensive over mudflats but can only be identified to the generic level macroscopically and are assigned to the genus Enteromorpha. It is believed that Enteromorpha sp. is what Eastwood (1977) refers to as Chaetomorpha, since it covers the area where he places the latter. Dr. Blackler (personal communication) assigned the Enteromorpha specimens taken to her laboratory as Enteromorpha intestinalis and said that the expert in Enteromorpha Dr. Dunn strongly believes that the five Enteromorpha species which have been recorded in the Eden estuary so far, are all varieties of Enteromorpha intestinalis.

Other macroflora species recognized are: The Chlorophyceae Ulva lactuca and Monostroma grevillei and the Pheophyceae Ascophyllum nodosum, Fucus spiralis, Fucus vesicu-

losus and Pelvetia canaliculata. They are all found loose on mud or connected with Mytilus edulis bands in patches from Guardbridge to Out Head usually in areas sheltered from wave action.

Towards the mouth of the Eden on bare sand Laminaria can be seen occasionally. Salicornia and Zostera marina are abundant in salt marshes.

B. Fauna.

GASTEROSTEUS ACULEATUS Linnaeus.

In June '78 2 individuals were found alive lying in the Kincaple Flat at low tide.

The most remarkable feature of Gasterosteus aculeatus is that the number of bony plates on the sides of the body varies with both salinity and latitude. Bertin (1925) believes that the plate number decreases regularly and continuously from North to South and from waters with high salinities to those with low ones. Heuts' (1947) experiments show that in high salinities at low temperature, the fishes with high plate numbers are favoured while those with lower plate numbers are selected against. Plate numbers may therefore be taken as an index of the selective value of the correlated physiological characters. Populations from brackish waters in Belgium have an average of 20-30 plates on each side of the body while fresh water populations from the same latitude have an average of 3 or 4 plates.

Heuts designated the fish with low mean plate number and small body as Type A and those with high plate numbers as Type B. Adult Gasterosteus of Type B migrate from sea water to fresh water in March and breed in fresh water in May. In

June the adults return to sea and the young animals follow in July-August.

The two individuals found in the Kincapple mudflat have 20 plates, being therefore adults of Type B favoured at high salinities and low temperatures. They seem most likely to have been on their way back to the sea.

Type B can tolerate salinities up to 10‰. Below 10‰ it loses the ability to osmoregulate and dies within a few days.

ECHINOCARDIUM CORDATUM (Pennant).

Echinoderms are strictly marine animals and osmotically conform to the environment. Their penetration into estuaries is therefore limited by tissue tolerance. Echinocardium cordatum may penetrate as far as 2‰. (McLusky, 1971). McIntosh (1875) refers to it as "very common off the West Sands". McIntyre (1958) records it as "occasional off shore". Distribution of the always fragmented shell over the estuary is shown in Fig. 3.1.

CARCINUS MAENAS (Linnaeus)

"Abundant everywhere between tide marks" (McIntosh, 1875). The only crab which penetrates well into estuaries in Britain. Carcinus maenas inhabits a wide range of habitats from open rocky shores to sheltered mudflats and salt marsh pools. It is most numerous where shelter is available and large numbers of small specimens may be found under stones in the middle reaches of the Eden estuary. C. maenas appears to be a generalised predator eating anything that it finds or catches. This wide range of feeding habits is coupled with an ability to osmo-

regulate at salinities lower than the blood concentration, so that the crab is well adapted to live in estuaries. The lowest salinity it can survive is 6‰.

BALANUS CRENATUS. Bruguiere

Recorded on mussel beds in the Eden estuary by Brown (1938). A typical sessile barnacle whose valves may be closed when the tide is out or when the salinity falls to a very low level. In British waters Balanus crenatus which has been acclimated to a low salinity, is able to tolerate lower salinities than individuals of the same species which have been taken from or acclimated to high salinities (Perkins, 1974). B. crenatus from around L.W.M. or the infra littoral, can tolerate salinities of 14-17‰ if they have been acclimated first. Distribution of B. crenatus broken plates in the Eden estuary is shown in Fig. 3.2.

COROPHIUM VOLUTATOR (Pallas).

"Abundant in brackish pools at mouth of the Eden" (McIntosh, 1875). "Abundant in soft mud in the Eden estuary" (Irvine, 1954).

Corophium species like other estuarine species are confined to specific substrates. C. volutator selects fine sand or mud and is not found in polluted conditions, clean sand or in black sulphurous mud. Within mud the animals form shallow U-shaped burrows. Provided there is a suitable substrate Corophium can be found where interstitial salinity is over 2‰. Given a choice they will choose salinities in the range 10-30‰ avoiding low salinities where they would be exposed to osmo-

regulatory work.

C. volutator's activity is controlled by an interaction of two activity rhythms, one tidal and one diurnal.

Laboratory experiments show that C. volutator is positively phototactic when in water (i.e. it swims towards the light), but negatively phototactic (i.e. it crawls away from light) when in air. This response must assist animals by encouraging them to burrow away from light when the tidal mud flats are exposed at low water and permitting them to swim when covered by water (McLusky, 1971).

EURYDICE PULCHRA Leach.

"Abundant at surface off East Rocks in autumn" (McIntosh, 1875). A marine species which penetrates a long way into estuaries and may be seen swimming swiftly in the rising tide. It is sometimes found in salt marsh pools, but this is often a case of stranding. Normally it appears to prefer open moving water and it will burrow into sand. It was found abundant buried in sand in site J 2. According to Soika (in Green, 1968) this species spends most of its time buried in sand and emerges to lead a pelagic life at night.

NEREIS DIVERSICOLOUR. O.F. Müller.

"Occasionally between tide marks" (McIntosh, 1875).

It penetrates down to 1‰ in British estuaries but does not live in fresh water. Above 22‰ it may be replaced by N. virens. Oglesby (1965) has pointed out that salinity is the principal controller of its distribution. Spawning occurs at temperatures above 5°C. The larvae is non-pelagic

and therefore is not washed out of the estuary by currents, neither there is any interchange between populations in different estuaries. Brown's suggestion that the larvae of N. diversicolor are carried down the Eden from their brackish water haunts higher up the estuary, and so colonize the mud at a lower tide level fails. N. diversicolor feeds on a wide variety of algae and detritus and is also a general predator on other estuarine animals. The worms tend to live buried in mud, where they are exposed to the relatively stable interstitial salinity rather than the overflowing water.

ARENICOLA MARINA (Linnaeus)

"Abundant everywhere in sandy ground" (McIntosh, 1875).

"It is found most commonly in the sandy regions near H.W. its distribution clearly influenced by the grade of mud or sand" (Brown, 1938).

Arenicola occurs on marine coasts as well as in estuaries in substrates composed of a mixture of sand and mud. It burrows forming a U-shaped burrow and ingests the sand and mud which are its food supply. The density of A. marina has been demonstrated by Brown (1938) and Bell (1979) to be controlled by the sediment type. Arenicola marina tolerates salinities down to 8‰.

MOLLUSCAN DISTRIBUTIONS

A. GASTROPODA

HYDROBIA ULVAE (Pennant)

"Extensively abundant in brackish pools near mouth of Eden" (McIntosh, 1875). "On mud in Eden Estuary" (D.E.G. Irvine, 1954). In this study living Hydrobia were found in

very fine sand at low energy marginal areas of the middle estuary, with highest densities up to 8 398 animals per m^2 in site D4 towards the head of the estuary (Figs. 3.3a, c). From dead populations density of up to 18 694 shells bigger than 2 mm per m^2 , were found in site D5. Very low densities 26-208 shells per m^2 were found towards the mouth of the Eden. Generally high densities of dead shells were found at marginal areas in the upper and middle estuary, as in the living Hydrobia (Fig. 3.3b).

Densities up to 60 000 per m^2 have been found in Denmark. Their success is explained by the manner in which during every tidal cycle they exploit two food sources. (Newell, 1962). At flood tide they float on the underside of the surface film of the water feeding on plankton. At ebb tide the snails detach from the surface film withdraw into their shells and sink to the bottom. After crawling for a while and feeding on detritus and diatoms they burrow under the mud surface where they stay until the next tide comes. Then they emerge to float in the shallow water taking advantage of the plankton available.

Several species of the Hydrobiidae are found in estuaries and show differences in their ecological preferences. In Denmark it was found by Muus (1963) that the approximate salinity ranges of the species were:

<u>Potamopyrgus jenkinsi</u>	0-15‰
<u>Hydrobia ventrosa</u>	6-20‰
<u>Hydrobia neglecta</u>	10-24‰
<u>Hydrobia ulvae</u>	10-33‰

To identify the species of Hydrobiidae 4 characteristics

are necessary 1) shell form 2) radula 3) copulatory organ 4) pigmentation. In the dead material from the Eden the only characteristic available was the shell form which alone was not enough, therefore the specimens were assigned to two categories: Hydrobia ulvae and Potamopyrgus jenkinsi.

The upshore distribution of Hydrobia ulvae is governed by its tolerance of desiccation. Stopford (1951) found that this species began to die after 4 days in dryness although some individuals could survive for about two weeks. This indicates that the upper limit will be about the level of the H.W.M.O.S.T. which cover the upper shore once a fortnight, but in general the snails will find better conditions lower on the shore.

Reproduction occurs during summer when in default of other hard surfaces, small capsules each containing a few eggs are deposited on the surface of the shell. Although these hatch as veligers, larvae life is very short with quick settlement on to the mud surface.

POTAMOPYRGUS JENKINSI

It is not recorded in the estuary or in St. Andrews Bay by Laverack and Blackler (1974), neither was it found living in this survey, at least not in the >2mm part of the samples, although it was noted in the Tay estuary. Distribution of the dead shells is very similar to Hydrobia's (Fig. 3.4) in very fine sand - Eastwood's Textural Facies III - with highest densities up to 1716 shells per m² in the middle estuary. Mainly at marginal areas of the upper and middle estuary it seems to avoid black sulphurous mud.

From general bibliography it appears that P. Jenkinsi is only found in the upper reaches of estuaries and has recently

invaded fresh water, where it has been very successful. It is found typically in fresh water extending in estuaries up to 15‰. All Hydrobiidae avoid running water preferring still conditions. Adults of P. Jenkinsi are tolerant to all salinities from fresh water to full sea water in all of which they move and feed actively. The young are more sensitive. Fresh water populations are born only in salinities 0-12‰ whereas the brackish populations are born in salinities from 0-18‰. Few larvae from fresh water or brackish origins can withstand a salinity 18‰ although a previous acclimation improves the survival rate.

PERIWINKLES are more or less stationary except when the tide recedes from them or on the arrival of a flowing tide. Littorines are herbivorous - change to the more specialized carnivorous diet comes later - making effective use of the taeniaglossid radula for scraping encrusting vegetation or rasping the surface of the larger seaweeds. Where rock is scraped these contents include a proportion of fine fragments representing a perceptible rate of erosion of up to 1 cm in 16 years.

LITTORINA LITTORALIS (Linnaeus)

"Very common between tide marks" (McIntosh, 1875, Irvine, 1954). In this study one living L. littoralis only, was found in the Kincaple Flat (Fig. 3.5a). Dead shells were seldom found in the Edenside Flat but were abundant everywhere in the Kincaple Flat (Fig. 3.5b). Densities clearly lower than L. saxatilis but still as high as 10 192 shells per m² were recorded in site H2 on very fine sand. L. littoralis occupies a wide zone from about H.T. level to extreme L.W.M.O.S.T. and is

connected with brown fucoid weeds. Its typical habitat is seaweeds (especially Fucus vesiculosus and Ascophyllum nodosum).

LITTORINA LITTOREA (Linnaeus)

"Extremely abundant between tide marks" (McIntosh, 1875, Irvine 1954, Sandison in Laverack 1974). Not a single living specimen was found in this survey or in Bell's survey (1978). Dead shells were found in all sorts of substrates mainly in the middle estuary (Fig. 3.6) in densities up to 1 118 shells per m².

Littorina littorea can live in salinities down to 10‰ and is often found in abundance in salt marsh creeks. L. littorea and L. saxatilis feed on detritus, diatoms and other small algae which they scrape up from the surface over which they move (Green, 1968). L. littorea show some hyperosmotic regulation in 10-16‰. It is seldom exposed for more than one consecutive low tide.

LITTORINA SAXATALIS (Olivi)

"Abundant on rocks near H.W" (McIntosh, 1875).

"M.T - H.W.S.T." (E. Sandison in Laverack and Blackler, 1974, Irvine, 1954).

A few living animals were found in the middle estuary (Fig. 3.5a). Dead shells of L. saxatilis reach the astronomical densities of 49 218 per m² in the middle estuary in very fine sand. Distribution of dead shells (Fig. 3.7) shows heavy populations in the middle and upper estuary with few occurrences towards the mouth of the Eden.

Typically a rocky shore animal it only penetrates estuaries where there are strong current movements and salinities

above 14‰. A brackish water form which will penetrate to 8‰ has also been noted. (McLusky, 1971). L. saxatilis has four subspecies that can withstand a range of exposure and of vertical distribution. All however, extend higher up the estuary under sheltered conditions. The high densities of L. saxatilis found in the Eden can be explained by the great tolerance of the animal to severe environmental conditions. It can go without food for several weeks, live in dry air for several days, live permanently in salinities from 8‰ up to more than twice the concentration of sea water and withstand immersion in fresh water for almost a week. Desiccation and osmotic stress are resisted by quiescence. The body is withdrawn into the shell and the mouth of the shell closed with the operculum (Green, 1968).

RETUSA OBTUSA (Kanmacher)

Two other species of the same genus are recorded in Laverack and Blackler (1974): Retusa alba as Cylichna obtusa and Retusa retusa as Cylichna truncata. It is not recorded in Bell's survey, although it was found living at the same time in this survey, in site C4 upper estuary in very fine sand (Fig. 3.5a). Dead shells appear in densities up to 1664 per m² their distribution following roughly that of Hydrobia (Fig. 3.8). This is easily explained by Retusa's feeding habits. However incredible Retusa feeds on the most rapidly moving British prosobranch Hydrobia ulvae. This was concluded from a photograph by Dr. S.T. Smith which shows an intact Hydrobia inside the stomach of R. obtusa (Green, 1968). Perhaps Retusa lies under the surface of the mud and sucks a Hydrobia into its pharynx as that animal passes overhead.

Generally Retusa is found burrowing in mud or muddy sand. The typical form (usually found in sand) has a distinct tapering spire to the shell whereas a variety which occurs in finer deposits (found in mud) lacks such a spire.

NUCELLA LAPILLUS (Linnaeus).

"Very abundant between tide marks" (McIntosh, 1875).

Widespread in the estuary on all sorts of substrate from coarse sand to mud mainly in the middle estuary (Fig. 3.9) in maximum densities of 364 shells per m². No live animals were recorded.

N. lapillus lives on exposed shores with its prey of barnacles, mussels and to a lesser extent limpets. From our distribution maps it seems that the highest density of Nucella lapillus dead shells coincides with the highest biomass of Balanus crenatus in site H2 - one extra argument that the dead shells are buried in situ, where they preyed on barnacles.

TRITONALIA ACICULATA

It is not mentioned in St. Andrews Bay Fauna and it was not found living in any survey of the Eden estuary so far. Dead shells of very small size were found in the middle and lower estuary in sand, near L.W.M. (Fig. 3.10).

GIBBULA CINERARIA (Linnaeus).

"Abundant on stones and rocks between and above tide marks" (McIntosh 1875). "Abundant under stones and in pools at East Rocks especially L.W.S.T." (Sandison in Laverack and Blackler, 1974). "Rare in deeper and more shady parts of tide pool at H.T., Hind Rock" (Irvine, 1954). "Common in tide pools

at East Rocks, but rarely found above H.T. or out of water" (Arnold, in Laverack and Blackler, 1974).

Only dead shells, mostly broken, were found in high energy environments at the mouth of the Eden (Fig. 3.11) not in total disagreement with their expected habitat - under stones and on seaweeds on the lower shore and down to about 20 m. G. cineraria is usually associated with brown fucoid weeds on which with algal debris it feeds. It is common from the level of H.W.N.T. to below tidal levels thus never exposed for more than one tidal period.

NATICA ALDERI (Forbes)

"With N. catena but less common on sandy grounds off West Sands" (McIntosh, 1875). "Two specimens only" (McIntyre, 1958).

Broken shells of Natica were sparsely found at the middle and lower estuary buried in sand (Fig. 3.12).

Common in shallow water off-shore they inhabit relatively clean sand. Carnivores, they feed on other infaunal animals, chiefly bivalves. Naticid boring can be distinguished because they are always bevelled on the outer side.

BUCCINUM UNDATUM. Linnaeus

"Common in pools off East Rocks" (McIntosh, 1875).

"Large specimens frequent in creels" (D.C. Arnold in Laverack and Blackler, 1974). Only a few broken shells were found in the middle estuary on sand and mud (Fig. 3.13). Living Buccinums wander freely over rocky and mixed sand and rocky shores, highly successful because nothing of animal origin, moribund or dead comes amiss. Living shells are common enough

in low shore pools, in the Laminaria zone and further offshore. During a long period of tidal exposure the animals can die of desiccation since they fail to retreat and close the aperture. The low densities of dead Buccinum undatum are thus explained (unfavourable environmental conditions in the estuary). However, living Buccinum has been recorded in the estuary by Brown (1938).

ACMAEA TESSULATA (Müller)

"Common under stones near L.W." (McIntosh, 1875).

Only small dead shells were found in the middle and lower estuary at M.T. level (Fig. 3.14).

A. tessulata is known to be confined in the lowest areas of the shore and down to depths of a few meters. It can resist long periods of desiccation high on the rocks. It occurs only round North shores from North Wales round to the Humber.

PATELLA SP.

"Patella species are generally abundant" (McIntosh, 1875).

Dead shells were found in the middle and lower estuary at different tide levels, on all types of substrate. (Fig. 3.14).

PATINA PELLUCIDA. (Linnaeus).

"Abundant on Laminaria" (McIntosh, 1875, Sandison in Laverack and Blackler, 1974).

Distribution of dead shells of Patina pellucida is shown along with Patella's in Fig. 3.14. Rarely found anywhere but on the fronds or within cavities of the massive holdfasts of Laminaria and so it is rarely exposed except at L.W.O.S.T.

"Two subspecies is what appear as distinct species in form and habitat. They are varieties of P. pellucida their differences

being the consequence of exposure of the growing animals to different environments". (Yonge and Thompson, 1976).

No records of Laminaria localities are kept but the sites where Patina was found are not far from the channel bed or L.W.M. where Laminaria can easily grow.

B. BIVALVIA

MYTILUS EDULIS. Linnaeus.

Extensive mussel beds occur at the edge of the river bed or large channels opening from it, mainly in the middle estuary. The distribution of mussels in these beds is irregular with bare areas between substantial beds and thus the results with the grid sampling system are biased. Densities of up to 2860 animals per m^2 were recorded from living populations (Fig. 3.15a, c). Dead populations show a universal distribution over the estuary, with a few valves found in the upper estuary where no mussel beds occur, heavy populations in the middle estuary where mussel beds can be seen-in densities up to 9204 valves per m^2 -, and a few valves again in the sand where conditions are unfavourable for mussels settlement (Fig. 3.15b). Predation marks are evident in many broken shells.

Regarding the settlement of the mussel spatfall previous workers (Geesteranus 1942, Kuenen 1942) assumed that the spatfall is scattered over an extensive area. Geesteranus (1942) observed that the young mussels have a marked tendency to settle in such a way that they fit into a groove or hollow. At first they settle on all sorts of substrata. "The main condition is that the substrate is firm and further that it is rough or contains corners, holes, cracks or grooves in which the animals can attach

themselves as firmly as possible". When the substrate no longer satisfies their thigmotactical needs, the mussels detach themselves and are transported by the currents. They settle again only when their thigmotaxis is satisfied. Geesteranus (1942) set up some experiments to decide whether the formation of mussel banks is the result of favourable combination of external factors (substrate, temperature, salinity, strength of current, food supply) or the mussels seek each other actively as a result of something like a social instinct. His experiments showed that the mussels do not find the mussel bed by chemoperception, but that they reach it more or less accidentally.

Kuenen (1942) studying the distribution of mussel beds on the intertidal sand flats near Den Helder found it probable that currents in combination with the condition of the substrate, have a primary influence on the distribution of mussels. The animals are transported constantly over the sands. As they are alive, the transport does not seem to harm them and they can attach themselves again if they find a suitable substrate. When the currents are strong enough they transport the mussels or sweep them from their place and this is surely the reason why the animals do not occur on the sand. The dead valves found in the sandflats of the Eden mouth may thus belong to animals which died there during transport or were transported there after death.

Also according to Kuenen (1942) the distribution of mussels is little influenced by salinity, temperature, predators, desiccation and want of oxygen. Analytically:

(a) Low salinities can be hardly of any importance except in

causing a marked reduction in growth rate and maximum size.

Death occurs below 4‰.

(b) The mussels near H.W.M. are exposed to more extreme temperatures than those further down nearer L.W.M. Low temperature e.g. strong frosts may kill all mussels which are uncovered. High temperature also delimits the area where the mussels can be found.

(c) Predators cannot be of any importance since they have no reason to eat mussels in one place and leave them in another.

(d) Desiccation is not very harmful as the mussels close their shells firmly as soon as they emerge from the water.

(e) The experiments seem to prove that mussels even after long periods of exposure to the air, very soon resume with their normal consumption of Oxygen.

"Mytilus edulis distribution depends both on the amount of food per unit of water and upon the current velocity.

More material is suspended in stronger currents. Mussels on the higher part of the flats have insufficient food at their disposal and this is the reason why they do not occur there normally" Kuenen (1942).

CARDIUM EDULE Linnaeus.

There is confusion in the literature over the two species of Cardium, C. edule and C. glaucum which recently have been put together as Cerastoderma edule by N. Tebble (1966). Peterson (1958) has studied the distribution of this species in Danish waters and found that C. edule did not occur in salinities below 20‰ while C. lamarki was found over a range from 5‰ to 60‰ in brackish to hypersaline waters. However only Cardium edule was identified in the Eden estuary by all investigators.

Living Cardium were recorded from the upper, middle and lower estuary burrowing in mud or sand, especially around mussel beds, where distinct cockle beds can be seen (Fig. 3.16 a, c). Densities up to 7000 animals per m^2 were found in muddy sand near L.W.M. in the middle estuary. Dead populations were also found everywhere in densities varying from 104 to 40 144 valves per m^2 (Fig. 3.16b).

Distribution of the dead shells reflects roughly the distribution of the living animals which is controlled by salinity, substrate, food, temperature, degree of exposure and predators (Kreger, 1940).

The most frequent habitat of the cockle is in slightly muddy sand, as in the Kincapple Flat where indeed the highest densities for both living and dead populations are met. Cardium feeds with the help of a short siphon extended into the water, which takes small planktonic organisms in suspension and detritus. Duration of time of submersion and current velocity are the two factors governing the availability of food. In stagnant water and near H.W.M. there is a lack of food - hence minimum densities at H.W.M. High current velocity is favourable, for it brings a water supply. Maximum growth takes place where the duration of submersion is longest and where it is accompanied by not too weak a current (Kreger, 1940) evidenced by biggest shells near L.W.M. at the mouth of the Eden.

Influence of high and low temperatures is very important and may cause the death of cockles over wide stretches. High temperatures can be dangerous because of the great contrast between the temperature of flood water and that of the flats exposed to the sun at low tide (McLusky, 1971). "Low temperatures

decrease the digging speed and so increase the risk of being washed away. Further, heavy frost may cause great mortality by covering the mud flats with a layer of ice beneath which the oxygen becomes depleted" (Green, 1961).

Degree of exposure influences the settling of spat. According to Kreger (1940) in sheltered areas the spat can settle successfully, whereas in areas with fast currents the spat is in danger of being washed away - hence poor populations in the high energy environments of the Eden estuary sandflats.

Besides fishes (e.g. Pleuronectes plates, P. flessus), birds (e.g. Haematopus ostralegus, Larus argentatus) are said by Kreger (1940) to feed on young cockles too. Predation marks evidenced in a considerable percentage of empty shells suggest that subtidal predators such as Buccinum undatum restrict the cockle to the intertidal zone in the Eden estuary.

SCROBICULARIA PLANA (da Costa)

Distribution of living Scrobicularia and dead shells is remarkably similar (Fig. 3.17a, b). Scrobicularia is confined in the upper and middle estuary to mud and muddy sand from H.W.M. to L.W.M. level. The highest densities met are: 182 animals per m² for living populations, 10712 valves per m² for dead populations.

Scrobicularia's absence from the lower estuary is justified by the fact that it does not osmoregulate except when the salinity falls below 30‰ (Freeman and Rigler in Green 1968). Indeed Scrobicularia is said by Yonge (1949) to be a brackish water indicator. The major limiting factor seems to be the substrate, since it does not appear in sand in the mouth of the Eden. Indeed Scrobicularia avoids burrowing in mobile sand where

it is prevented from maintaining the long narrow burrows for the siphons. Instead it is well adapted to live buried in deep soft mud. The foot is large and capable of burying the animal in a short time. Buried at a depth down to 30 cm in black mud it avoids predators such as the Oystercatcher Haematopus ostralegus. Contact with the surface is maintained by means of long siphons which can be retracted to avoid predators or low salinities. The inhalant siphon sucks in water from above the surface of the mud together with deposits, thus exposing the animal to variation in salinity. It withstands low salinities for a long time either by withdrawing its siphons or by closing its valves until favourable conditions return. So it is recorded living at salinities as low as 2‰ for a short time.

Scrobicularia plana is known to compete for space with Macoma balthica. Data from a few sites are as follows:

Site	DEAD POPULATIONS number of valves/m ²		LIVING POPULATIONS number of animals/m ²	
	Scrobicularia	Macoma	Scrobicularia	Macoma
B 4	3 926	14 976	26	78
B 5	1 092	1 170	52	*416
D 4	2 912	2 652	*182	286
F 3	286	4 082	52	26
F 4	2 106	8 190	26	178
H 2	*10 712	*24 536	-	208
I 2	2 366	5 460	52	286

From the above table it can be seen clearly that while the highest densities for dead populations of the two species coincide (no evidence of competition for space), they do not coincide for the living populations, the relative abundances and scarcities of which are complementary.

MACOMA BALTHICA (Linnaeus)

Living Macoma is confined to the upper and middle estuary with maximum densities in the Kincaple Flat of 416 animals per m² (Fig. 3.18a,c). McIntosh (1875) reports Macoma as abundant on sandy beaches at the mouth of the Eden, and results from the dead population (Fig. 3. 18b) agree with both observations. Macoma valves are found everywhere with highest densities in Edenside and Kincaple flats up to 29 536 valves per m², in muddy sand at middle tide level.

Macoma's universal distribution over the Eden estuary can be explained by its life habits. Temperature is not likely to be a limiting factor, Macoma's great resistance to low temperature being indicated by its occurrence in the Gulfs of Finland and Bothnia where the sea freezes for several months a year. Being a deposit feeder Macoma burrows in mud and sand and moves about frequently in search of food. Its distribution depends on the amount of food available and the amount of time available for feeding, that is, on the tidal level. This is clear in the Eden, where Macoma's densities are least near H.W.M. where feeding time is minimum. Newell (1965) found that populations of M. balthica in the Thames estuary were denser where the grain size of deposit was finer. The higher populations in fine deposits were attributed to increased densities of microorganisms. This too, seems to be the case in the Eden estuary where high densities occur in very fine sand in the mudflats. The main food of Macoma is derived from the digestion of microorganisms in the deposits that are sucked up by the inhalent siphon and the abundance of this food is related to the grain size of the deposits.

TELLINA FABULA Gmelin

"Common on sandy grounds with T. tenuis" (McIntosh 1875). Living Tellina fabula was not found, but results from dead populations show a distribution very similar to that of T. tenuis, hardly overlapping with Macoma's (Fig. 3.19). Dead shells were found in sand from the lower reaches of the middle estuary flood tidal delta around Out Head, to the mouth of the Eden, in beaches exposed to wave action with no evidence of the shells being transported long distances. On the contrary the thin shells would hardly withstand transportation without any breakages and many valves were not only found whole but articulated as well and buried in situ. Substrate seems to be the controlling factor of T. fabula, as suggested by its distribution in the Eden estuary.

TELLINA TENUIS da Costa

"Very common on sandy grounds" (McIntosh 1875).

Tellina tenuis occur in sandy grounds and its distribution does not seem to overlap with Macoma's as seen in Fig. 3.20 (a.b.). A deposit feeder, it rather replaces Scribicularia and Macoma in higher salinities and coarser clearer deposits. Perkins (1956) found indications of an inverse relation between the numbers of Macoma and Tellina tenuis in a traverse of a sand bank near the mouth of the Dee estuary. The same holds true, for living populations of the two species in the sand flats near the mouth of the Eden, as the following table reveals.

Site	Macoma	T. tenuis
	No. of animals/m ²	No. of animals/m ²
K 5	78	26
L 5	-	78
L 11	-	26
J 3	104	-
J 6	-	78
J 7	-	78

Dead populations seem to be heavy at the mouth of the Eden whereas but few valves were found in the lower reaches of the middle estuary, both areas comprising sandy substrates associated with strong currents (flood tidal delta). Holme (1950) found that some populations were not randomly distributed in the sand but were fairly evenly spaced. He suggested that siphonal contact may be the clue that Tellina uses to estimate the distance from its nearest neighbour.

MYA ARENARIA Linnaeus

"Frequently in muddy sand at mouth of Eden" (McIntosh 1875).

"Occurs sparingly in mud estuary" (Brown 1938).

Living Mya arenaria occurs in muddy sand in the upper and middle estuary (Fig. 3.21a). Dead shells were found all over the estuary. In the Kincaple Flat, they reach densities of 650 valves per m² while less occur in the Edenside Flat and around Out Head in muddy and sandy substrata (Fig. 3.21b). Most of the empty valves of Mya arenaria were disarticulated but still close together and buried in a living position. Besides shell orientation, the fact that the ratio of left to

right valves is about 1, in most sites strongly suggests that no transportation has taken place. In Mya transportation is easily recognizable because of the different speeds of the left and right valves which are thus transported different distances from the living place (Schäfer, 1972).

Mya penetrates to the upper estuarine regions perhaps because flagellates are more numerous than diatoms in the plankton there and Mya's growth rate depends on the concentration of flagellates in the phytoplankton (Green, 1968). The rate of feeding of Mya decreases with decreasing salinity. Below 4‰ no feeding takes place. Thus, besides food sources the distribution of Mya is limited by the salinity tolerance of the shells. Small specimens do not tolerate salinity variation as well as large.

MYA TRUNCATA. Linnaeus.

"Abundant off the mouth of the Eden" (McIntosh 1875).

It does not occur with M. arenaria. Only a few broken valves were found in sand, at the mouth of the Eden, in agreement with McIntosh (1875) (Fig. 3.24 b).

LUTRARIA LUTRARIA (Linnaeus)

"Common in muddy sand at the mouth of the Eden" (McIntosh 1875).

Only broken valves were found, a few in muddy sand in the middle estuary, many in sand at the mouth of the Eden (Fig. 3.22). A very interesting area was spotted in the North Bank at the Eden, near Sanctuary Spit, where whole big valves of Lutraria lutraria are abundant. Still no living animal was found in our samples from the nearby site. The very

fragmented valves in some sites do not necessarily mean transportation in any great distance. They may be the result of to-and-fro movements in exposed to wave action areas.

ABRA ALBA (Wood)

"From deep water, rare" (McIntosh 1875).

"Generally distributed off shore, common to abundant" (McIntyre 1958).

Thin shells of A. alba often broken, were common in sand downstream, from the middle estuary towards the mouth of the river (probably replacing Scrobicularia) and at all tide levels. (Fig. 3.22).

Elsewhere Abra alba is often found in enormous numbers in offshore muds and muddy gravels where organic debris is most abundant. From the distribution of organic matter in the Eden estuary (Fig. 3.31) it can be seen that this is not a limiting factor for Abra's distribution. Rather, the substrate controls its distribution.

SOLENI-ENSIS

Two species of *Ensis* are recorded in St. Andrews Bay. *Ensis ensis* as "frequent on sandy grounds" by McIntosh (1875) and *Ensis siliqua*, as "abundant in sand at L.W.S.T." by McIntosh (1875).

Only broken shells, some very fragmented, were found in sand in the middle and lower estuary (Fig. 3.22). One valve was recorded in muddy sand, near Guardbridge, most probably transported there in the channel. Again the fragmented state of the valves does not imply transportation over long distances. It may be due to wave action or to-and-fro movements of the shells.

Ensis distribution is in accordance with its life habits. The genus is intolerant of reduced salinities and on account of this is absent from all except the outer areas of the Eden estuary.

MONTACUTA FERRUGINOSA (Montagu)

"Common in deeper waters of Bay" (McIntosh, 1875).

"Occasional off shore" (McIntyre, 1958).

Tiny thin valves of *Montacuta ferruginosa* were found whole, in sand, from the lower reaches of the middle estuary to the mouth of the Eden in places where *Echinocardium cordatum* occurred (Fig. 3.1). Its co-occurrence with *Echinocardium cordatum* is explained by its life habits. Young individuals of *Montacuta* are attached to spines on the under surface of *E. cordatum*. Larger ones are free in the anal region of the burrow (Yonge and Thompson, 1976). The well preserved thin valves found where *E. cordatum* occurs, suggest burial in the place of occurrence.

NUCULA NUCLEUS (Linnaeus)

"Common in bay" (McIntosh, 1875).

Nucula nucleus is known to inhabit clay, organic rich mud and muddy medium-grained sand from shallow water down to about 150 m. This is not the case in the Eden estuary where its distribution is controlled by the salinity rather than the substrate, or food sources. Always found buried in sand (Fig. 3.23) in the substrates, poorest in organic matter, the small valves though very fragile were sometimes still articulated and in living position. It can be deduced from the above that little transportation if any, has taken place.

THRACIA SP.

"Common on sandy ground off West Sands" (McIntosh, 1875).

The shells of Thracia have very smooth surface and are extremely fragile. The convex shell is almost paper thin and collapses unless handled with the greatest care. This is the reason why in a high energy environment, such as the lowest reaches and mouth of the Eden estuary, they were found very fragmented, which made identification to species level impossible. Buried in sand between tide marks, its distribution is in agreement with McIntosh's as can be seen in Fig 3. 23.

BARNEA CANDIDA (Linnaeus)

"Rare; apparently much more common in sublittoral region" (McIntosh, 1875).

Another paper-thin shelled bivalve of which not a single valve was found whole. Broken valves were found in muddy sand and sand, in the middle and lower estuary, from H.T.M. to L.T.M. levels (Fig. 3.23). Barnea candida is a rock borer (in clay

and soft rock), that can also burrow into wood. Its distribution in the Eden is not in agreement with its life habits, and therefore it is suggested that its odd occurrence is due to postmortem transportation.

HIATELLA ARCTICA (Linnaeus)

Hiatella arctica is not recorded in St. Andrews Bay by Laverack and Blackler (1974), but it is recorded as living in the Tay estuary by Alexander et al. (1935). Only dead shells were found during this study, in sand, at the mouth of the Eden and on the West Sands at all tide levels (Fig. 3.24). Its distribution is not easily explained having in mind Hiatella's life habits. Transportation would be a good reason if the small valves were not found mostly whole and bearing no evidence of transportation.

GARI FERVENSIS (Gmelin)

"Abundant on sandy grounds off West Sands" (McIntosh, 1875).

"Single specimens only in deeper water" (McIntyre, 1958).

A few shells of Gari fervensis were found around the Out Head, in sand at all tide levels, possibly connected with Hiatella arctica (Fig. 3.24). Distribution of Gari in the Eden estuary is in accordance with the animal's life habits. Suspension feeders with wide and short siphons they burrow in sand from the lower shore down to about 50 m depth. Being shallow burrowers they are in danger from predators and starfish.

CORBULA GIBBA (Olivi)

"In few fathoms off East Rocks" (McIntosh, 1875).

Dead shells of Corbula were common in muddy sand and sand in the middle estuary, less at mouth of the Eden (Fig. 3.24).

Corbula gibba is known as being well adapted for life within every grade of bottom material. Being a shallow burrower, the animal seldom emerges in nature once it is buried. In Marseilles, Corbula gibba is recorded with Thryasira flexuosa in a sub-normal zone indicative of pollution (Perkins, 1974). In Scandinavia it has increased steadily in abundance over the 40 years period during which the pollution of the areas found, has increased steadily (Perkins, 1974). Little information is available on pollution in the Eden estuary, to be confident that pollution is the limiting factor in Corbula's distribution but it appears from the distribution of Enteromorpha (another indicator of pollution) that the middle estuary is the most polluted part of the Eden estuary.

MUSCULUS DISCORS. (Linnaeus)

"Occasional on Fucus and Himanthalia near L.W." (McIntosh, 1875).

A few dead shells were found in well sorted sand in the middle estuary from H.T. to L.T. levels (Fig. 3.25). Its distribution agrees with its expected habitat which is under rocks and among seaweeds and other invertebrates from the middle shore downward. Seaweeds and other invertebrates are abundant in the middle estuary.

ANOMIA SP.

"Very common on stones and Laminaria, at East Rocks, H.T. downwards" (E. Sandison in Laverack and Blackler, 1974).

Only single, tiny, very thin valves were found frequent in sand near L.W.M. in the lower estuary (Fig. 3.25). The animals live attached to other shells to whose shape they often conform.

PECTEN SP.

"Occasional in deep water" (McIntosh, 1875).

A few small usually broken valves were recorded in the middle estuary in sand and at the sandflats at the mouth of the Eden in high energy environments, often with Anomia (Fig. 3.25). Mainly near L.W.M. Pecten appears to penetrate well into the middle estuary and dead valves were present at H.W.M. in site G 6 where they may be attributed to post-mortem transportation, but it is also likely that the animals swam there freely. All Pectinacea begin life byssally attached resting on their right valve. With growth they become free and are capable of swimming while some forms retain byssal attachment and become cemented by the lower right valve.

VENERUPIS SP.

"Abundant in muddy sand between tide marks" (McIntosh, 1875).

Two valves only, articulated and in the living position, were found in the Kincapple Flat, in muddy sand at H.T. level (Fig. 3.25). No other evidence of Venerupis living or dead in the whole estuary was recorded. The state and position of

the valves reveal that Venerupis lived there and was not transported by the currents. It is therefore enigmatic that it is totally absent anywhere else in the estuary.

ASTARTE BOREALIS (Schumacher)

The two species of the genus (A. montaquii and A. sulcata) that are recorded by McIntosh (1875) are both frequent in deep water in St. Andrews Bay. During this study only a few broken valves of Astarte borealis were found in the North bank of the Eden in the flood-tidal delta, buried in sand at H.T. and L.T. levels (Fig. 3.26). The sediments of the area are transported and deposited in high energy environments (Eastwood's Textural Facies I). This does not imply that Astarte has been transported, but in the absence of living specimens this seems the most reasonable explanation of its distribution.

ARCTICA ISLANDICA (Linnaeus)

"Common in deep water" (McIntosh, 1875). "Obtained alive only when thrown on West Sands after storms" (Arnold in Laverack and Blackler, 1974). "Occasional in deep water" (McIntyre, 1958).

Only one fragmented unusually thick valve was found buried in sand at the mouth of the Eden. The state of the valve is alone enough to conclude transportation over a long distance. Arctica is a plankton feeder, with no siphons, protected by a thick shell. It occurs in sand and sandy mud from low shore levels to fair depths and is a major food for bottom living fish. There may be a connection between Arnold's "thrown on West Sands" animals and the fragmented valve found in site K 5.

DOSINIA SP.

A few shells were found scattered over the estuary at all tide levels buried in sand and muddy sand (Fig. 3.26). Their odd distribution is explained partly by their recorded occurrence elsewhere in all grades of substrata up to coarse gravel. Unfortunately no information specifying their salinity tolerance is available to justify Dosinia's penetration so far into the estuary, so the transportation of dead shells assumption can not be rejected.

OSTREA EDULIS Linnaeus.

Ostrea edulis is not mentioned in the St. Andrews Bay fauna although it is recorded in estuaries and is widely distributed in the North Sea. Small, well preserved valves, were common in sandy substrates from the middle estuary to the mouth of the Eden, at all tide levels (Fig. 3.27). The reason Ostrea does not penetrate further into the estuary may be pollution (evidenced by Corbula gibba and Enteromorpha sp. so far). The state of the small, thin shelled valves supports the belief that no transportation has taken place.

CRASSOSTREA ANGULATA (Lamarck).

Crassostrea too is not mentioned in the St. Andrews Bay fauna, the reason probably being that while the more extensive surveys of the fauna took place in the end of the nineteenth century by McIntosh (1875), Crassostrea only recently reached the Atlantic, English Channel and North Sea. Previously it was confined to the Mediterranean (Perkins, 1974). However once it appeared in the new environment it spread

rapidly and came to occupy large areas formerly occupied by Ostrea alone. Crassostrea is capable of penetrating further into estuaries than Ostrea. In some American estuaries Crassostrea lives permanently in salinities down to 12‰ and can tolerate lower salinities for short periods.

In the Eden one single valve was found in sand by the channel bed in the lower estuary (Fig. 3.27). Being very small and with extremely thin shell, it broke although handled with extra care. It is believed that the animal lived there since salinity, substrate, tide level and temperature agree with the life habits of the species (Green, 1968). The optimum conditions for reproduction is 20-25‰ salinity. Optimum development takes place faster at 18-27°C at 28-35‰. It requires higher temperatures than Ostrea and the adult tolerance range is also wider than the common oyster's. The adults living up to 35°C are very successful in estuarine conditions, on flats exposed at each tide and will survive in turbid conditions. Pollution and predators are the limiting factors for Crassostrea too.

DONAX VITTATUS (da Costa).

"Very abundant on sandy ground at a few fathoms depth" (McIntosh, 1875).

Up to 40014 valves per m² of Donax vittatus were collected in the sand flats at the mouth of the Eden. Less but yet high densities of Donax valves, were found in sandy and muddy substrates in the middle and outer estuary at all tide levels (Fig. 3.28). Predation marks on a considerable percentage of valves, suggest that predators may be responsible for the often found fragmented valves. Wave action in the open beaches at the mouth of the Eden is also to be held

responsible for the state of the valves.

Besides substrate, food sources seem to be the limiting factor controlling Donax distribution in the Eden estuary. Inhabitants of exposed beaches, the last area where detritus collects, Donax live close below the surface in the surf zone, feeding on the material raised by the surf. The siphons are short, serving to draw in suspended matter. They move up and down with the breaking waves, retaining position by virtue of their powers of instant burrowing. The animals are in constant danger of being uncovered, the instant reaction to which is reburial.

VENUS STRIATULA da Costa

"On sandy grounds in a few fathoms" (McIntosh, 1875)

"Generally common on all off shore grounds" (McIntyre, 1958).

Venus striatula valves were found in well sorted and medium sand in the lower reaches of the middle estuary and at the mouth of the Eden, in areas influenced by tidal currents (Fig. 3.29). The highest densities occur in exposed sandy areas and reach 4 446 valves per m².

Substrate and abundance of food are the major factors controlling distribution. Venus feeds by filtering plankton which is abundant in the exposed areas it was found (Perkins, 1960). Being a shallow burrower it lives in a range of sediment grades from fine to muddy sand around and below L.W.M., in outer estuaries. It is recorded in the Tay estuary as well as in the Solway Firth. It may be associated with Echinocardium cordatum.

A low percentage of valves shows predation marks of Natica alderi. It was noticed that the highest densities of Venus valves coincide with those of Natica alderi shells.

Boring of V. striatula is around the lower margins of the shell and young bivalves are most frequently attacked.

SPISULA-MACTRA.

The big shells of the two species were mostly broken but tiny thin shells of Spisula solida and Mactra corallina were preserved whole buried in sand. Densities up to 3500 valves per m² were recorded towards the mouth of the Eden. Fewer shells occurred in the middle estuary (Fig. 3.30).

In the Solway Firth estuary Mactra corallina occurs in coarse-medium exposed sand and in fine sand while Spisula solida occurs only in fine sand with Mactra corallina.

TABLE 3.1.

LIVING MOLLUSCA RECORDED IN THE EDEN

	McIntosh, 1875	Wilson, 1910	Brown, 1958	Bell, 1978	Bell, 1979	R.Z., 1978
BIVALVES	Cardium edule	Cardium edule	Cardium edule	Cardium edule	Cardium edule	Cardium edule
	Mytilus edulis	Mytilus edulis	Mytilus edulis	Mytilus edulis	Mytilus edulis	Mytilus edulis
	Macoma balthica	Solen	Macoma balthica	Macoma balthica	Macoma balthica	Macoma balthica
	Mya arenaria		Mya arenaria	Mya arenaria	Mya arenaria	Mya arenaria
	Mya truncata		Tellina tenuis	Tellina tenuis	Tellina tenuis	Tellina tenuis
	Lutraria lutraria		Scrobicularia plana	Scrobicularia plana	Scrobicularia	Scrobicularia
			Donax vittatus			
GASTROPODS	Hydrobia ulvae	Purpura lapillus	Purpura lapillus	Hydrobia ulvae	Hydrobia ulvae	Hydrobia ulvae
	Limpontia capitata	Aporrhais per pelicani	Chiton marginatus	Littorina littorea	Littorina saxatilis	Retusa obtusa
			Limpontia capitata		Littorina littorea	Littorina saxatilis
			Buccinum undatum		Littorina littoralis	Littorina littoralis
			Hydrobia ulvae		Chiton marginatus	
			Littorina obtusata		Limpontia capitata	
			Littorina rudis		Cylichna obtusa	
			Littorina littorea			
			Cylichna obtusa			

TABLE 3.2.

LIVING MOLLUSCA

	Eden Estuary	Tay Estuary	Firth of Forth Estuary
BIVALVES	<i>Cardium edule</i>	<i>Cardium edule</i>	<i>Cardium edule</i>
	<i>Mytilus edulis</i>	<i>Mytilus edulis</i>	<i>Mytilus edulis</i>
	<i>Macoma balthica</i>	<i>Macoma balthica</i>	<i>Macoma balthica</i>
	<i>Mya arenaria</i>	<i>Mya arenaria</i>	<i>Mya arenaria</i>
	<i>Mya truncata</i>	-	-
	<i>Scrobicularia plana</i>	<i>Scrobicularia plana</i>	-
	<i>Tellina tenuis</i>	<i>Tellina tenuis</i>	<i>Tellina tenuis</i>
	-	-	<i>Tellina tabula</i>
	<i>Lutraria lutraria</i>	-	-
	<i>Donax vittatus</i>	-	-
	<i>Solen</i>	-	-
		<i>Venus striatula</i>	
		<i>Hiatella gallicana</i>	
		<i>Hiatella arctica</i>	
	<i>Spisula solida</i>		
	<i>Modiolus modiolus</i>		
	<i>Modiolus barbatus</i>		
GASTROPODS	<i>Hydrobia ulvae</i>	<i>Hydrobia ulvae</i>	<i>Hydrobia ulvae</i>
	<i>Retusa obtusa</i>	-	<i>Retusa obtusa</i>
	<i>Littorina saxatilis</i>	<i>Littorina saxatilis</i>	-
	<i>L. littoralis</i>	<i>L. littoralis</i>	-
	<i>L. littorea</i>	<i>L. littorea</i>	-
	<i>Nucella lapillus</i>	<i>Nucella lapillus</i>	-
	<i>Buccinum undatum</i>	<i>Buccinum undatum</i>	-
	<i>Aporrhais pes pelicani</i>	-	
	<i>Chiton marginatus</i>	-	
	<i>Limopontia capitata</i>	-	
	<i>Retusa alba</i>	-	
		<i>Potamopyrgus jenkinsi</i>	
		<i>Patella vulgata</i>	
		<i>Acmaea testudinalis</i>	
	<i>Gibbula cineraria</i>		
	<i>Orchidoris fusca</i>		

TABLE 3.3.

FROM ST. ANDREWS BAY
FAUNA LISTS.RECORDED
AS LIVING
IN TAY-FORTHRECORDED
AS LIVING
IN EDEN

DEAD MOLLUSCS

DEAD MOLLUSCS	RECORDED AS LIVING IN EDEN	RECORDED AS LIVING IN TAY-FORTH	
1. <i>Macoma balthica</i>	+	Tay - Forth	Abundant on sandy beaches at mouth of Eden - McIntosh
2. <i>Scrobicularia plana</i>	+	-	Common in muddy sand at mouth of Tay - McIntosh
3. <i>Cardium edule</i>	+	Tay - Forth	Abundant around mussel beds in Eden - McIntosh
4. <i>Mya arenaria</i>	+	Tay - Forth	Frequent at muddy sand at mouth of Eden - McIntosh
5. <i>Mytilus edulis</i>	+	Tay - Forth	Adults in several beds in Eden
6. <i>Solen ensis</i>	+	-	Frequent on sandy grounds
7. <i>Tellina fabula</i>	-	Forth	Common on sandy ground with <i>T. tenuis</i> - McIntosh
8. <i>Tellina tenuis</i>	+	Tay - Forth	Very common on sandy ground with <i>T. tenuis</i> - McIntosh
9. <i>Spisula - Mactra</i>	-	Tay	Abundant in sandy grounds off West Sands
10. <i>Montacuta ferruginosa</i>	-	-	Common in deeper water of bay. Occasional off-shore
11. <i>Venus striatula</i>	-	Tay	Generally common on all off-shore grounds - McIntyre
12. <i>Dosinia</i> sp.	-	-	Abundant in deep water - McIntosh
13. <i>Donax vittatus</i>	+	-	Very abundant on sandy ground at a few fathoms depth. McIntosh
14. <i>Lutraria lutraria</i>	+	-	Common in muddy sand at mouth of Eden
15. <i>Pecten</i> sp.	-	-	Occasional in deep water - McIntosh
16. <i>Ostrea edulis</i>	-	-	Not mentioned
17. <i>Thracia</i> sp.	-	-	Common on sandy grounds off West Sands - McIntosh
18. <i>Abra alba</i>	-	-	From deep water rare - McIntosh. Generally distributed off shore, common.
19. <i>Anomia</i>	-	-	Very common on stones and <u>Laminaria</u>
20. <i>Nucula nucleus</i>	-	-	Common in bay - McIntosh
21. <i>Hiatella arctica</i>	-	Tay	Not mentioned
22. <i>Gari fervensis</i>	-	-	Abundant on sandy ground off West Sands - McIntosh
23. <i>Corbula gibba</i>	-	-	In few fathoms, off East Rocks - McIntosh
24. <i>Mya truncata</i>	+	-	Abundant at mouth of Eden
25. <i>Musculus discors</i>	-	-	Occasional on <u>Fucus</u> near L.W.
26. <i>Arctica islandica</i>	-	-	Obtained alive only when thrown on West Sands after storms
27. <i>Astarte borealis</i>	-	-	Frequent in deep water. Breeding in July
28. <i>Crassostrea</i>	-	-	Not mentioned
29. <i>Venerupis</i> sp.	-	-	<i>V. pullestris</i> : Abundant in muddy sand between tide marks
30. <i>Barnea candida</i>	-	-	Not mentioned
1. <i>Hydrobia ulvae</i>	+	Tay - Forth	On mud in Eden estuary
2. <i>Potemopyrgus jenkinsi</i>	-	Tay	Not mentioned
3. <i>Littorina saxatilis</i>	+	Tay	Abundant on rocks near H.W. - McIntosh
4. <i>Littorina littorea</i>	+	Tay	Extremely abundant between tide marks - McIntosh
5. <i>Littorina littoralis</i>	+	Tay	Very common between tide marks - McIntosh
6. <i>Nucella lapillus</i>	+	Tay	Very abundant between tide marks
7. <i>Tritonalia aciculata</i>	-	-	Not mentioned
8. <i>Retusa obtusa</i>	+	Forth	In deep water occasional - McIntosh
9. <i>Natica alderi</i>	-	-	With <i>N. catana</i> on sandy grounds - McIntosh
10. <i>Buccinum undatum</i>	+	Tay	Common in pools at East Rocks
11. <i>Gibbula cineraria</i>	-	Tay	Abundant on stones and rocks between and above tide marks
12. <i>Patella</i>	-	Tay	Generally abundant
13. <i>Acmaea tessulata</i>	-	Tay A. testudinialis	Common under stones near L.W. - McIntosh
14. <i>Patina pellucida</i>	-	-	Abundant on <u>Laminaria</u> - McIntosh

BIVALVES

GASTROPODS

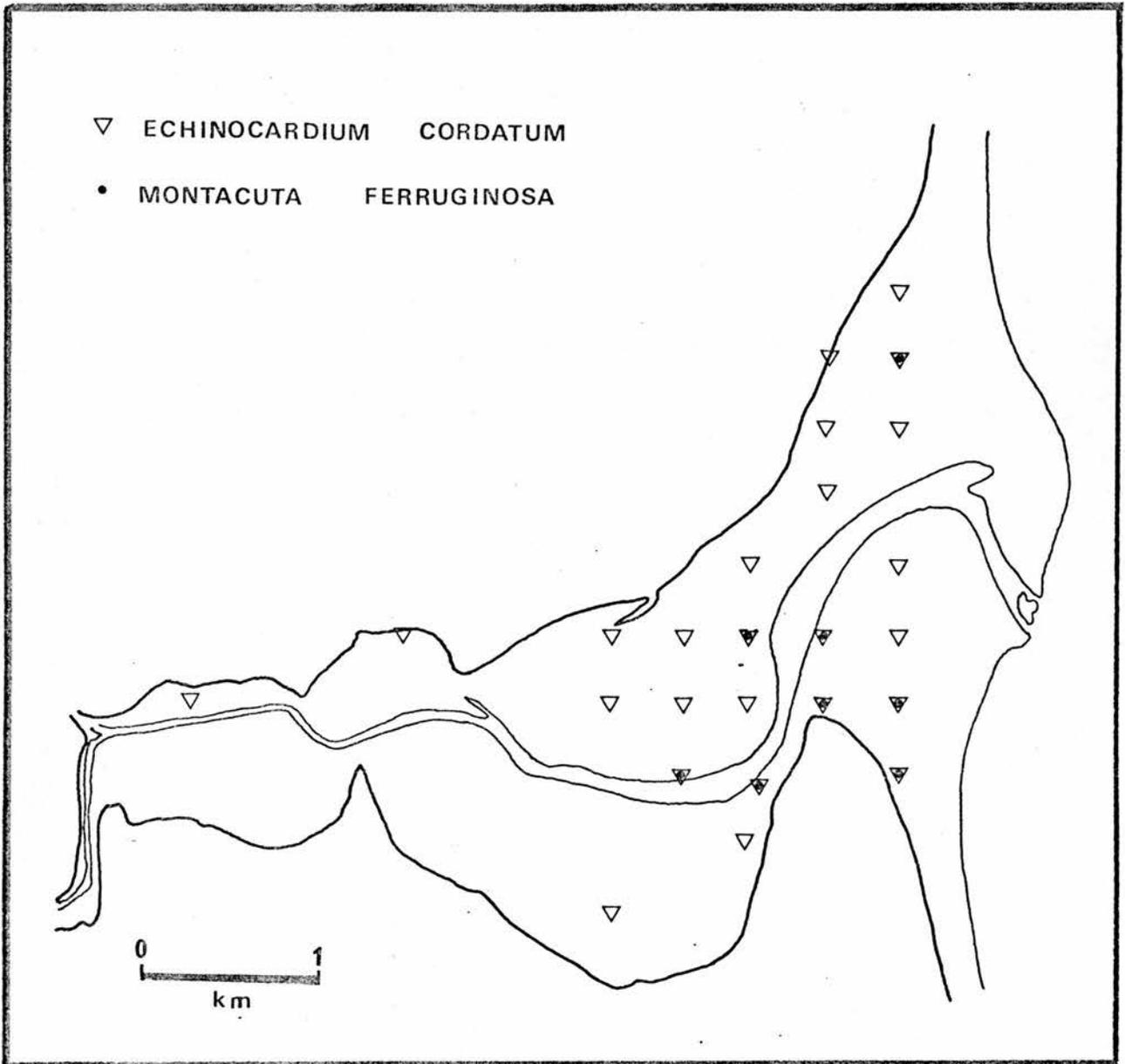


Fig.3.1 Distribution of Echinocardium cordatum & Montacuta ferruginosa dead populations.

BALANUS

CRENATUS

- 1 - 10
- 10 - 100
- 100 - 1000
- >1000

BIOMASS in gr* per m²

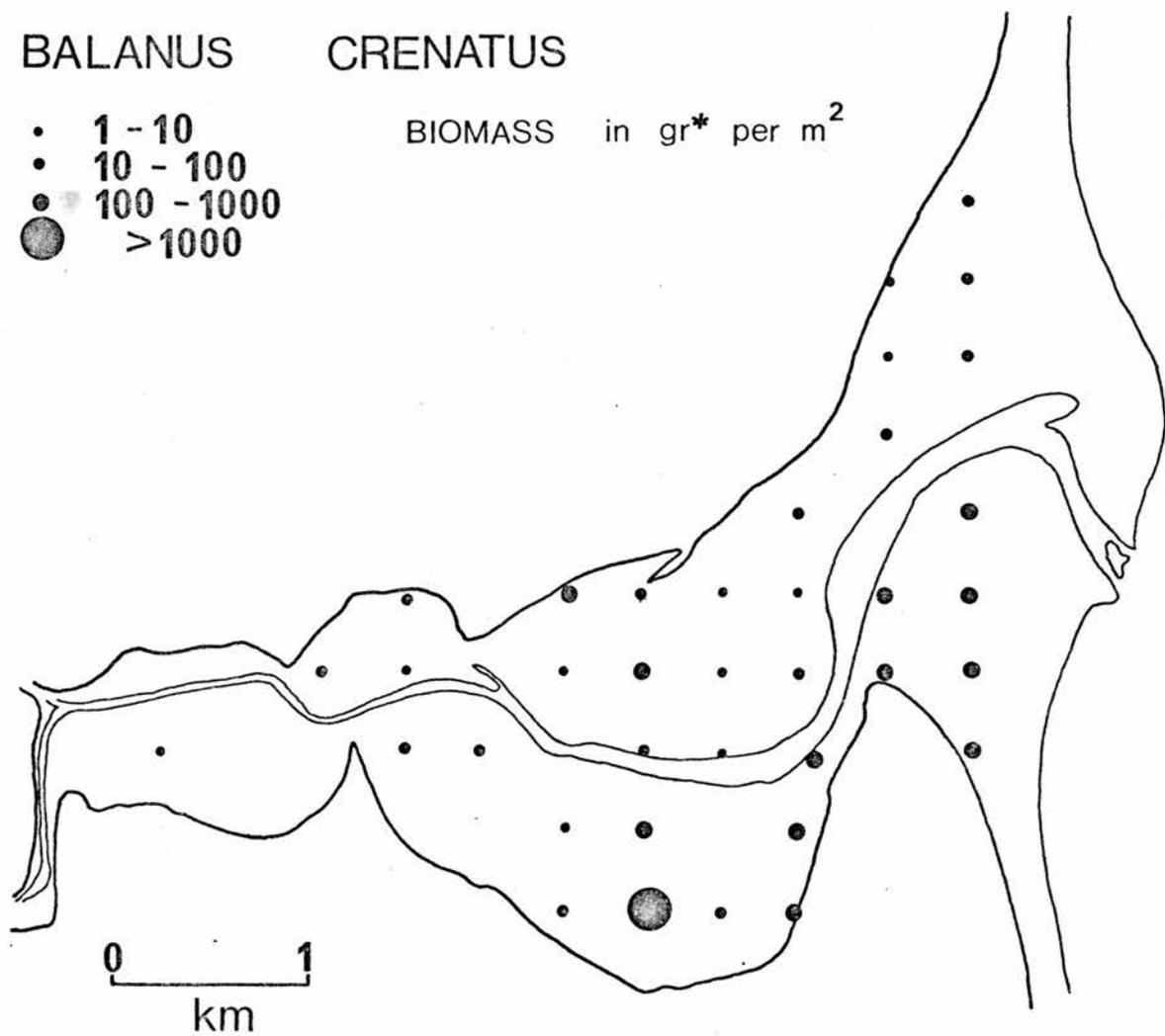


Fig.3.2 Distribution of Balanus crenatus dead population.

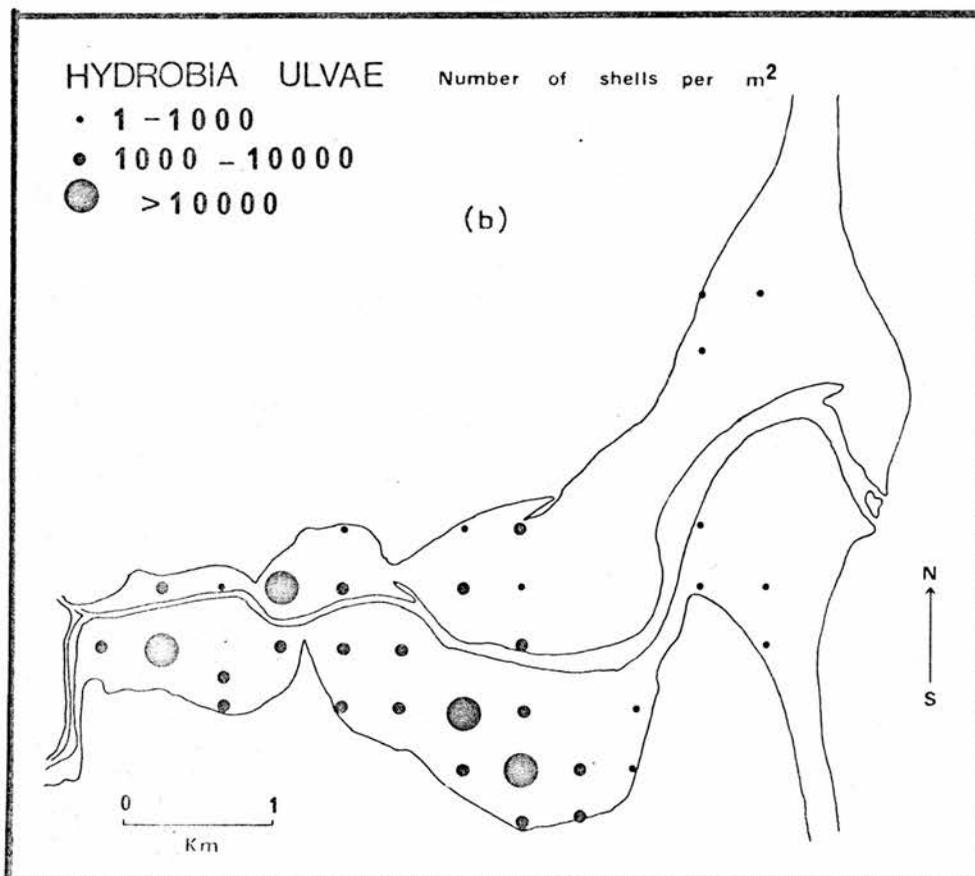
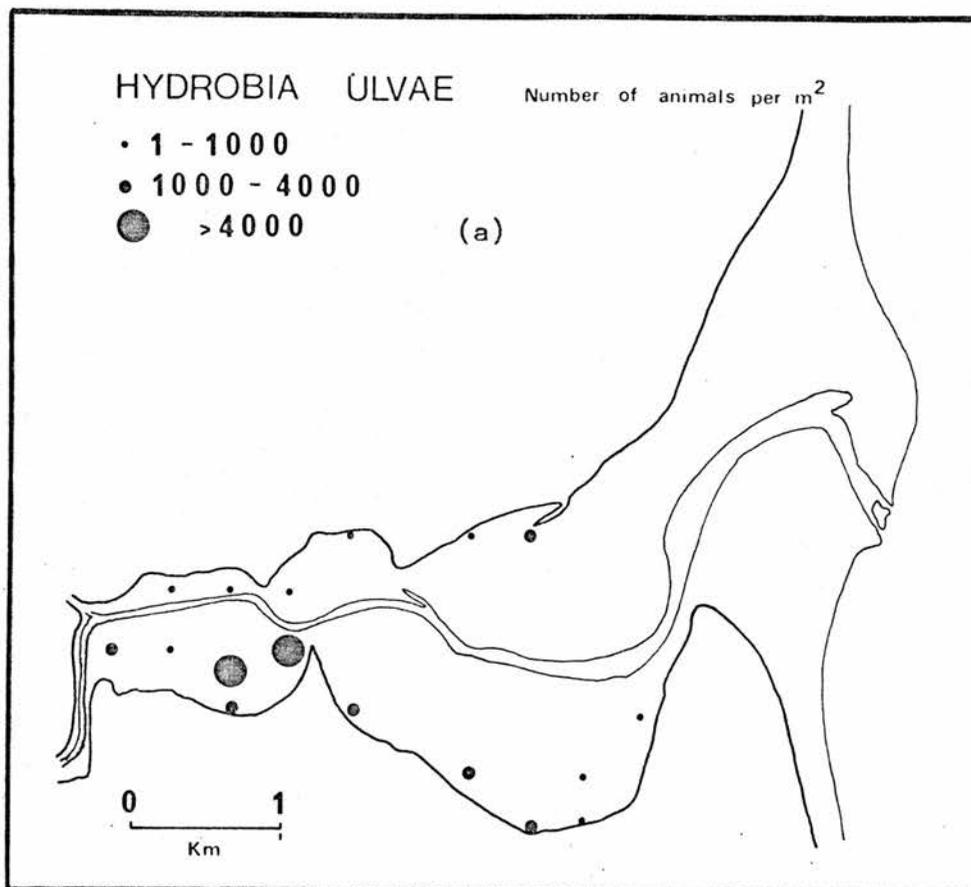


Fig.3.3 Distribution of Hydrobia ulvae : (a)living & (b)dead populations.

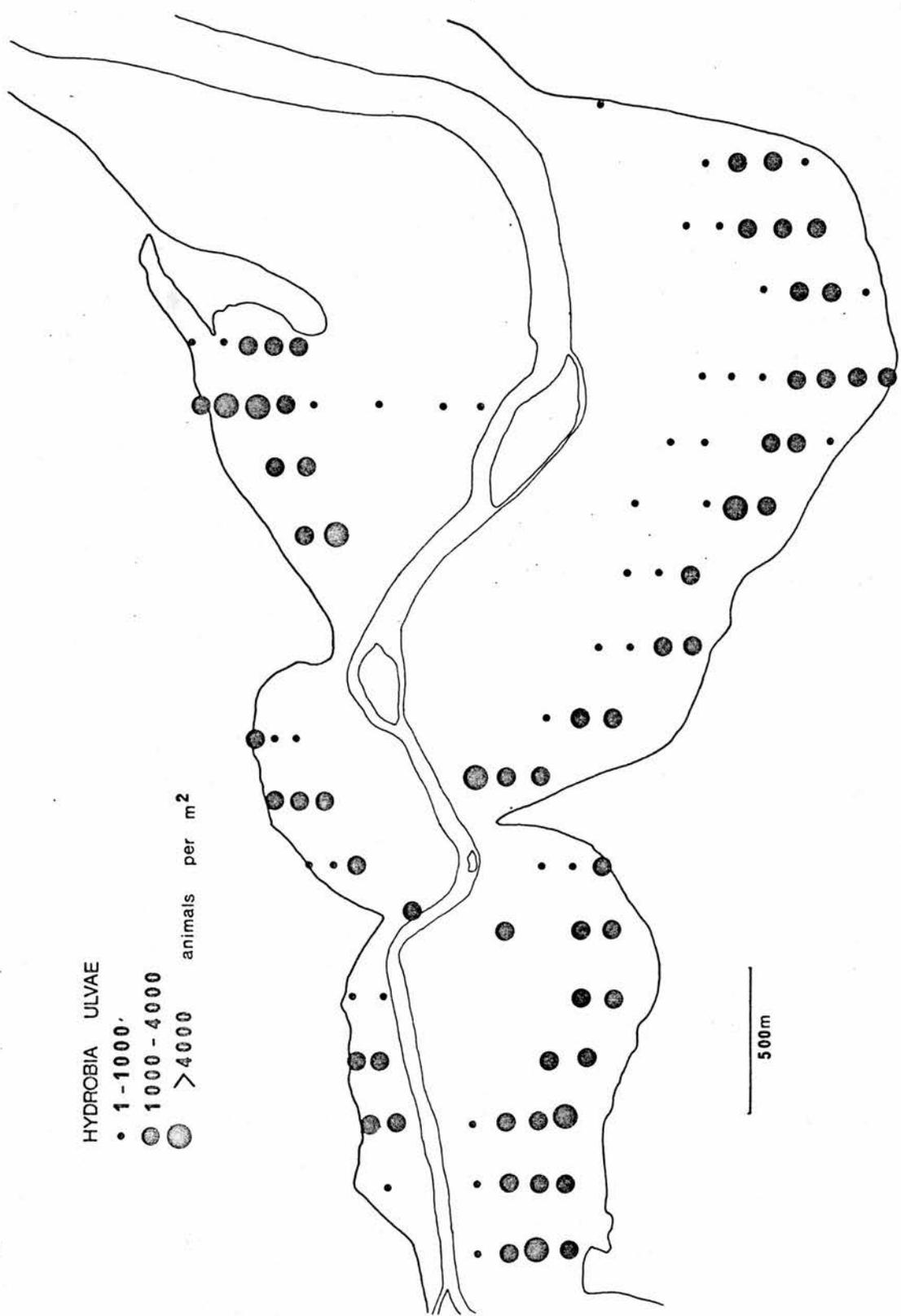


Fig. 3.3(c) Distribution of Hydrobia ulvae living population (Bell's 1978 data)

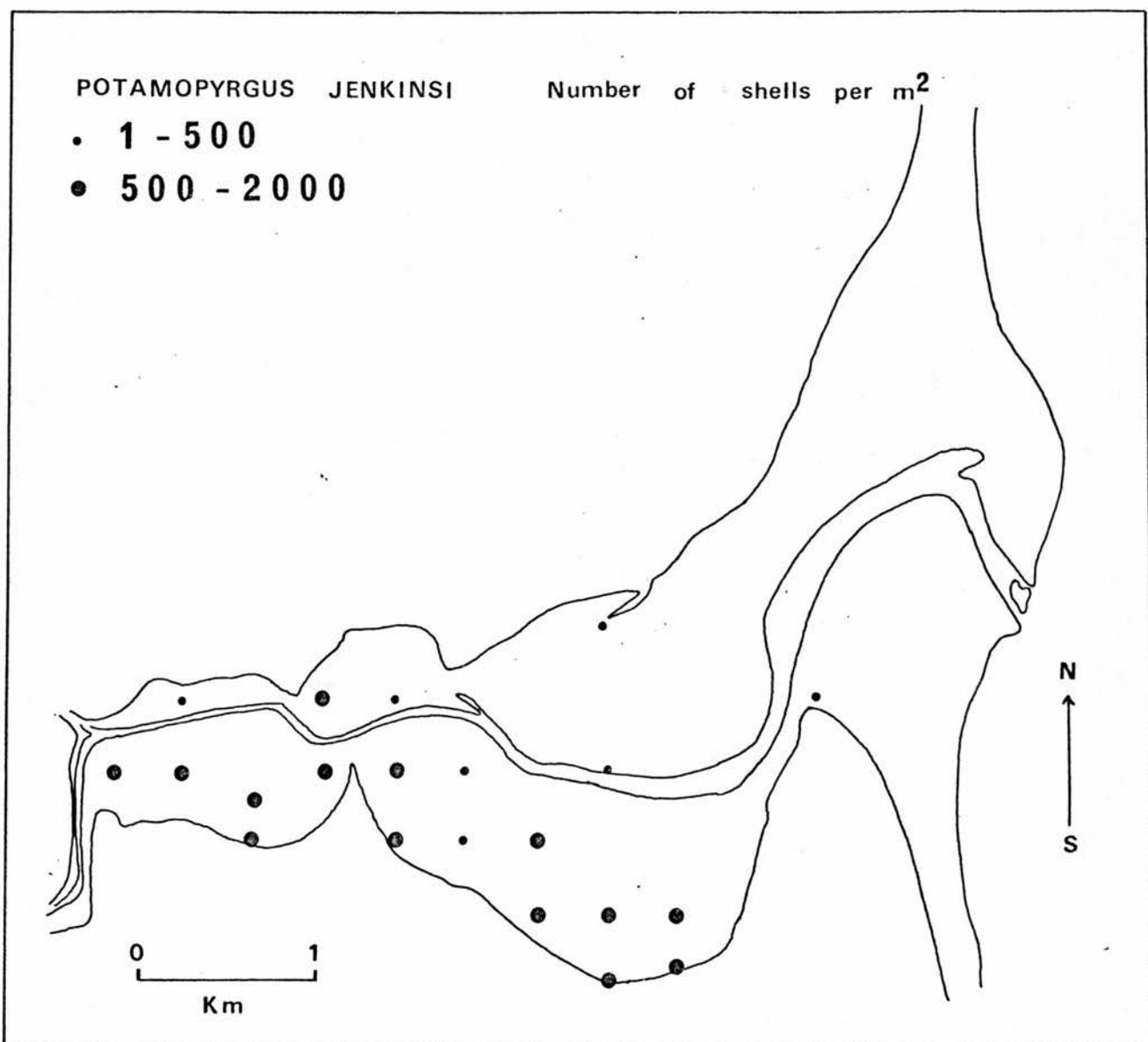


Fig.3.4 Distribution of Potamopyrgus jenkinsi dead population.

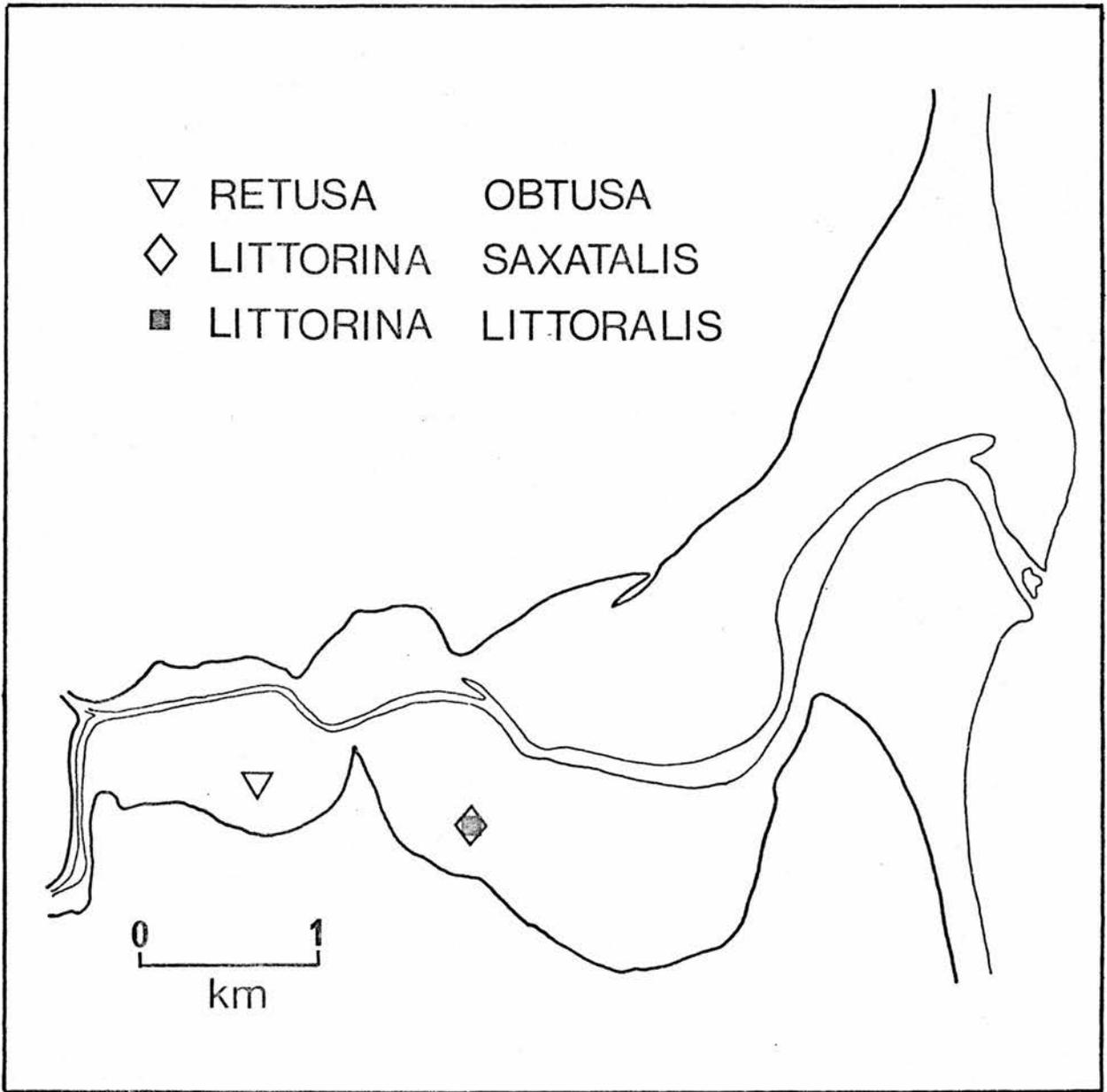


Fig.3.5(a) Distribution of Retusa obtusa, Littorina saxatilis & Littorina littoralis living populations. Only presence of the above species is illustrated.

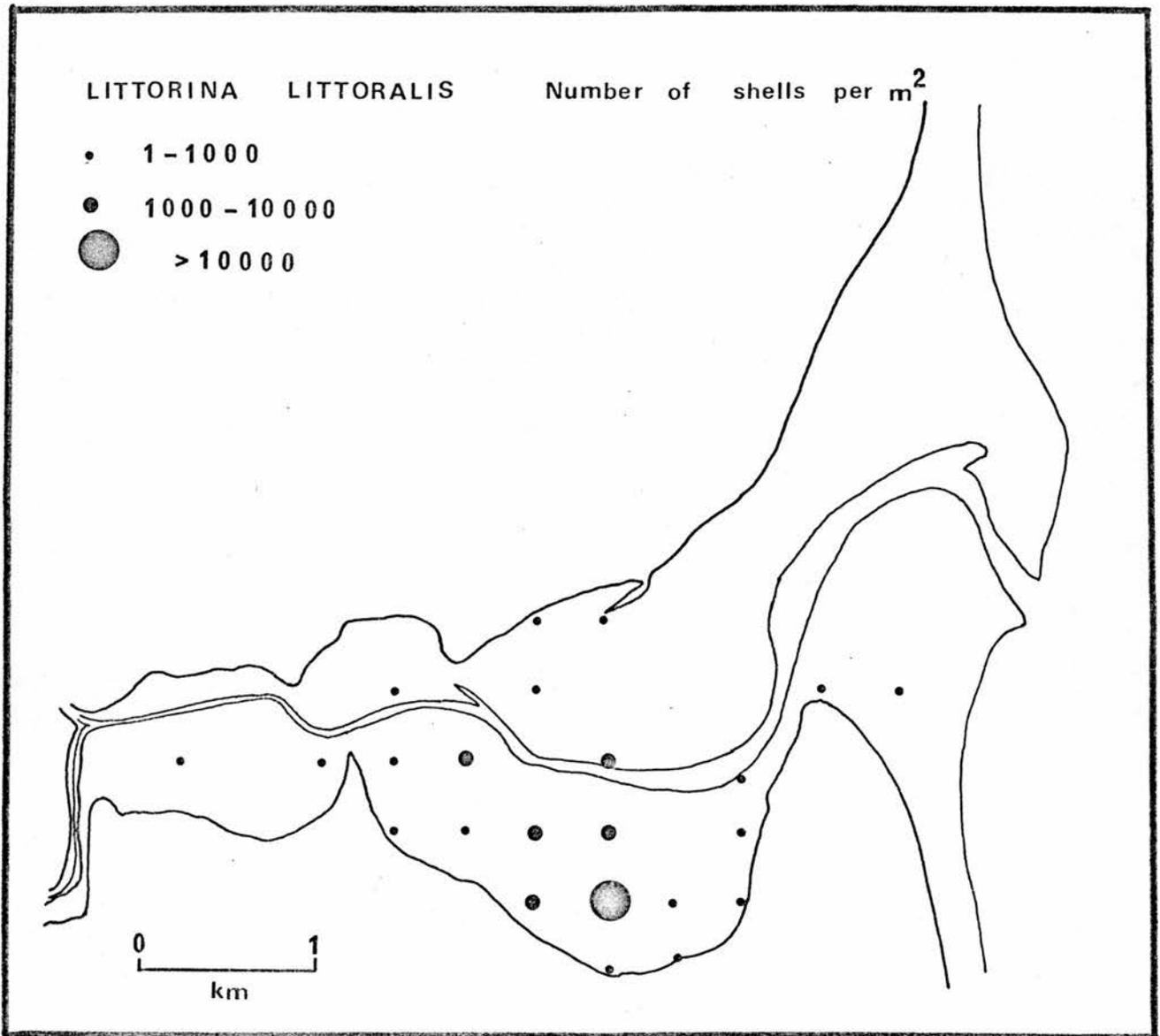


Fig.3.5(b) Distribution of Littorina littoralis dead population.

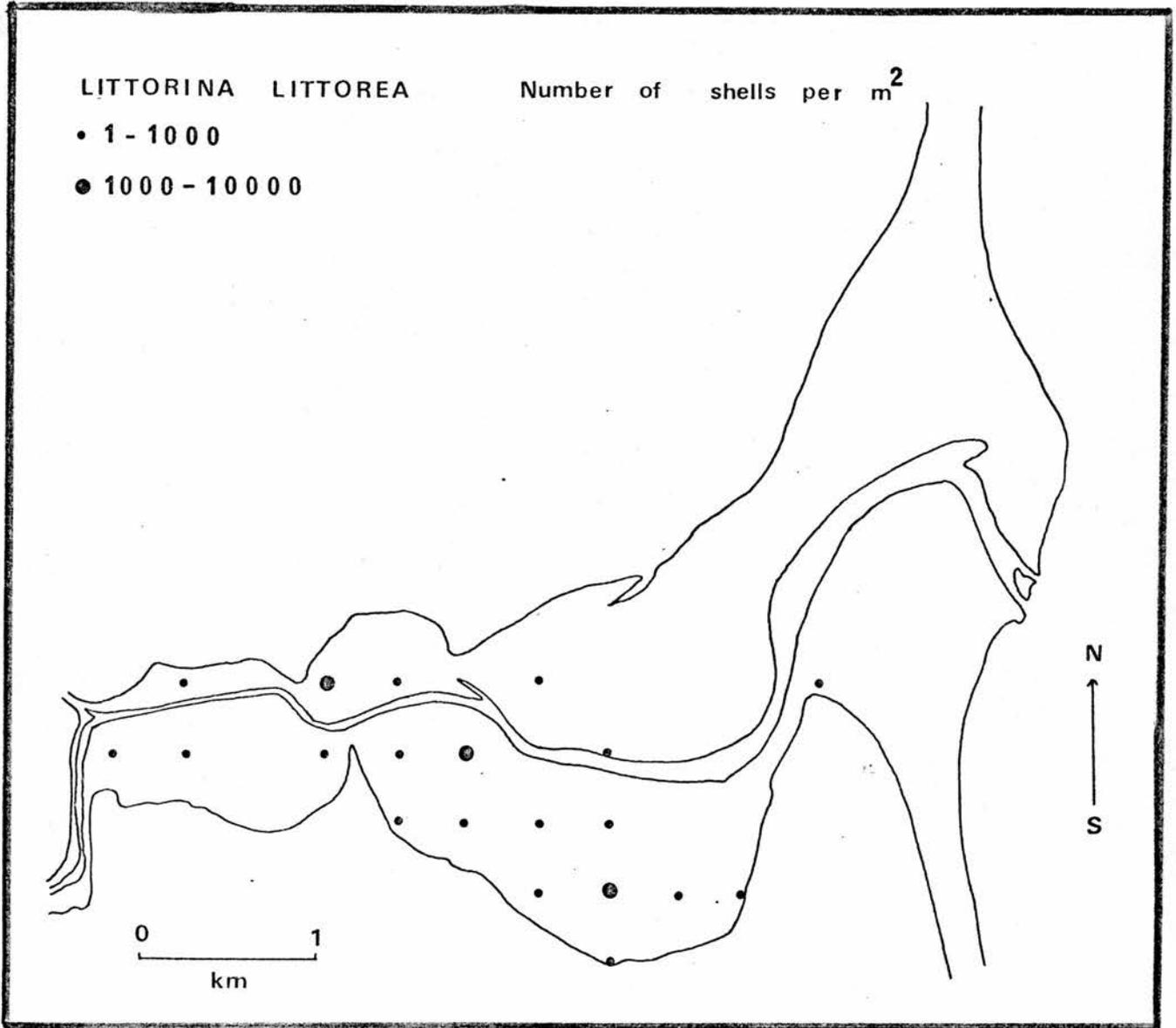


Fig.3.6 Distribution of Littorina littorea dead population.

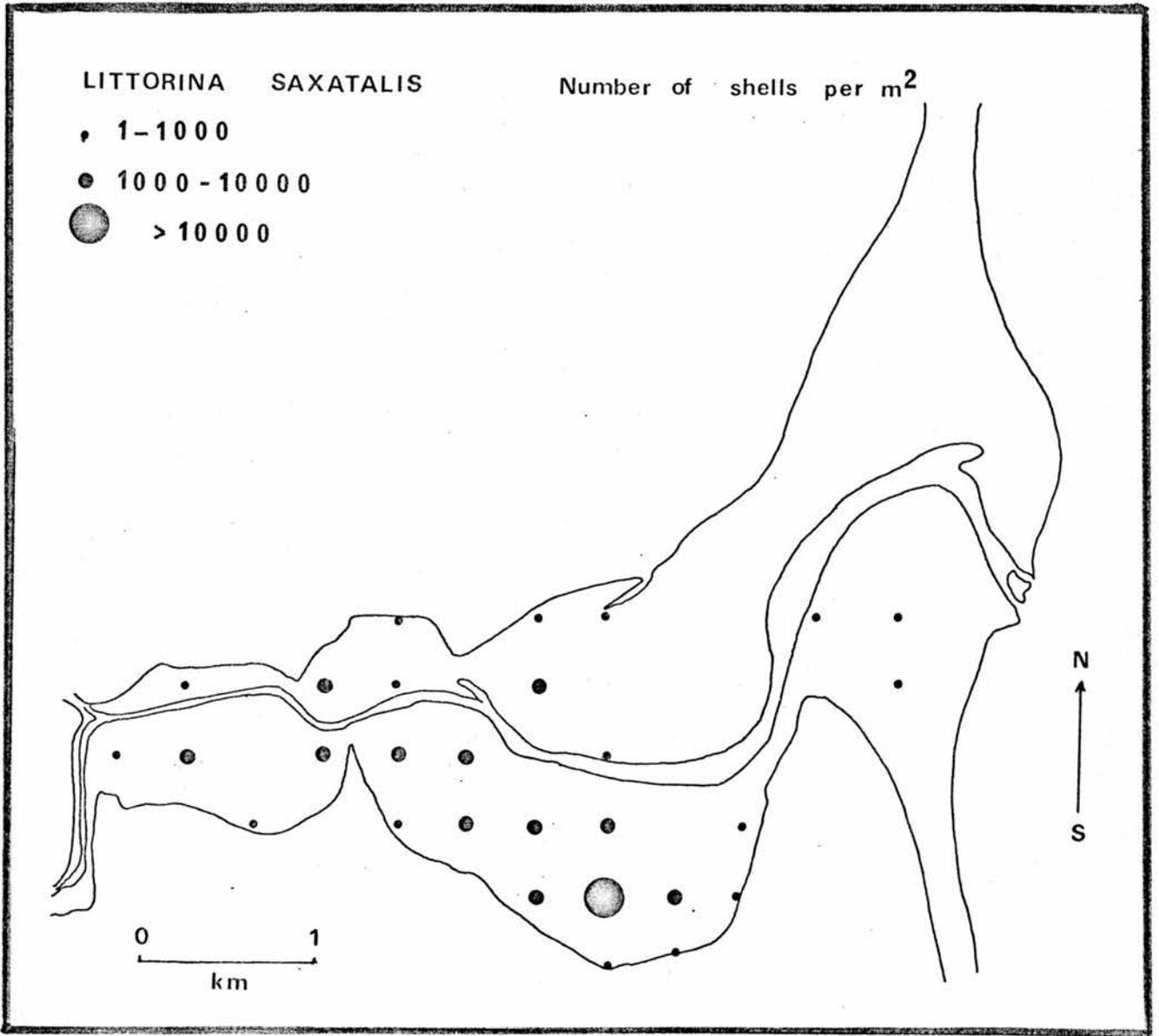


Fig.3.7 Distribution of Littorina saxatilis dead population.

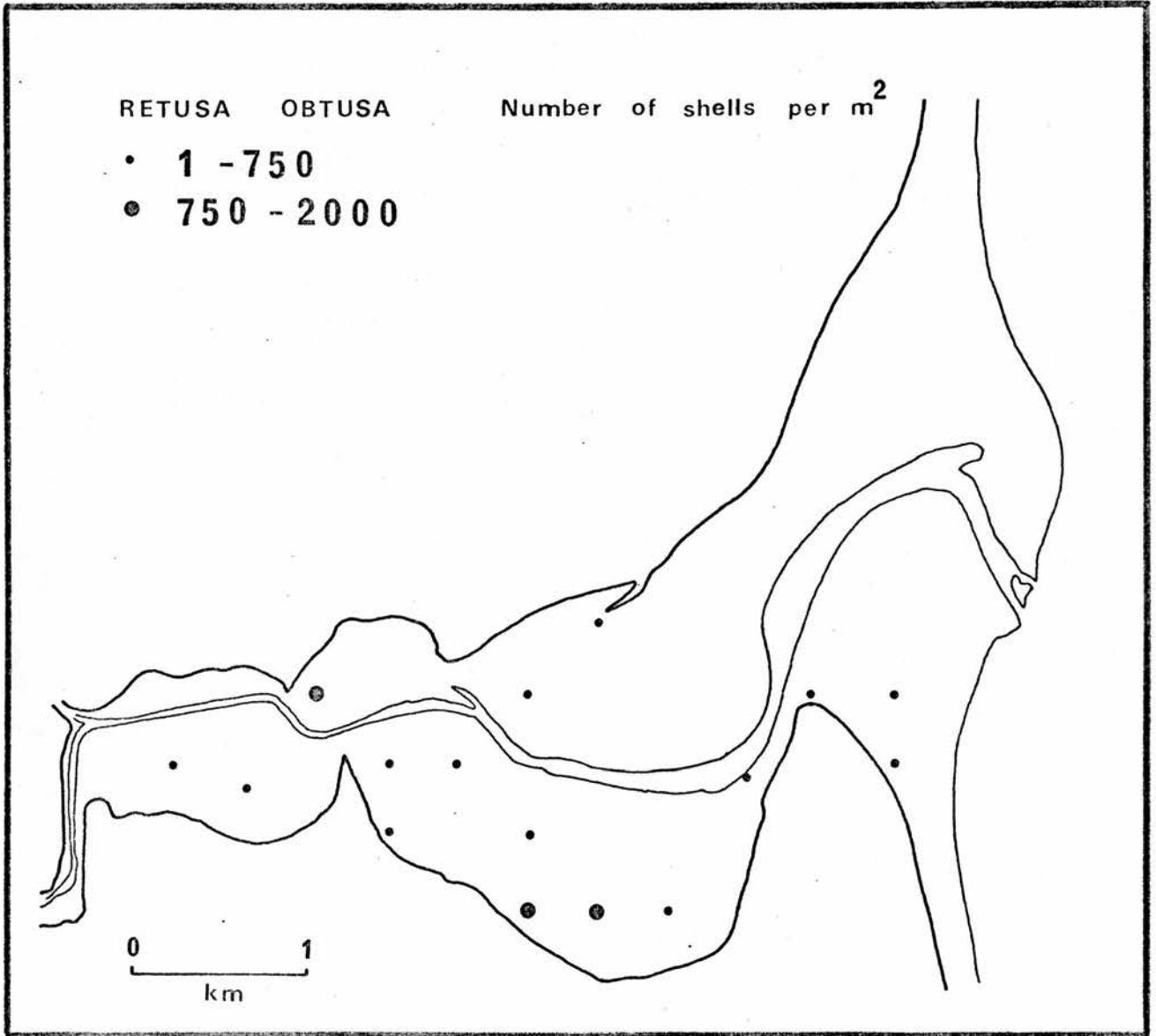


Fig.3.8. Distribution of Retusa obtusa dead population.

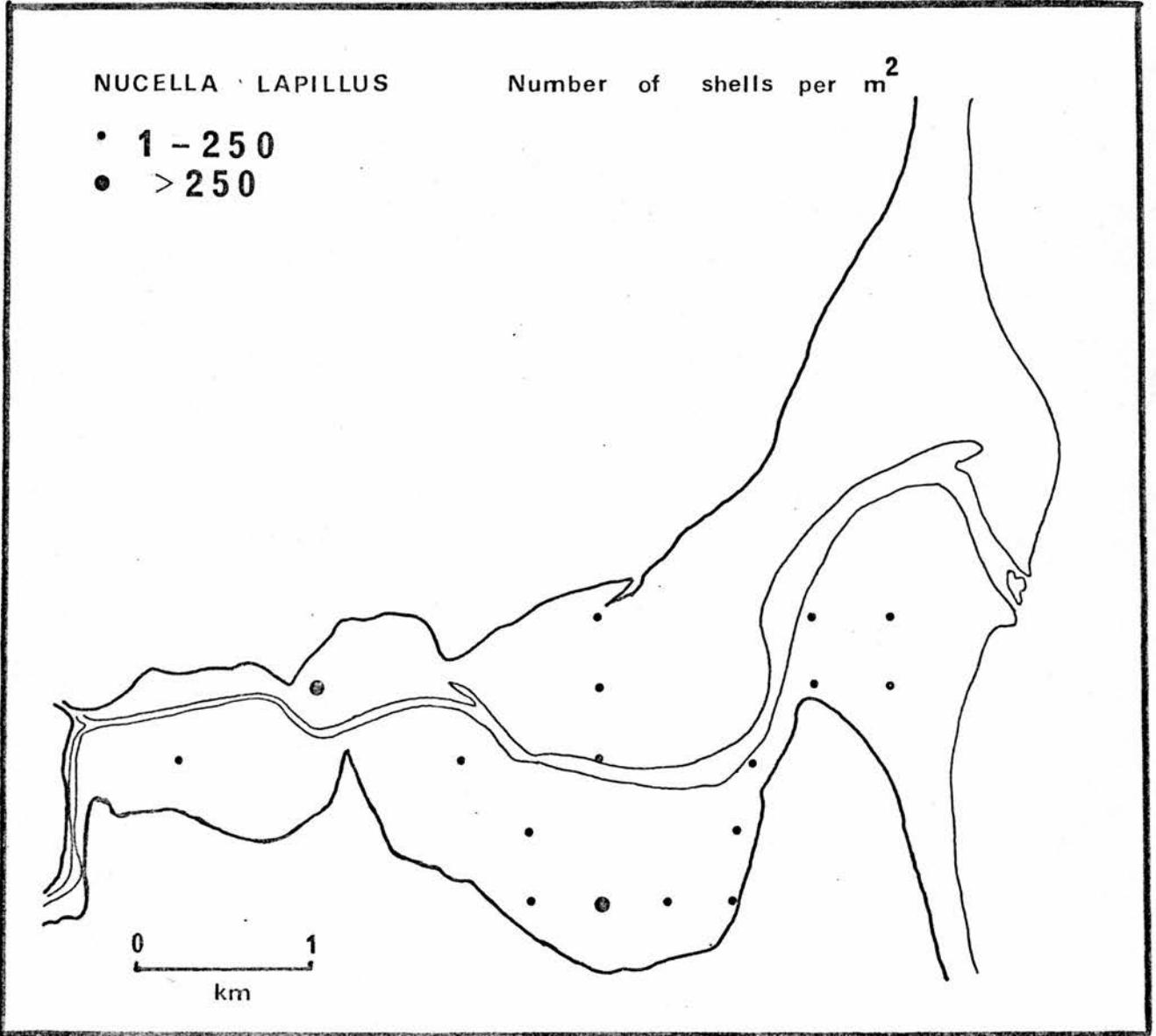


Fig.3.9. Distribution of Nucella lapillus dead population.

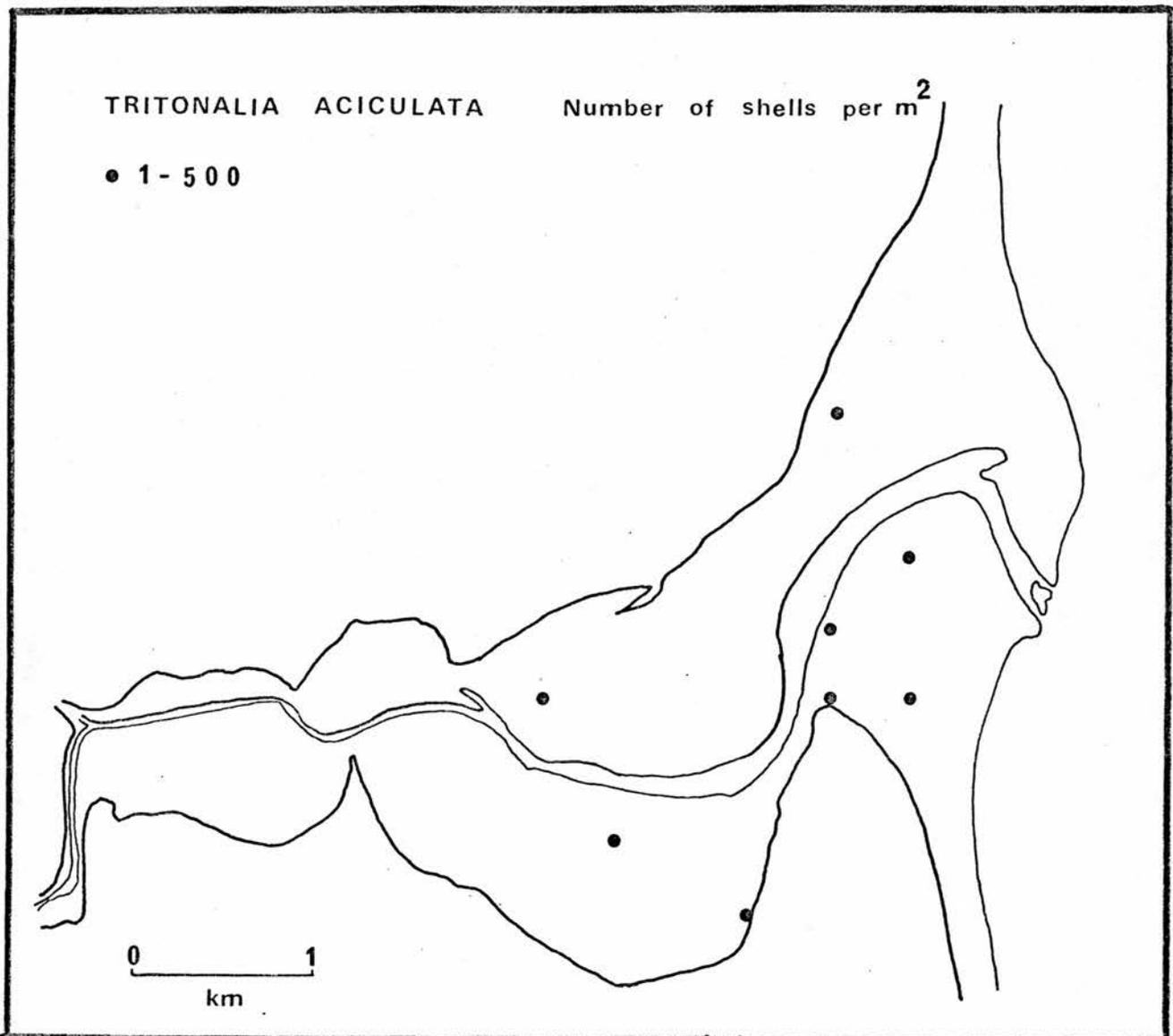


Fig.3.10. Distribution of Tritonalia aciculata dead population.

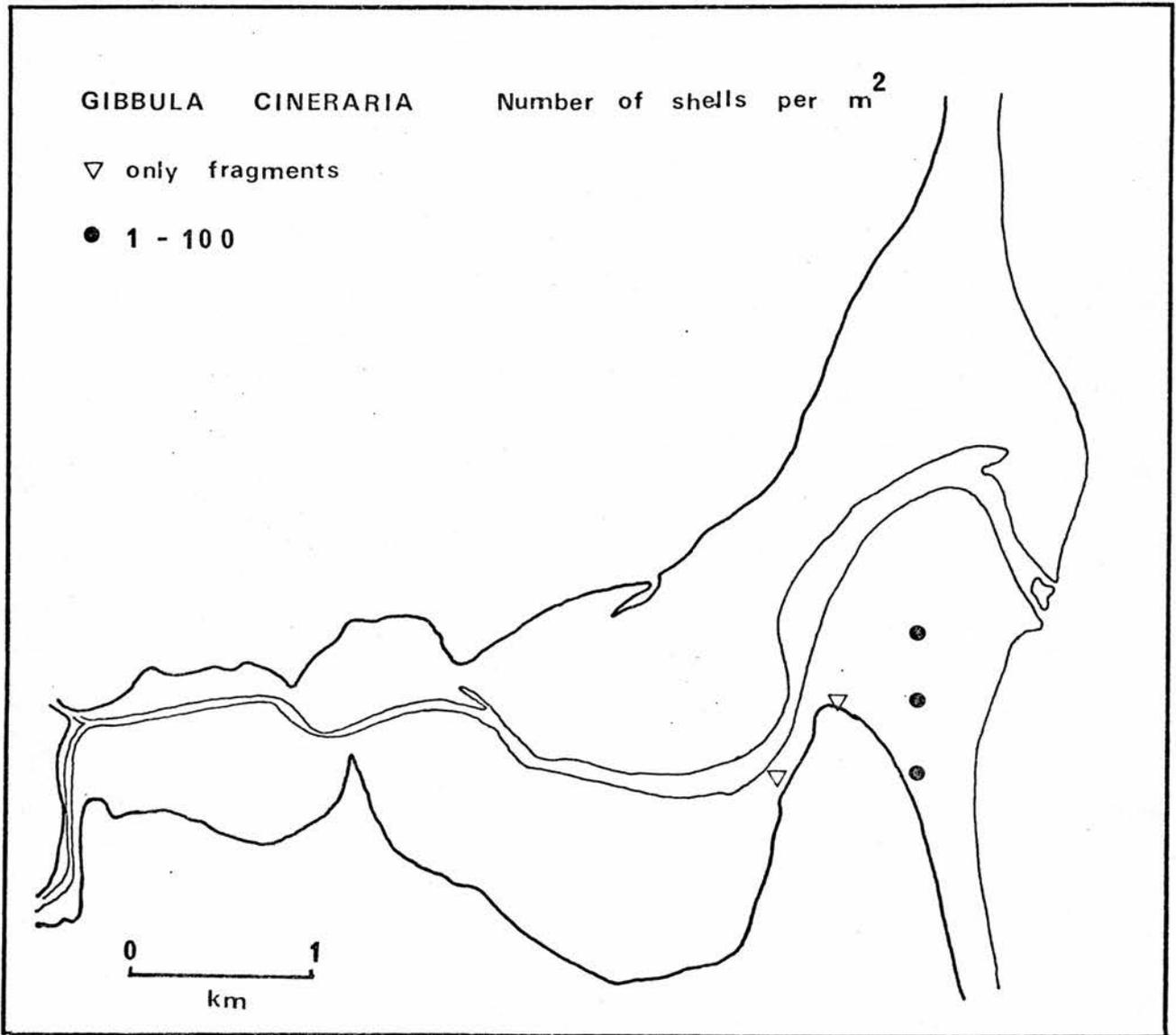


Fig.3.11. Distribution of Gibbula cineraria dead population.

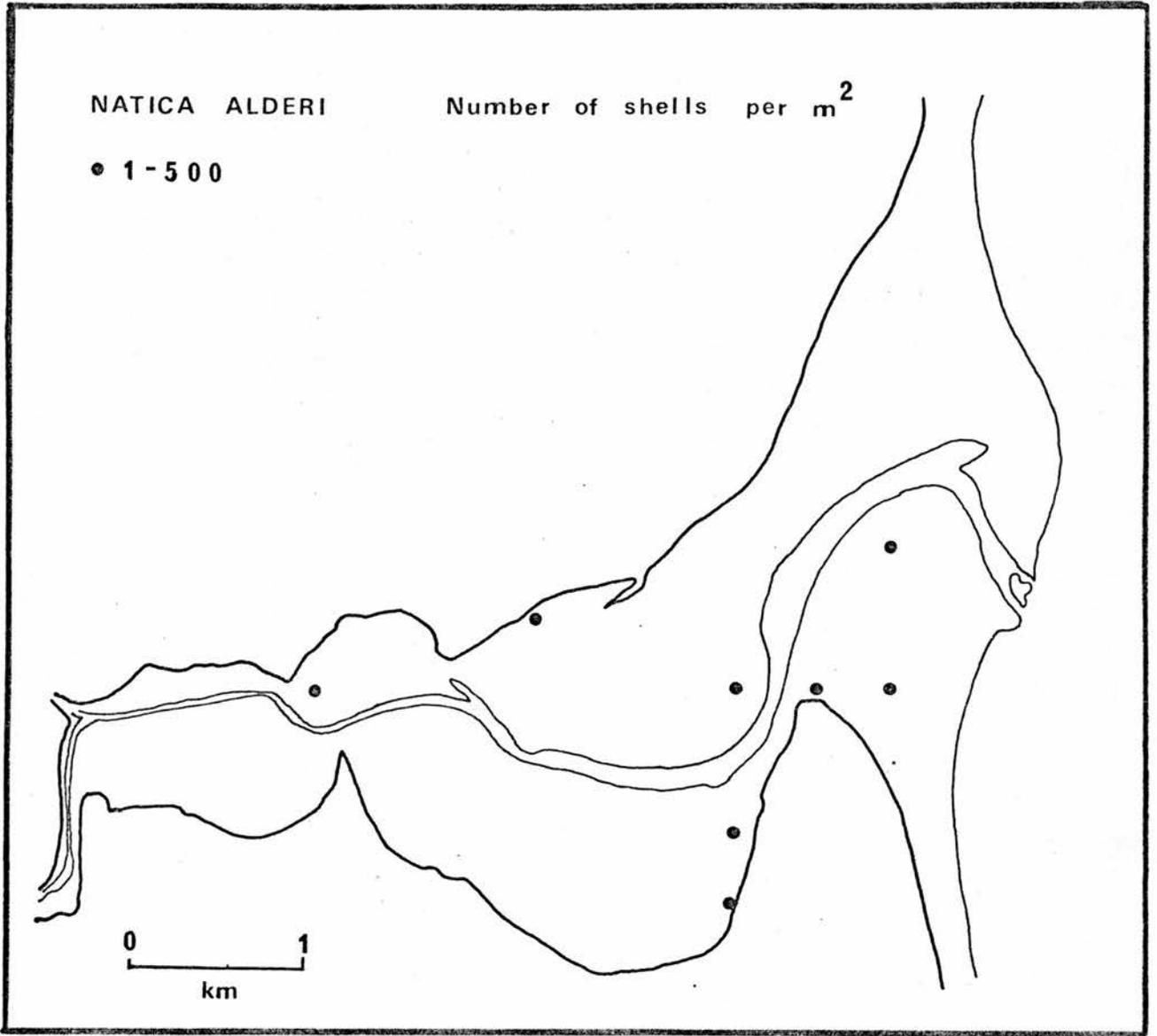


Fig.3.12. Distribution of Natica alderi dead population.

BUCCINUM UNDATUM

▽ presence

● 1 - 200 shells per m²

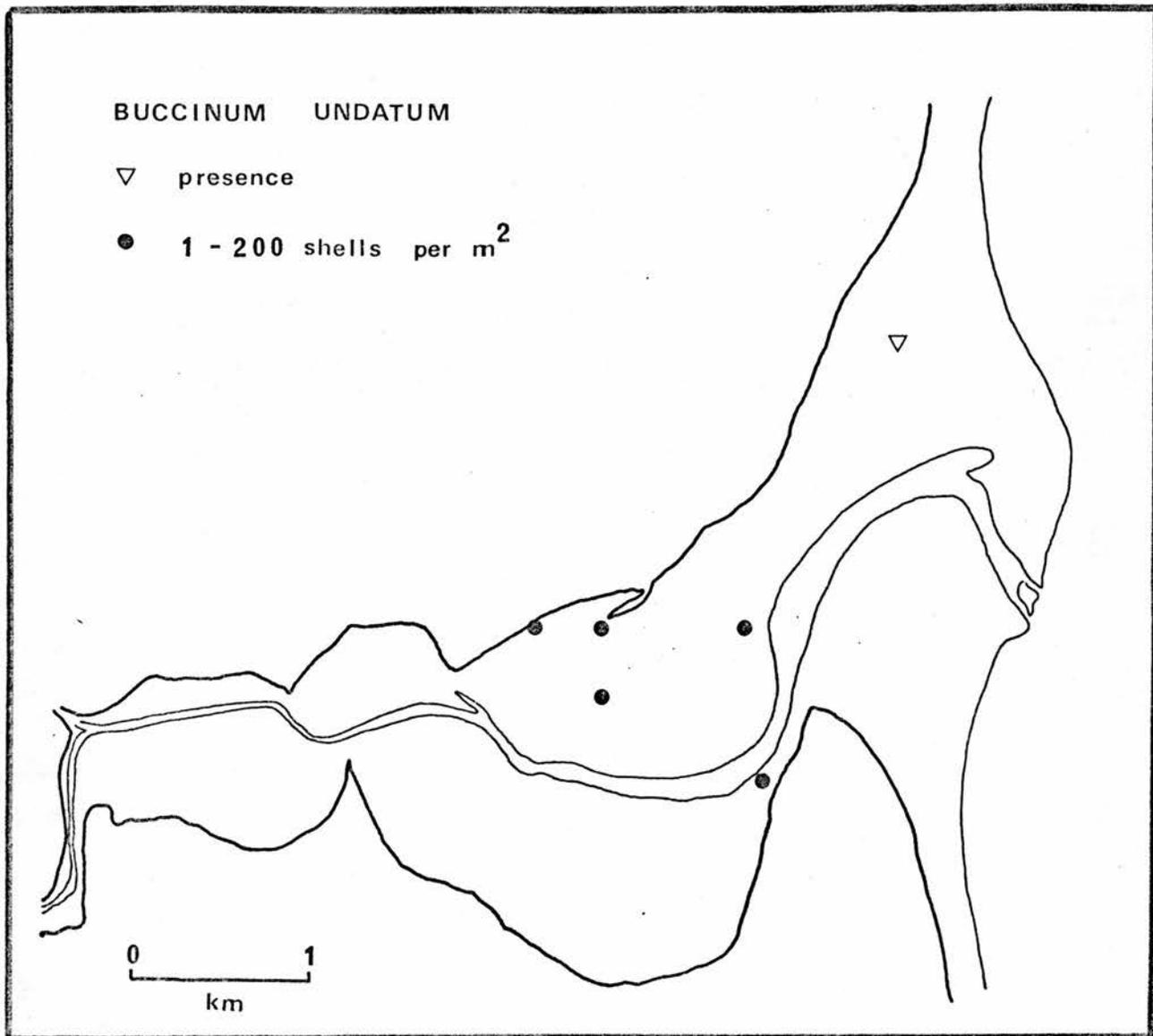


Fig.3.13. Distribution of Buccinum undatum dead population.

ACMAEA TESSULATA A.T

PATINA PELLUCIDA P.P

PATELLA SP. P.S

● 1-150 shells per m²

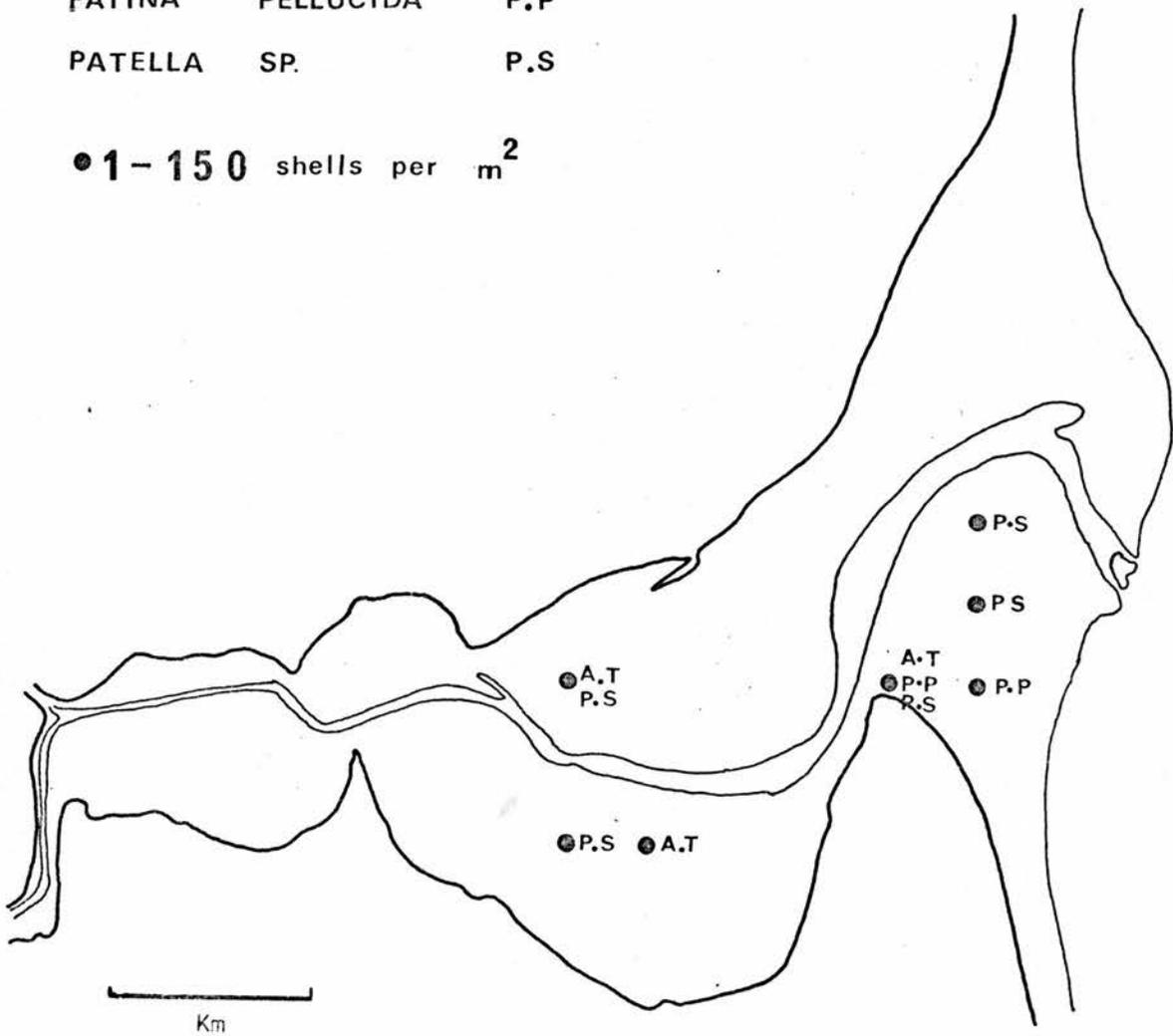


Fig.3.14. Distribution of Acmaea tessulata, Patina pellucida & Patella sp. dead populations.

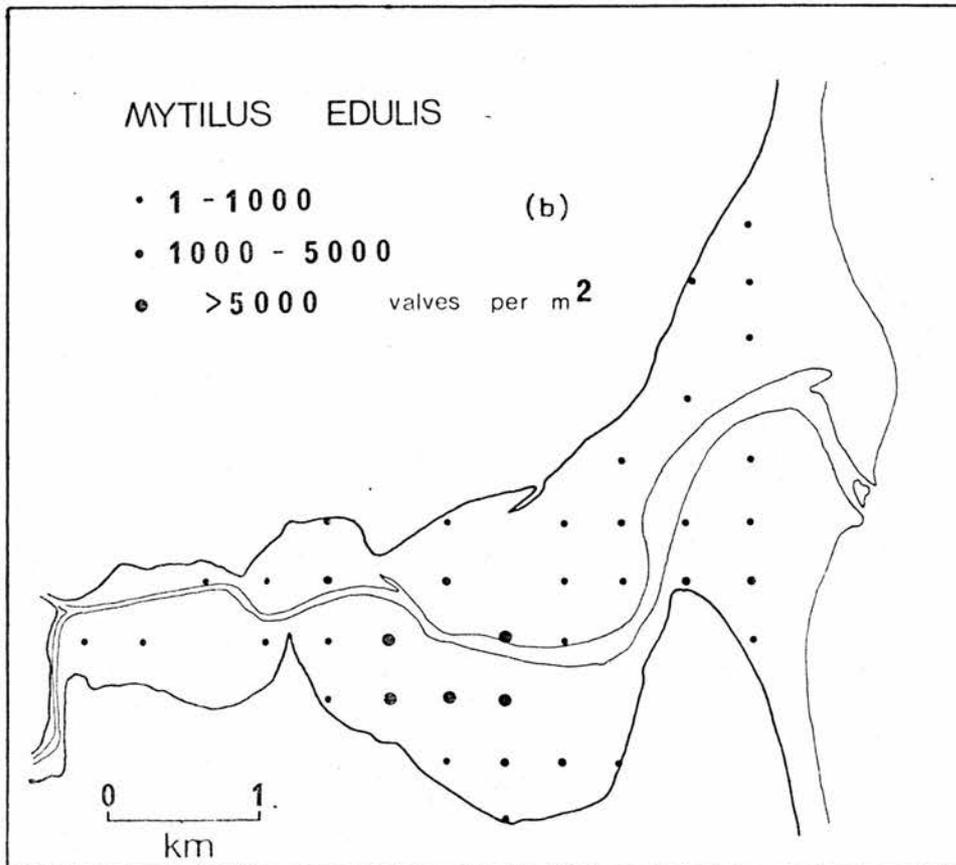
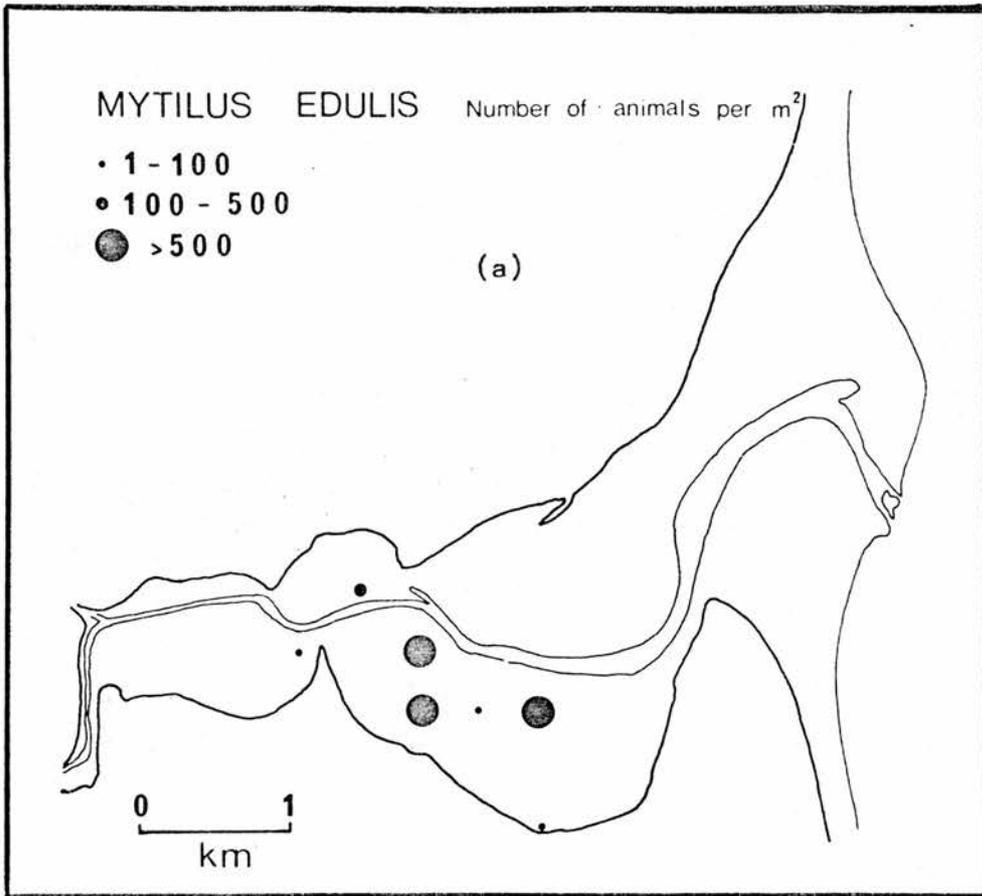


Fig. 3.15 Distribution of Mytilus edulis: (a) living & (b) dead populations.

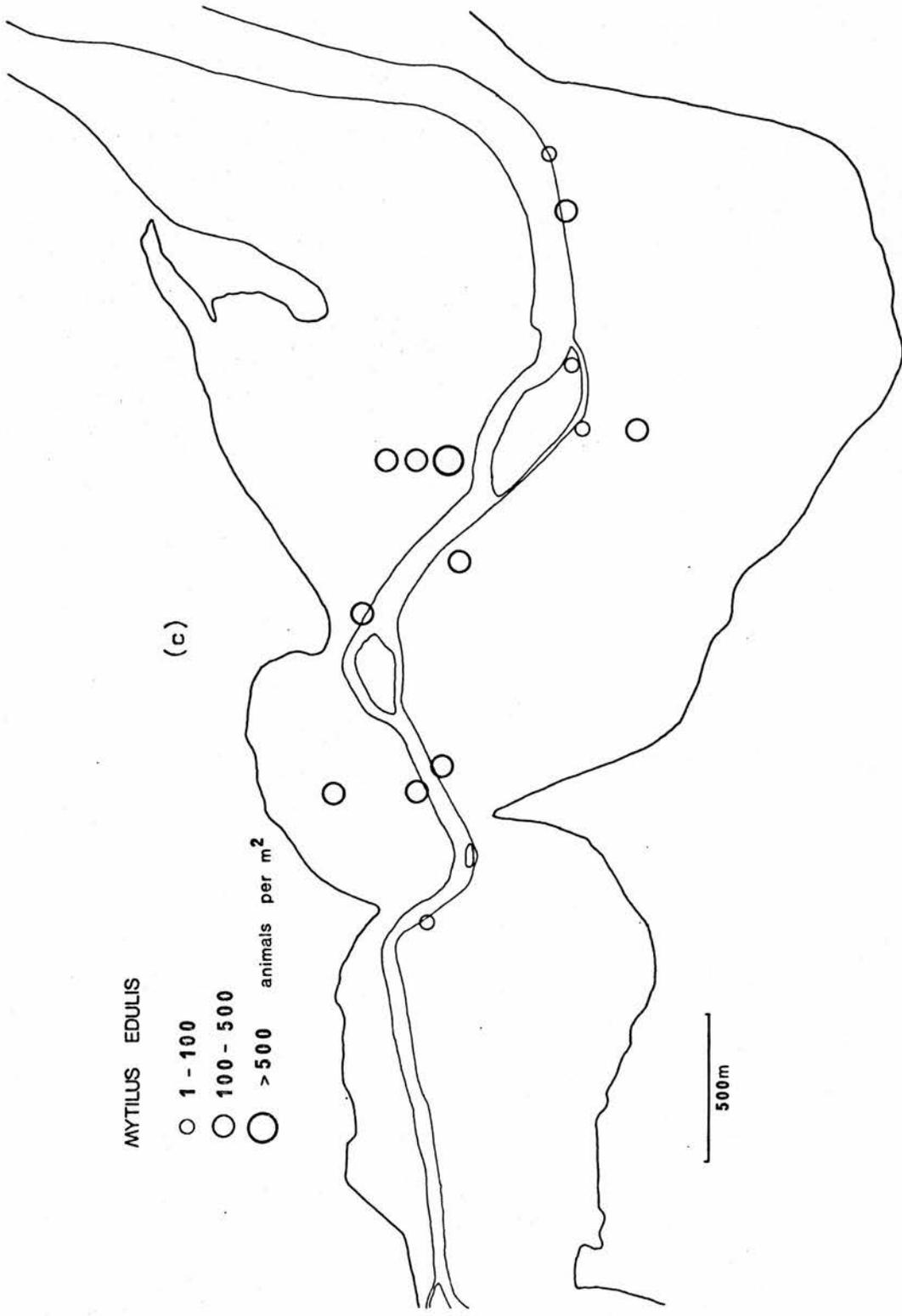


Fig.3.15.(c) Distribution of Mytilus edulis living population (Bell's 1978 data)

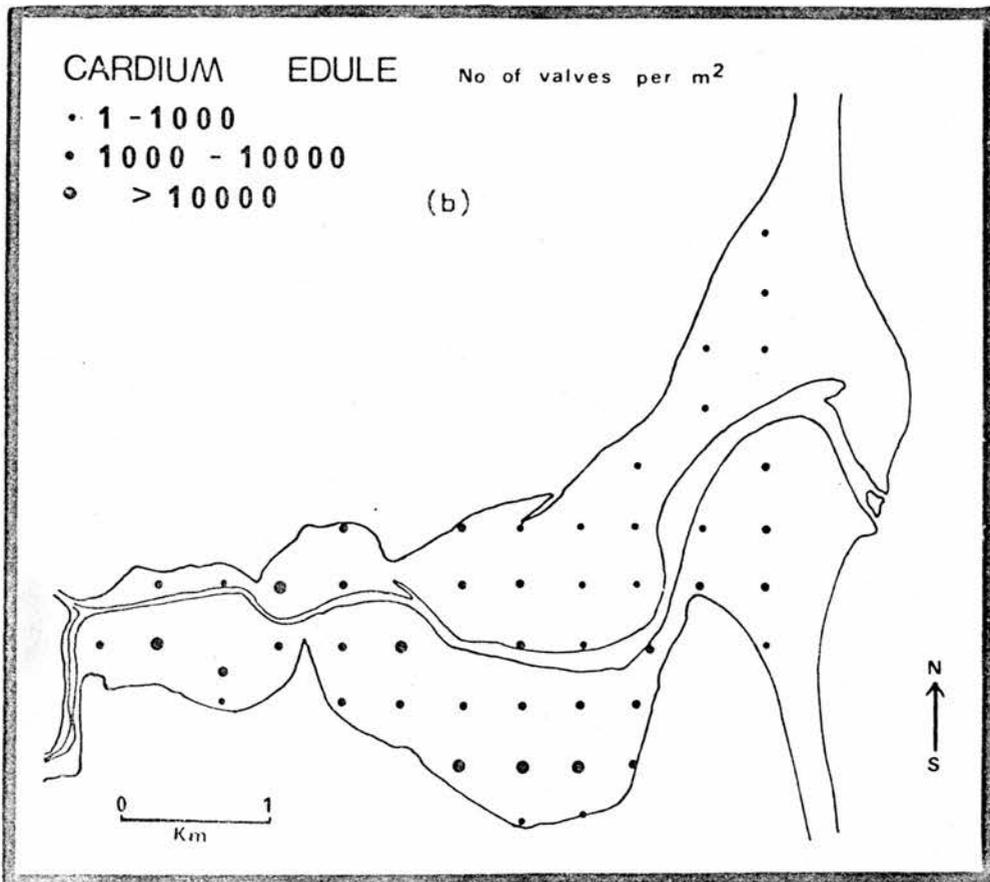
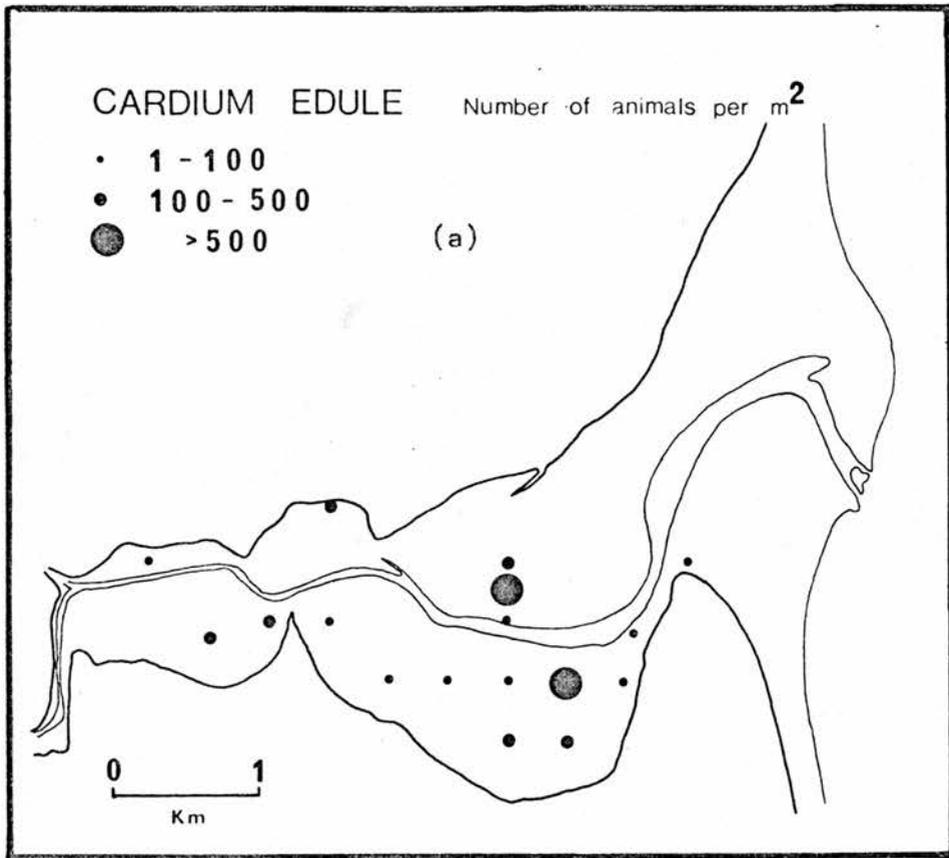


Fig.3.16. Distribution of Cardium edule: (a) living & (b) dead populations.

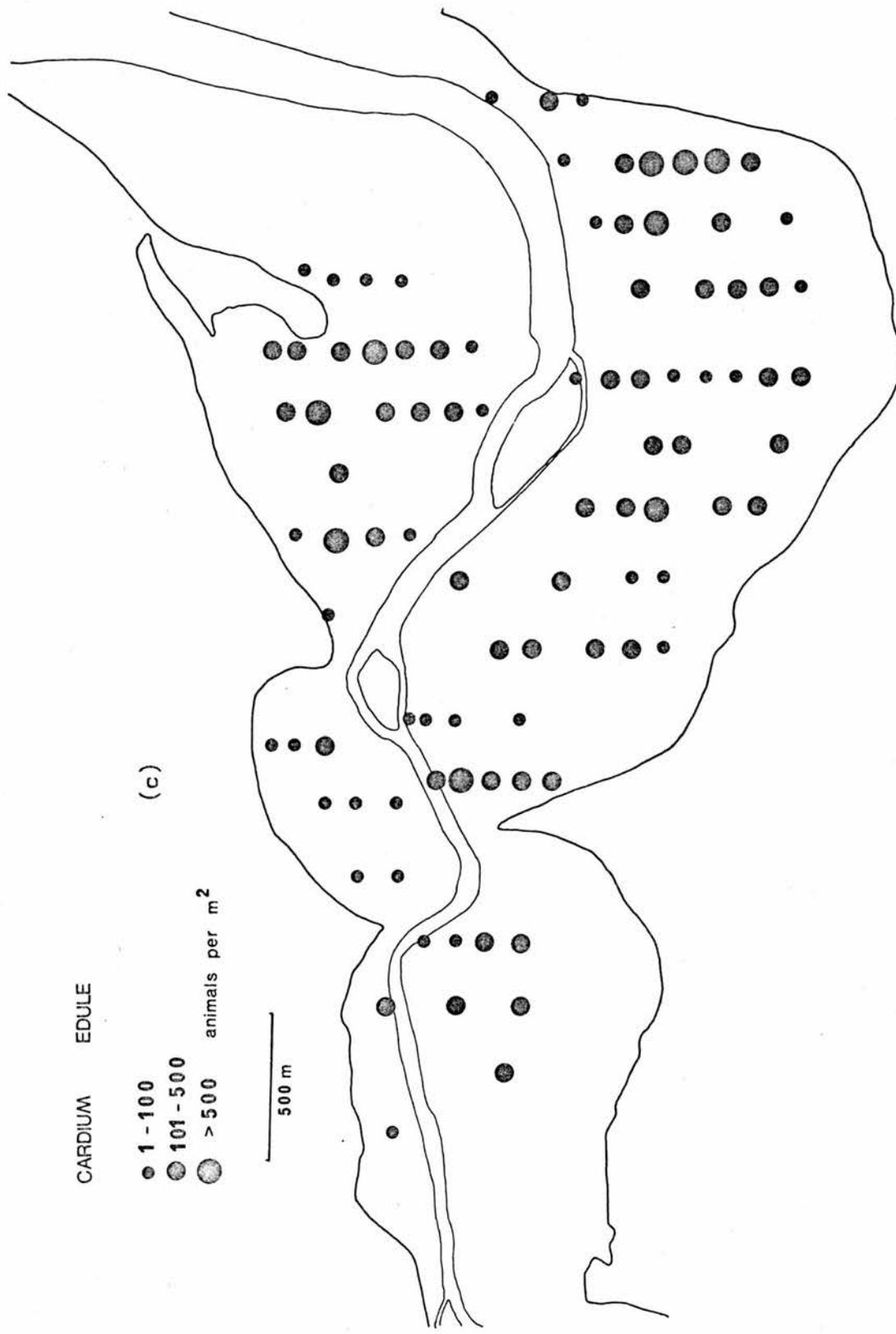


Fig.3.16 (c) Distribution of Cardium edule living population (Bell's 1978 data)

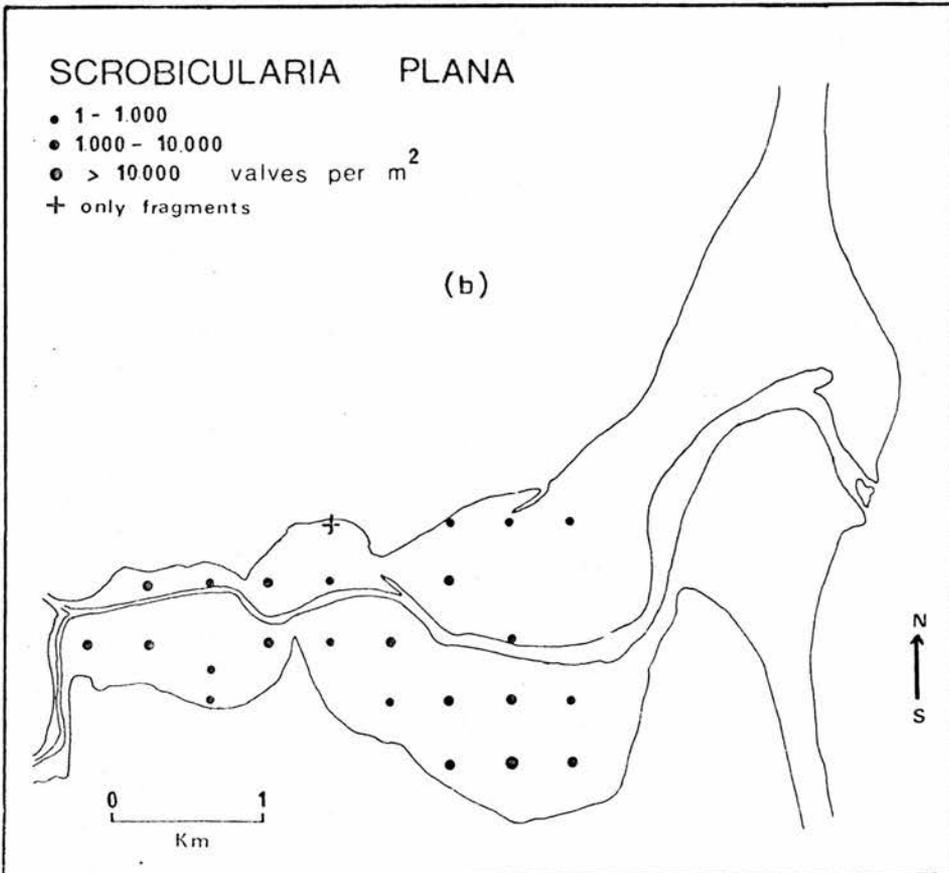
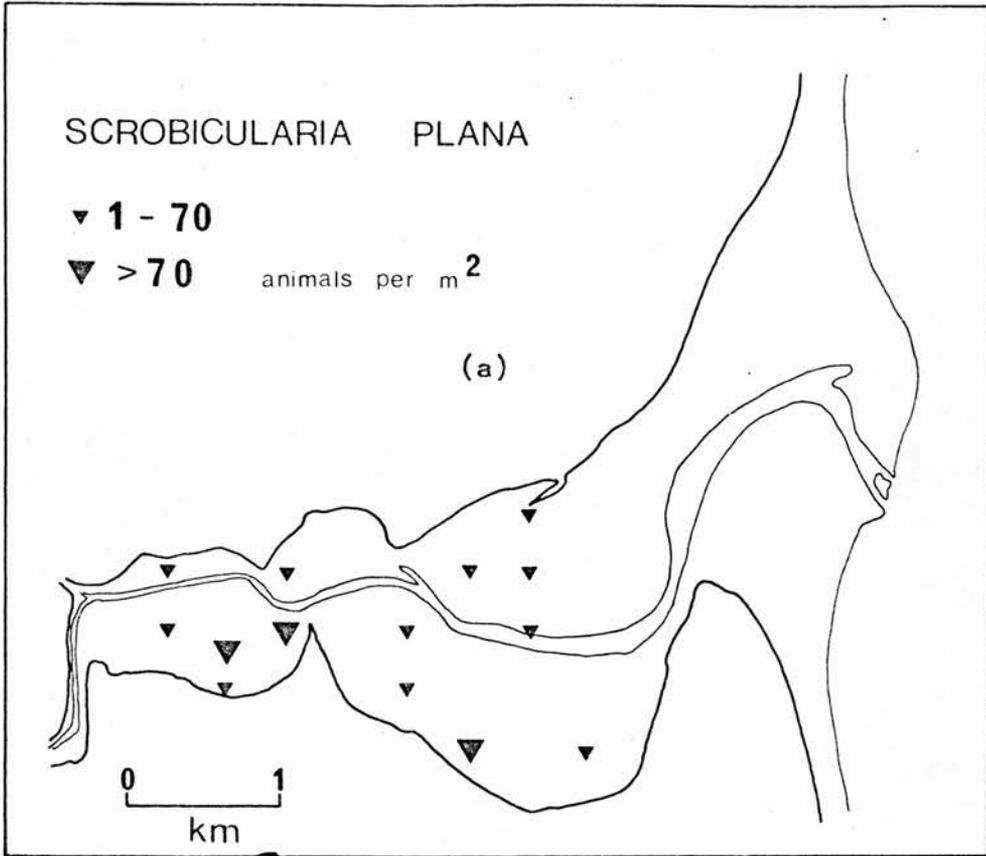


Fig.3.17. Distribution of Scrobicularia plana:
 (a) living & (b) dead populations.

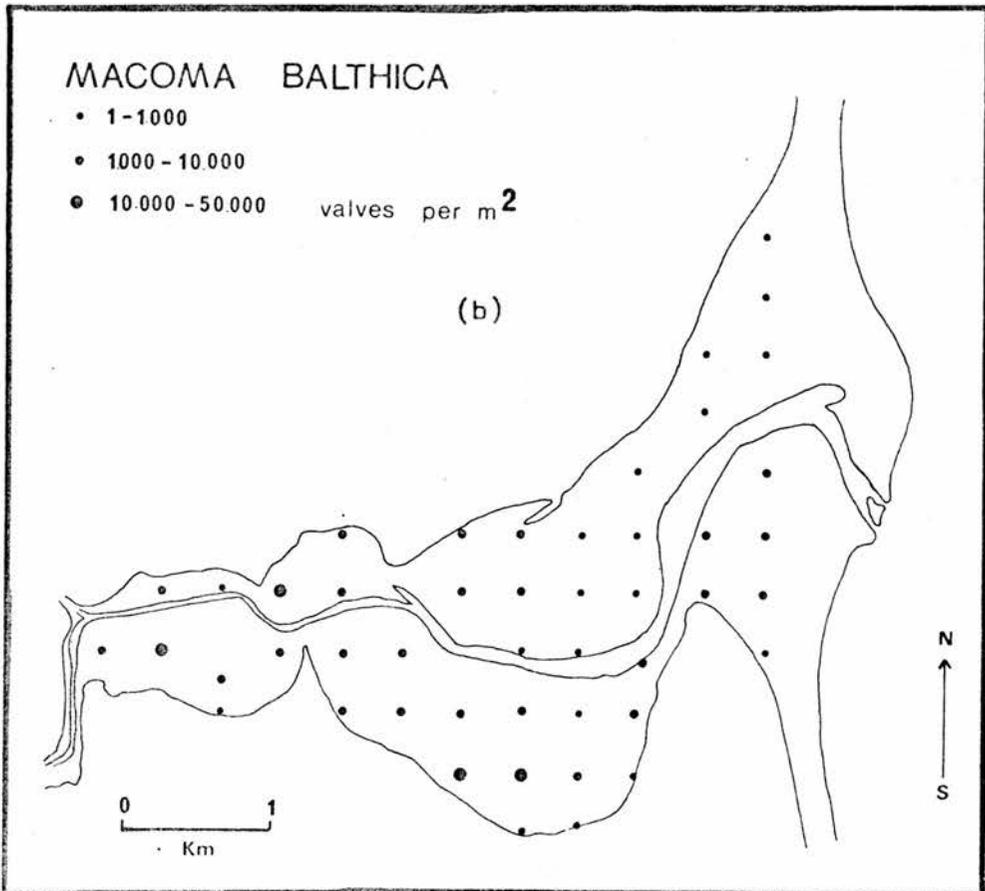
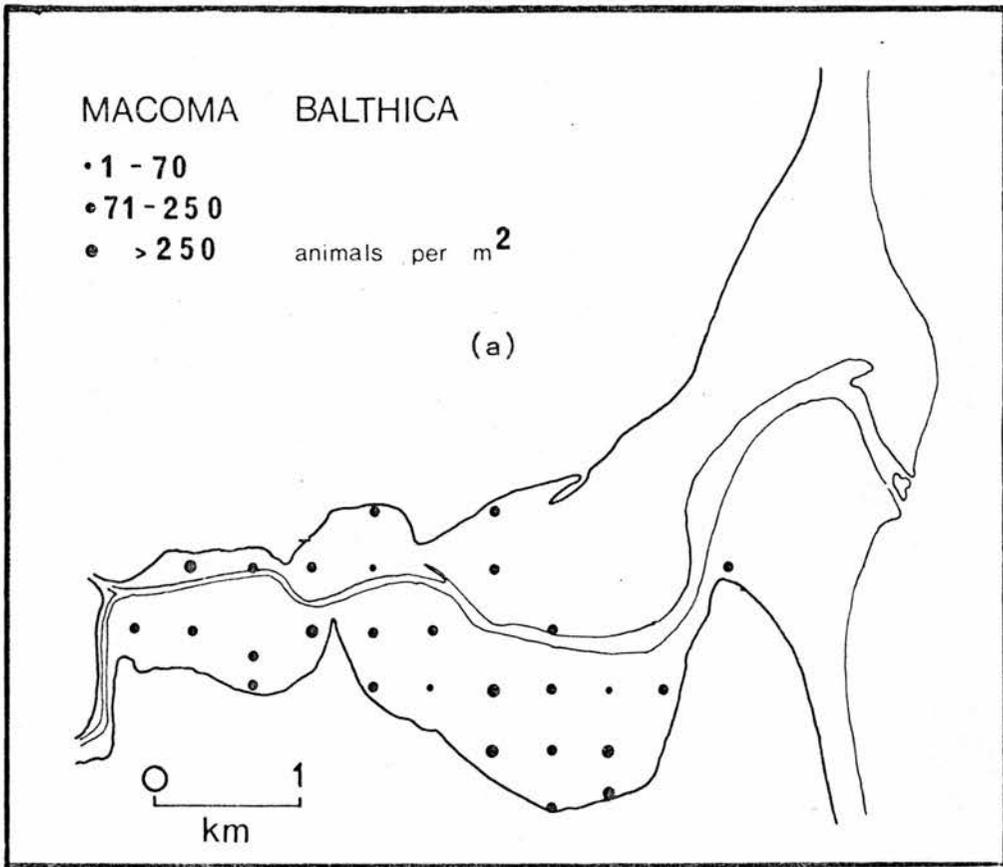


Fig. 3.18. Distribution of Macoma balthica: (a) living & (b) dead populations.

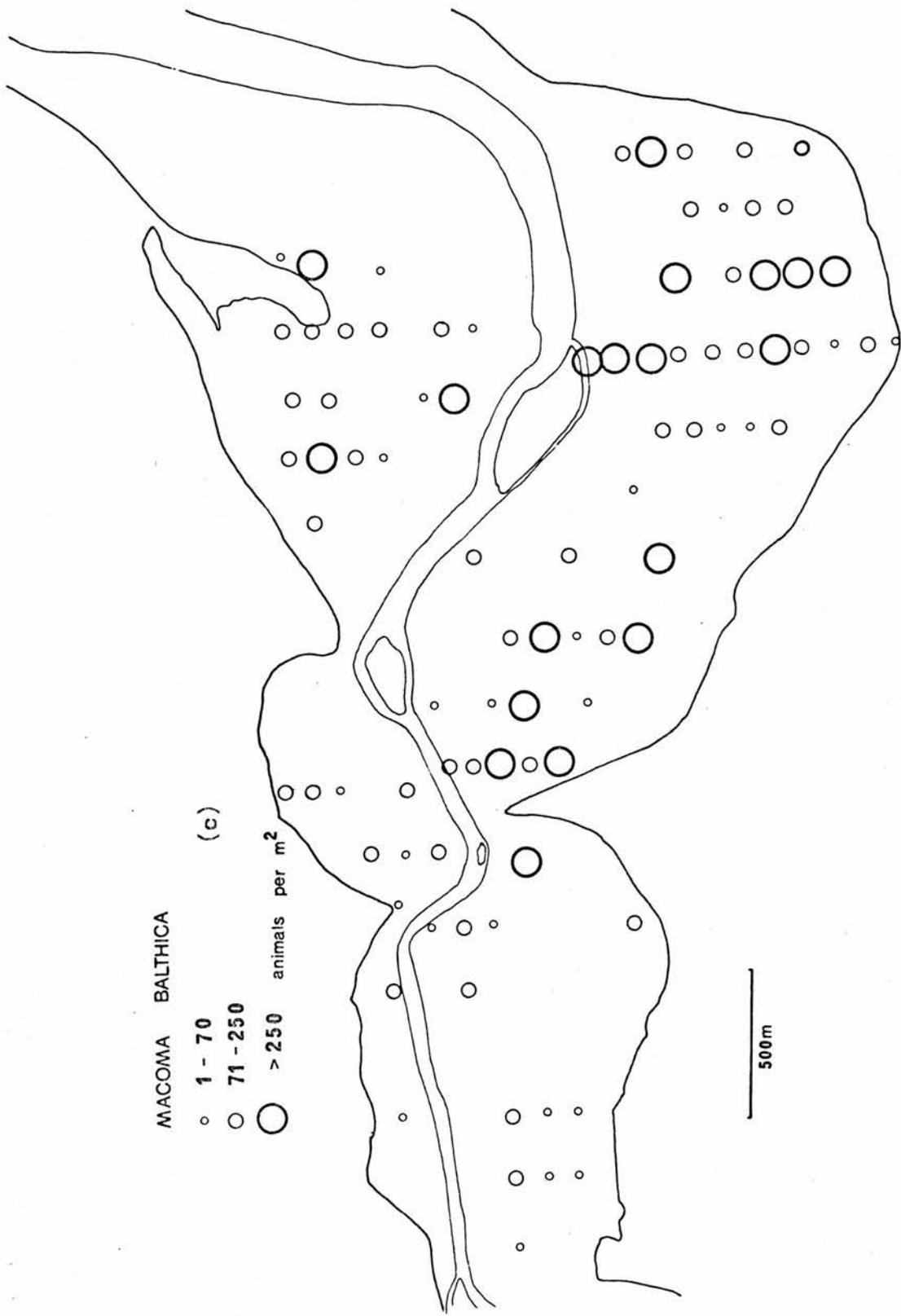


Fig.3.18. Distribution of Macoma balthica living population (Bell's 1978 data)

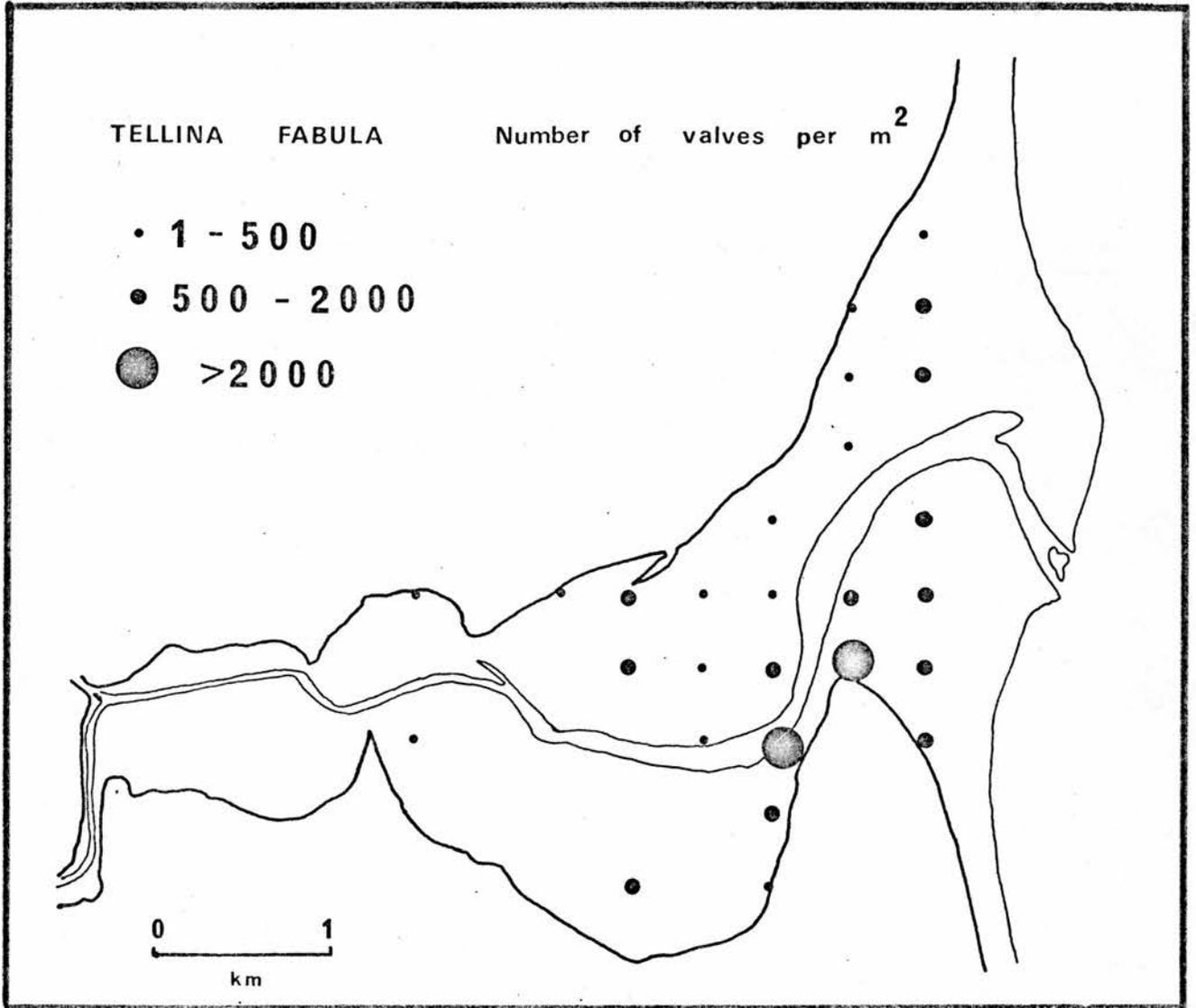


Fig.3.19. Distribution of Tellina fabula dead population.

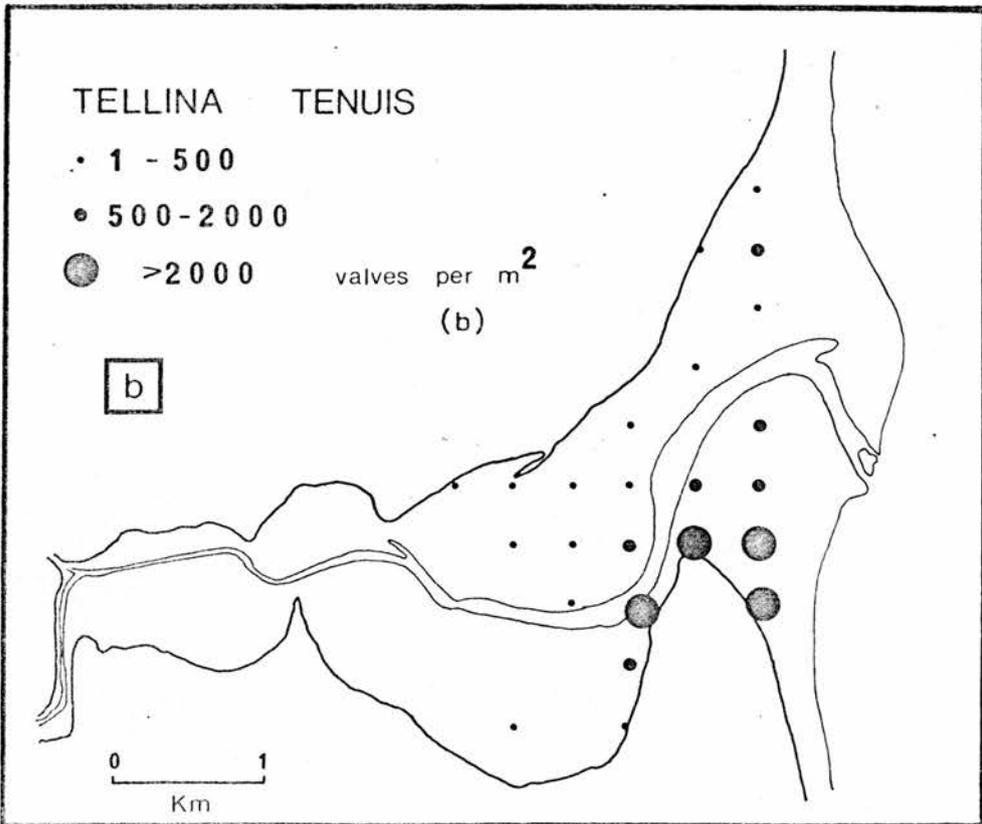
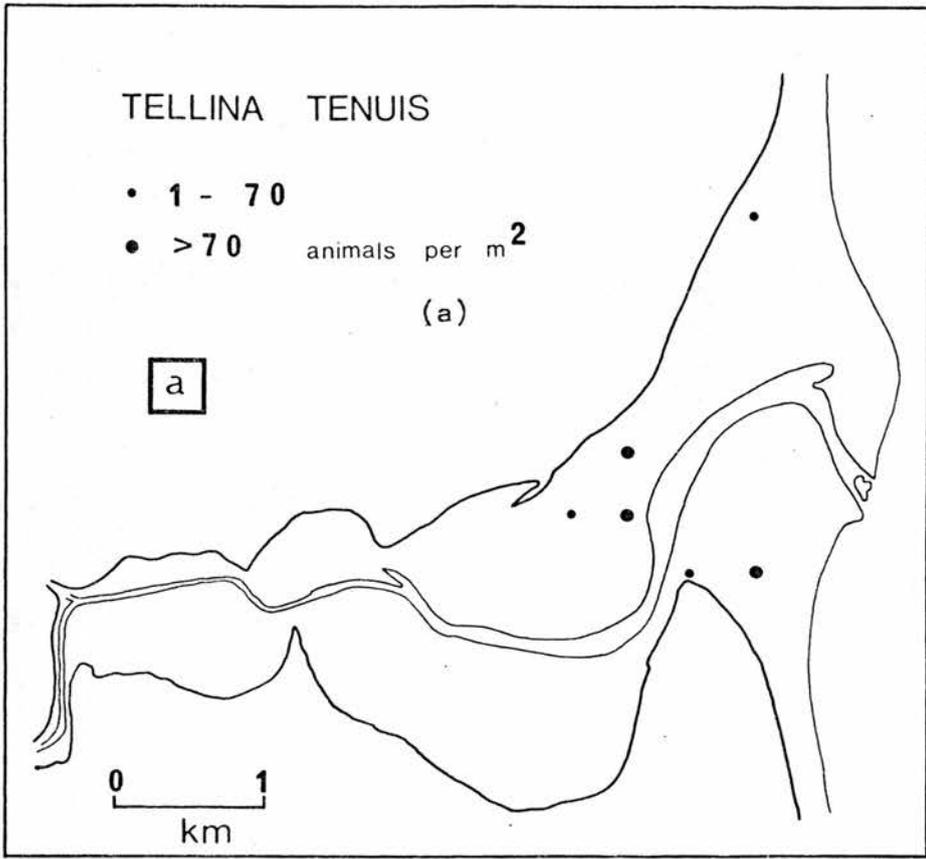


Fig.3.20. Distribution of Tellina tenuis: (a)living & (b)dead populations.

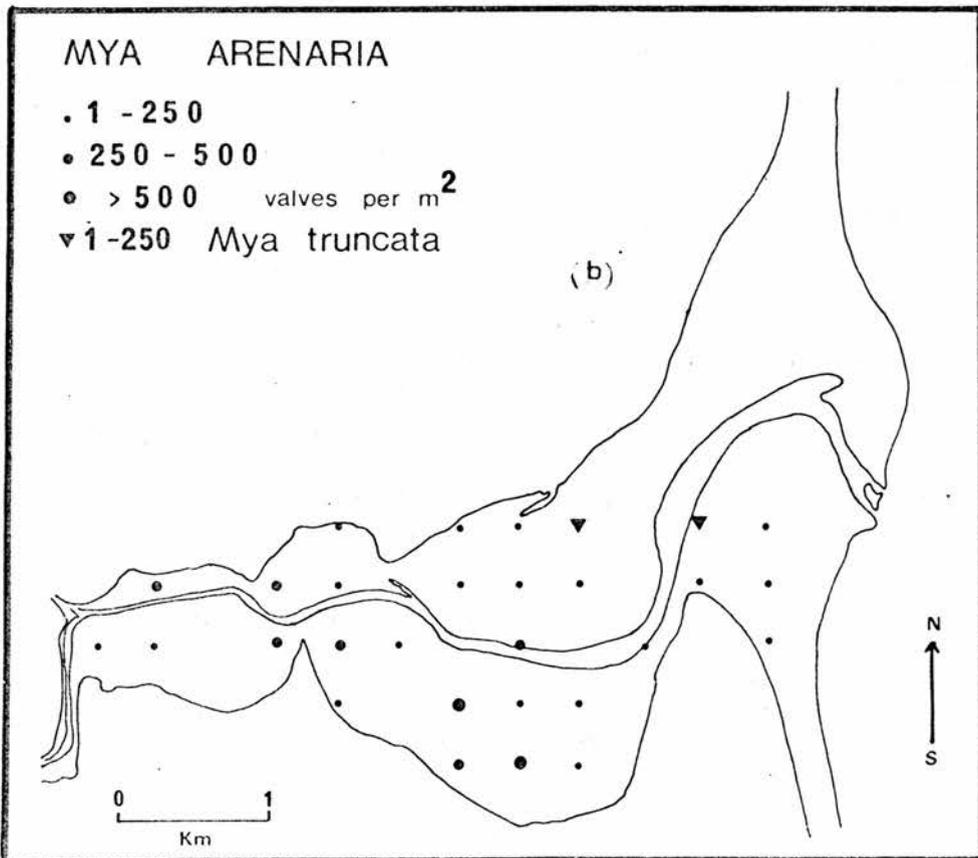
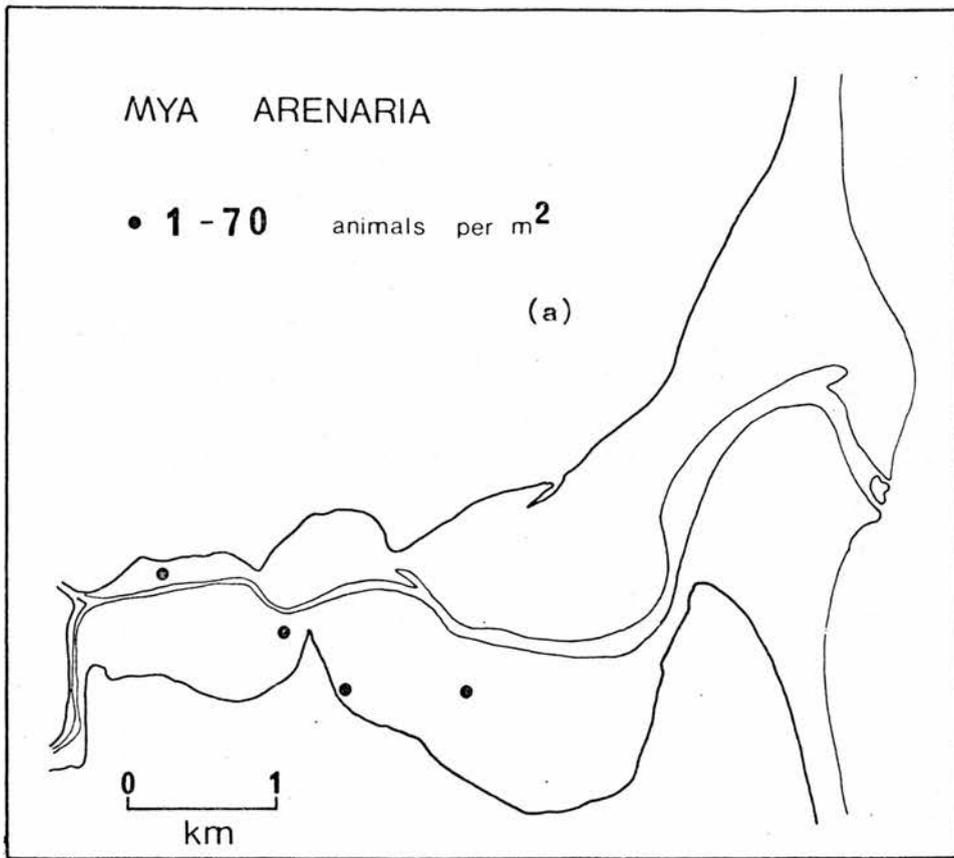


Fig.3.21. Distribution of *Mya arenaria* : (a) living & (b) dead populations.

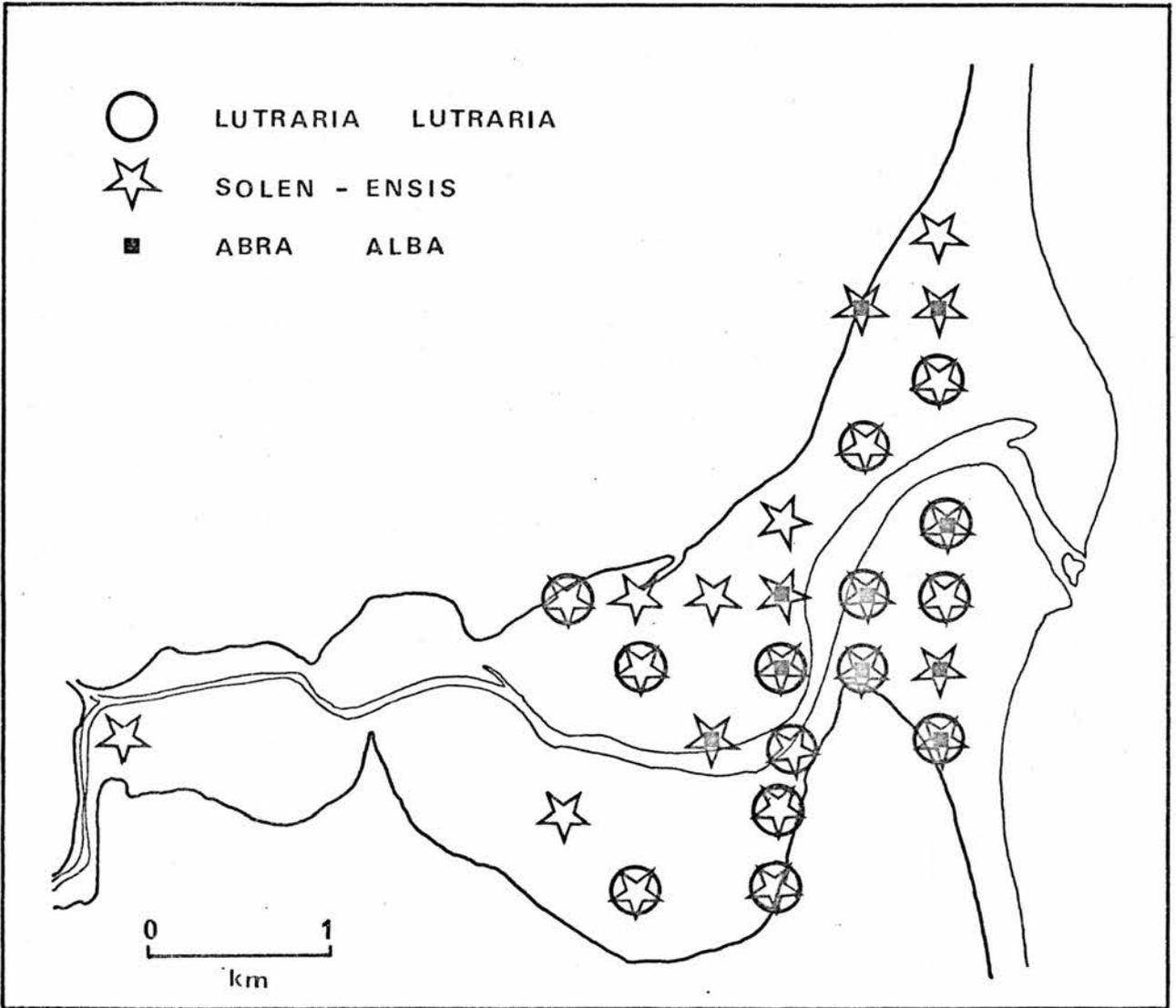


Fig.3.22. Distribution of Lutraria lutraria, Solen-ensis & Abra alba dead populations. Only presence of the above species is illustrated.

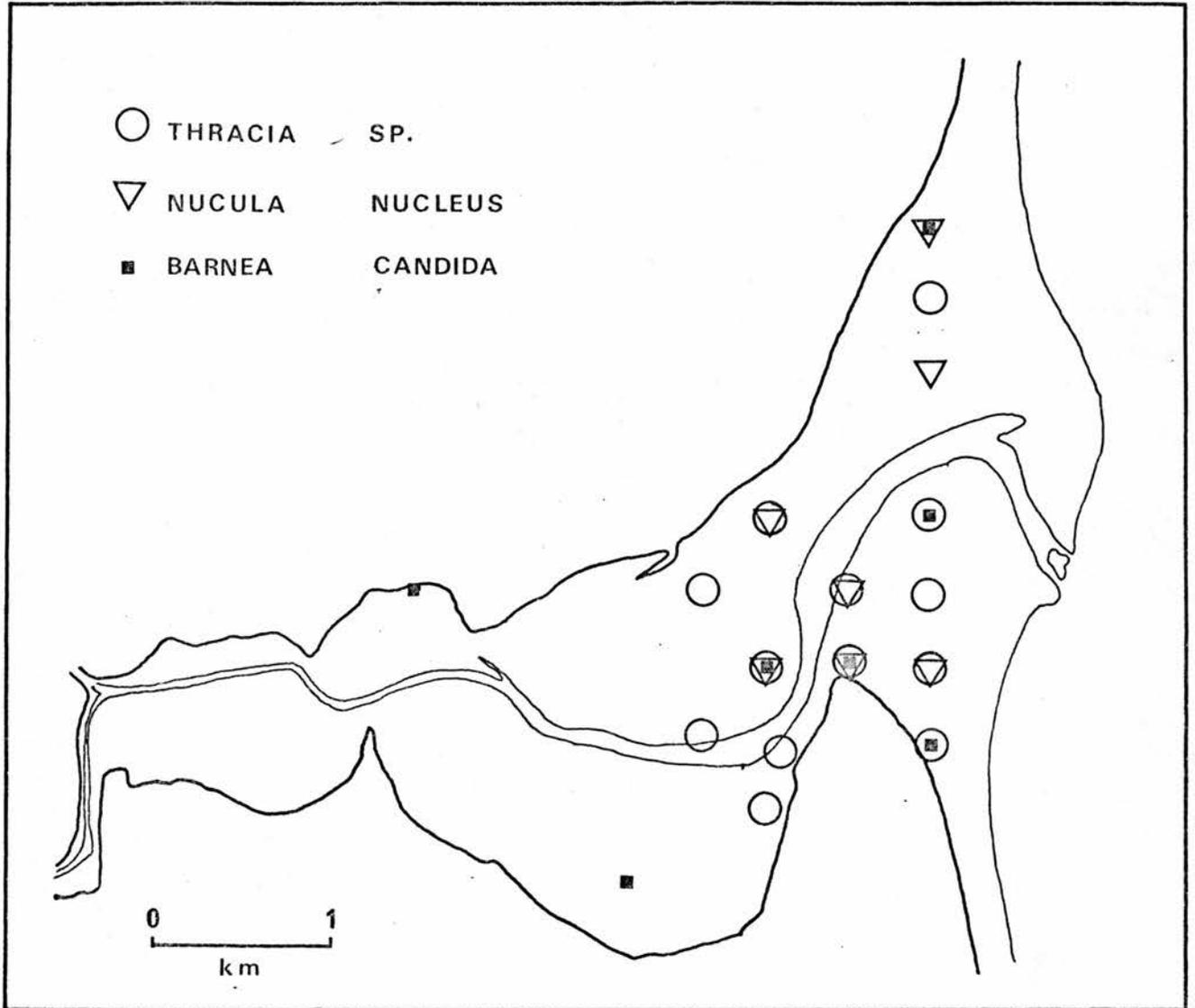


Fig.3.23. Distribution of Thracia sp. , Nucula nucleus & Barnea candida dead populations. Only presence of the above species is illustrated.

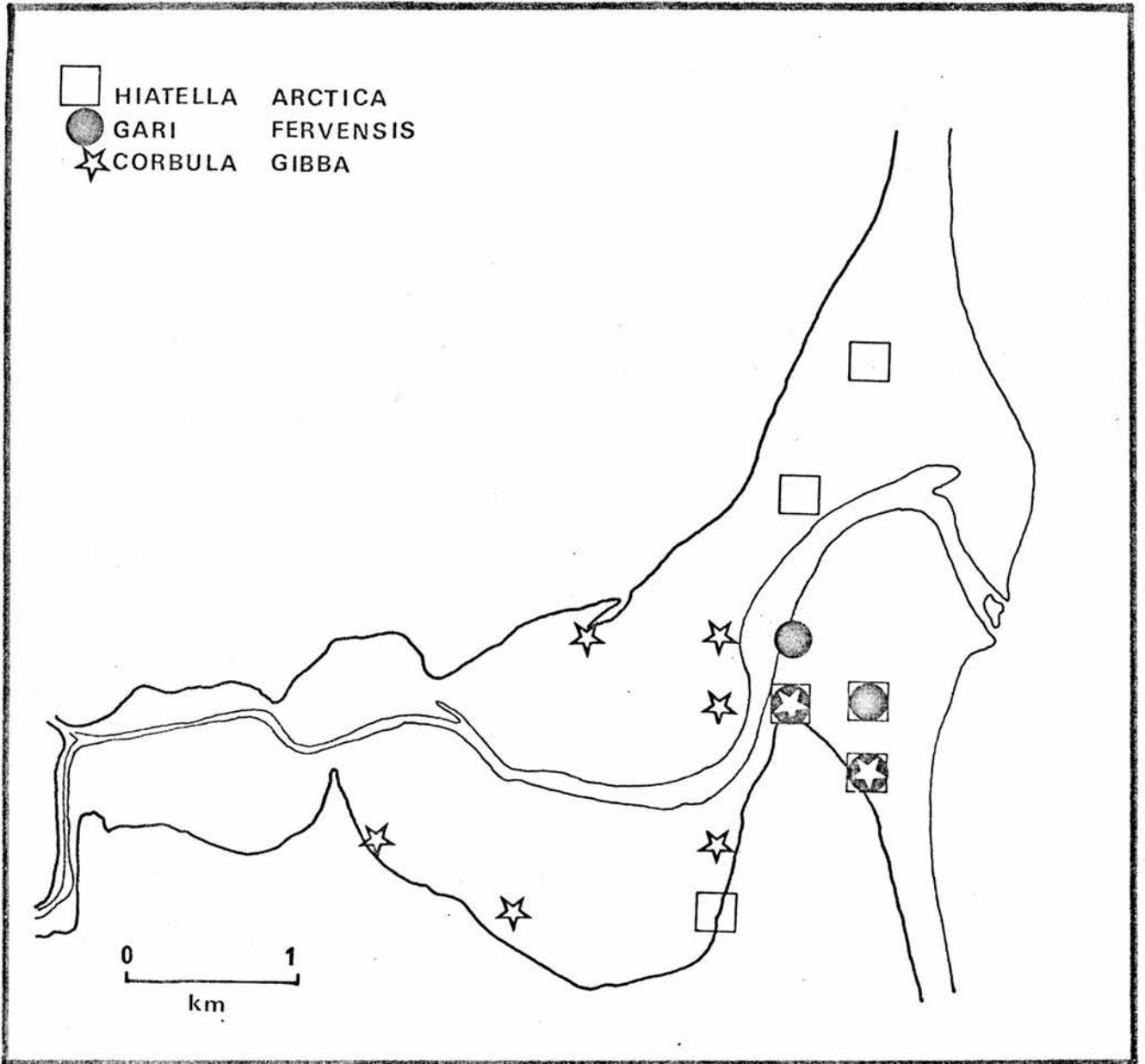


Fig.3.24. Distribution of *Hiatella arctica*, *Gari fervensis* & *Corbula gibba* dead populations. Only presence of the above species is illustrated.

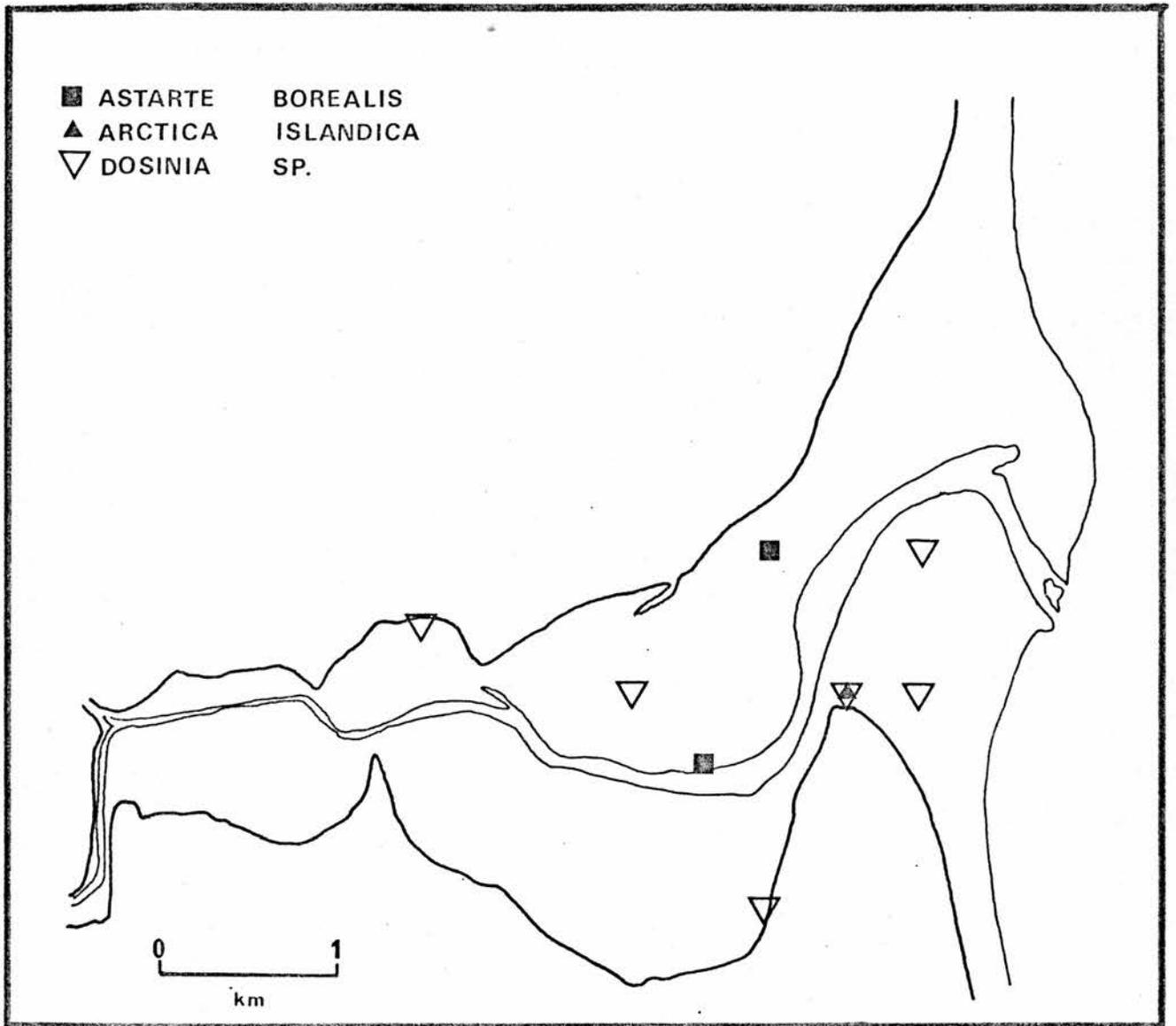


Fig.3.26. Distribution of *Astarte borealis*, *Arctica islandica*, & *Dosinia* sp. dead populations. Only presence of the above species is illustrated.

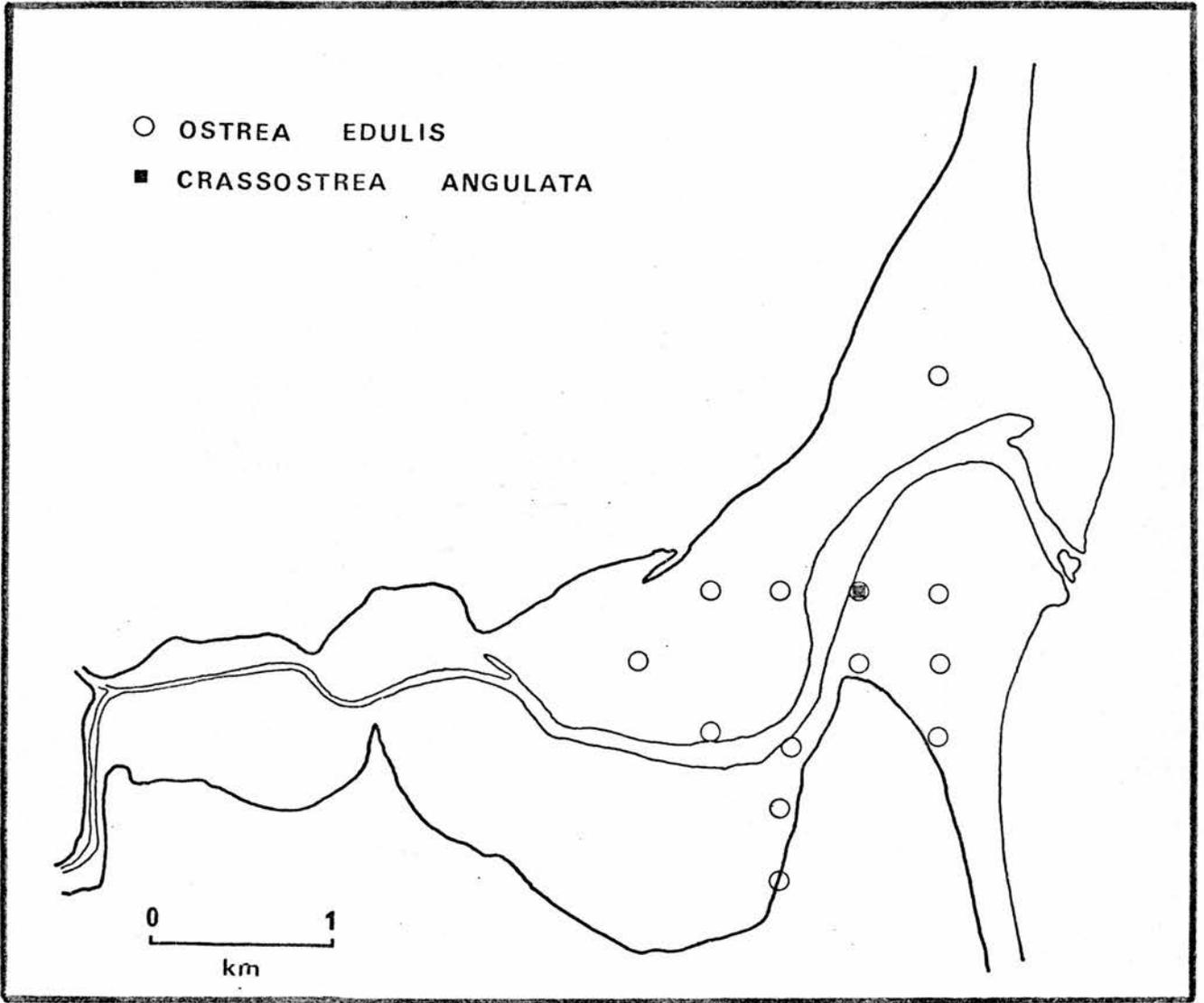


Fig. 3.27 Distribution of *Ostrea edulis* & *Crassostrea angulata* dead populations. Only presence of the above species is illustrated.

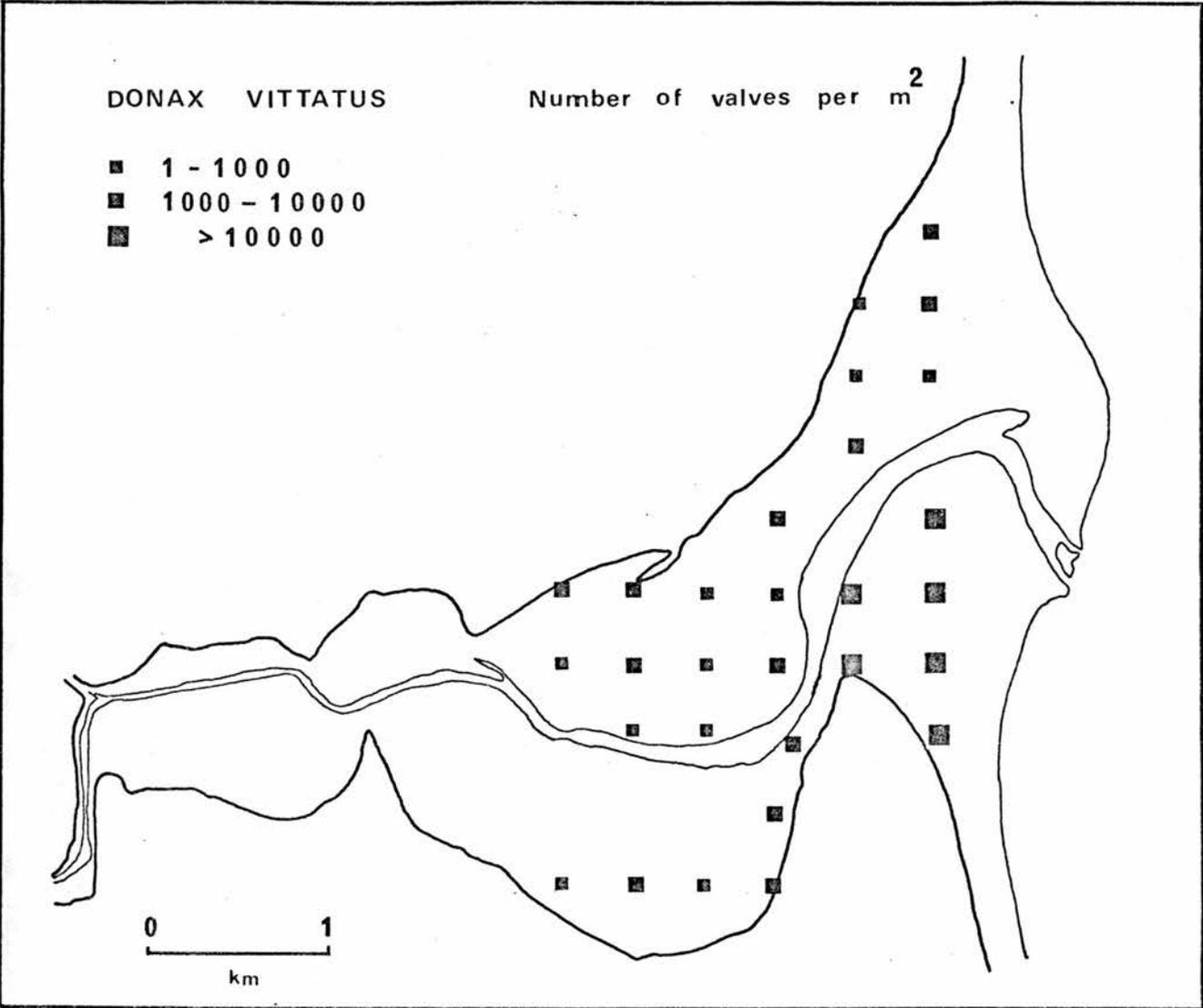


Fig. 3.28 Distribution of Donax vittatus dead population

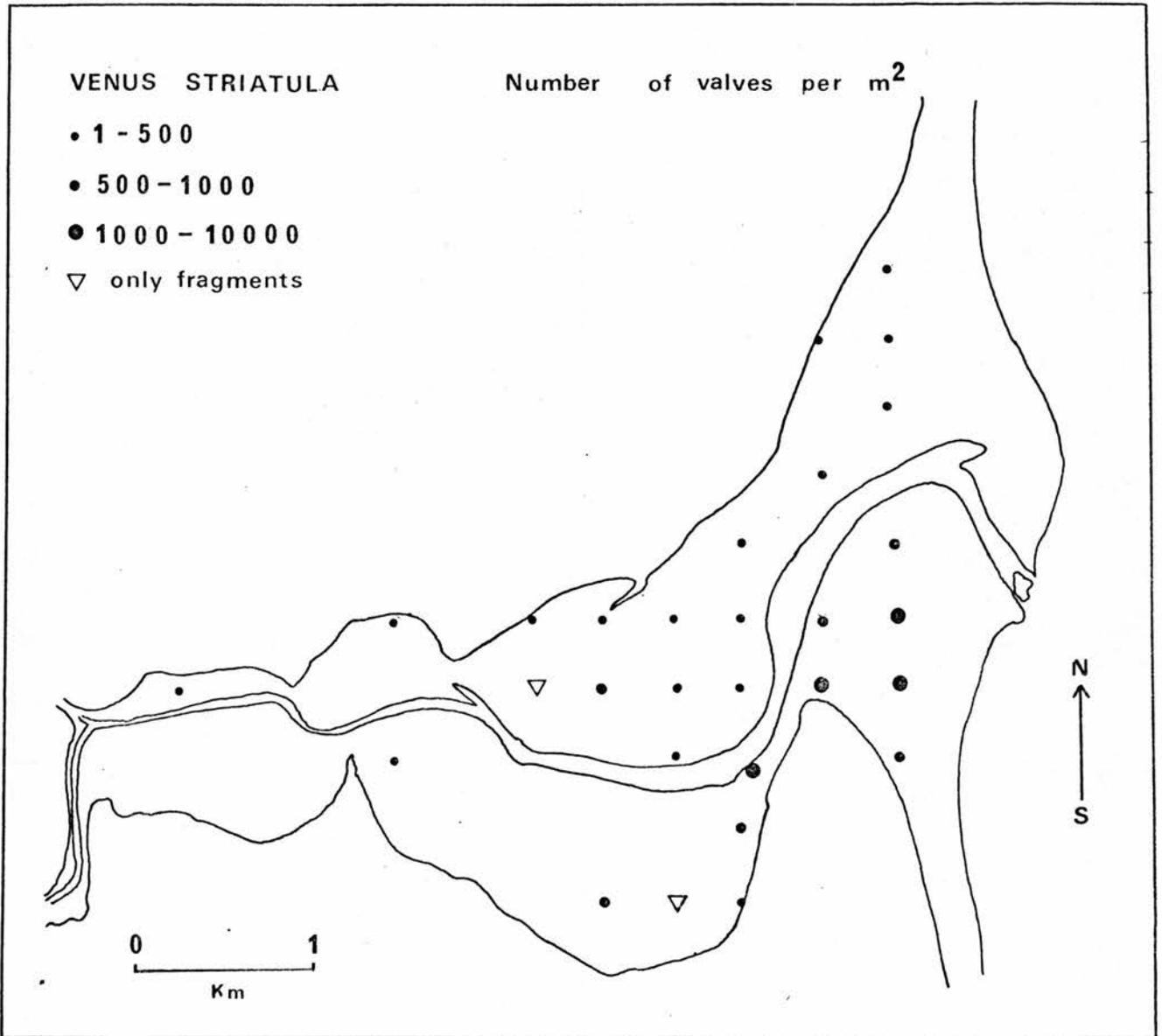


Fig. 3.29 Distribution of Venus striatula dead population

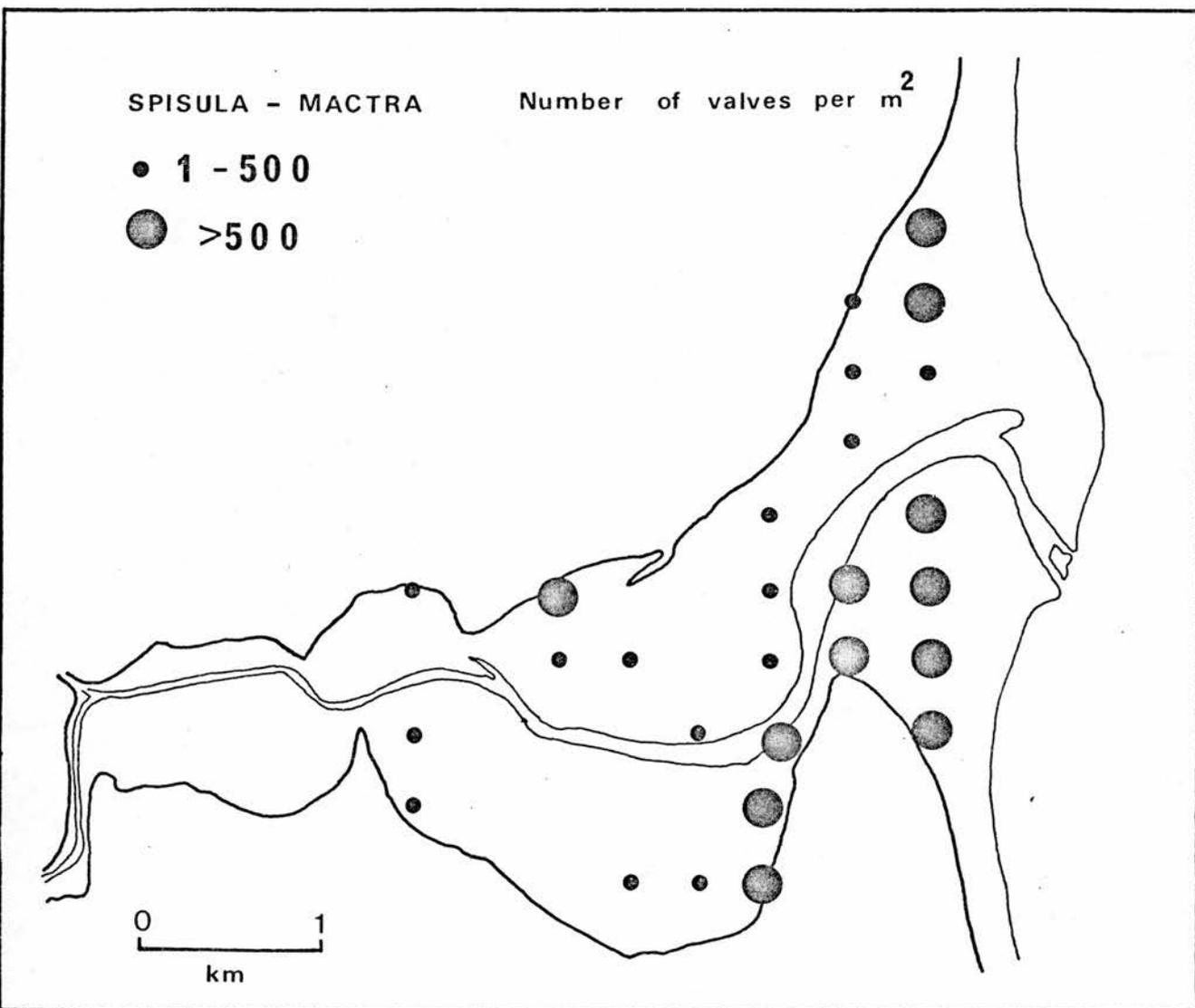


Fig. 3.30 Distribution of Spisula-Mactra dead population

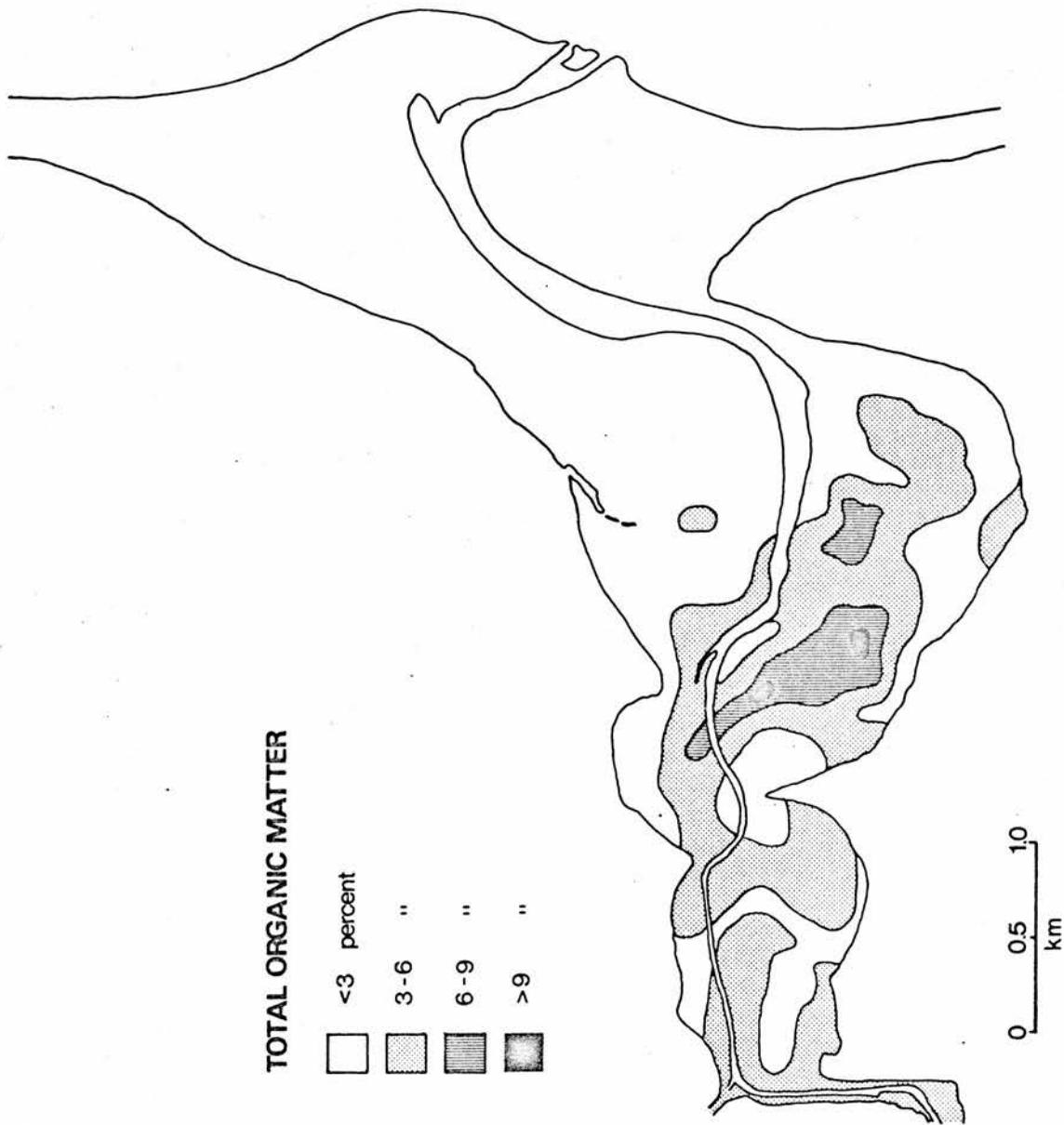


Fig.3.31. Distribution of total organic matter in the Eden estuary (after Eastwood, 1977).

CHAPTER 4.

PALEOECOLOGICAL CONSIDERATIONS

DIVERGENT VIEWS.

The subfossil populations of Mollusca have often been the object of paleoecological studies concerned with the discrimination of life and death assemblages.

"Life assemblage" is the definition given by Boucot (1953) as equivalent to "biocoenosis" meaning "community of life comprising the living organisms situated within a particular area". Other forms proposed for life assemblage are: "fossil community" by Craig (1953) "death assemblage buried in situ" by Johnson (1960) and "living population" by Craig and Oertel (1966).

"Death assemblage" is also suggested by Boucot (1953) to mean, "thanatocoenosis" implying a "community of death, comprising the aggregated remains of organisms that in many cases never constituted a biocoenosis but were brought together by physical agencies such as wave and current action, which operated after they died". Other definitions given for death assemblage are: "fossil assemblage" by Craig (1953), "dead population" by Craig and Oertel (1966) and "transported fossil assemblage" by Fagerstrom (1964).

As Rollins and Donahue (1975) state, many palaeo-ecologists have been unwilling to examine seriously fossil assemblages from the point of view that such assemblages might reflect once-living-organism communities.

Imbric (1956) suggests that the paleontologist, lacking contrary evidence, must often make the assumption that specimens found together at the same locality did in fact live together.

Käesler (1966) in defining his biofacies takes as given that effects of transportation and mixing of faunas are not great enough to obscure biofacies relationships completely.

However the assumptions have become realities in many cases. Recent extensive studies have revealed locations where the fossil assemblages were buried in situ. Four such cases are known.

1. Johnson (1965) notes that "the death assemblages of Tomales Bay appear to represent with sufficient accuracy, for most paleoecological purposes, the species composition of the life assemblages from which they were derived."

2. Warne (1971) examining the Molluscan assemblages in Mugu lagoon, states "Species and assemblages of Mollusca shells accumulating in the lagoon undergo little postmortem transportation. There is a good correlation between live and dead representatives of the same species in the same samples".

3. Turney and Perkins (1972) on the basis of size frequency distributions and condition of shells, conclude that transportation of shells larger than silt size is not significant in Florida Bay and that wind driven currents can move shells around locally and on the edges of the mud banks, but no faunal dislocations are produced.

4. Peterson (1976) states: "within sample comparisons at Mugu Lagoon and at Tijuana Slough revealed reasonably good fidelity between the presence and absence of living and dead species, indicating that negligible post-mortem mixing had occurred within the high energy sand habitat".

LIFE DEATH ASSEMBLAGES DISCRIMINATION CRITERIA

Discrimination of fossil assemblages as life and death assemblages is difficult and one must evaluate as many criteria as can be reasonably applied. The criteria suggested by various workers (Boucot (1953), Olson (1957), Boucot et al. (1958),

Johnson (1960), Craig and Hallam (1963), Sheldon (1965), Craig and Oertel (1966) and Hallam (1967) and summarized by Fagerstron (1964) are:

- 1) size frequency distributions
- 2) ratio of articulated to disarticulated valves
- 3) ratio of opposite valves
- 4) dispersion of fossils
- 5) population density
- 6) community density
- 7) faunal composition and diversity
- 8) orientation of clastic particles (including fossils)
- 9) texture
- 10) sorting and structure of sedimentary aggregate
- 11) lithofacies relationships
- 12) surface condition of fossils
- 13) ratio of whole to fragmented valves.

One more criterion investigated in PART II, and used by Maddocks (1966) and Warne (1971), is by comparison of a) communities (biofacies) and b) distribution patterns (biotopes) constructed by numerical analysis and based on the separate live and subfossil assemblages in all of the samples.

The Eden estuary dead Mollusca populations are in fact subfossil populations. The term "subfossil" is used here to denote remains of animals found lying or buried in sediment, that are not strictly recent but not "pre-historic" either. The above criteria applied to fossil assemblages can also be applied to subfossil ones and their evaluation in the Eden estuary subfossil molluscan assemblages is attempted. Most of the criteria deal with bivalves and only a few can be applied to gastropods.

Direct detailed observations on the shells of each species in each sample from the Eden estuary, revealed that the following criteria can be applied in distinguishing a subfossil life assemblage in an estuarine environment:

- (1) dispersion of fossils
- (2) faunal composition and diversity
- (3) population density
- (4) surface condition of shells
- (5) ratio of opposite valves

Other criteria tested but not found applicable in the Eden subfossil assemblages are:

- (1) size-frequency distributions
- (2) ratio of articulated to disarticulated valves
- (3) ratio of whole to fragmented valves

These criteria are discussed below.

SUCCESSFULLY APPLIED CRITERIA

1. DISPERSION OF (SUB)FOSSILS

The dispersion of (sub)fossils refers to the horizontal and vertical distribution of individuals belonging to the same subfossil species. The horizontal dispersion of all Mollusca species was examined in CHAPTER 3 and found most valuable in recognising life assemblages. The distributions of dead populations according to the species life habits are illustrated in Figures 3.3 to 3.30. Information on vertical distribution was lost due to sampling methods.

2. FAUNAL COMPOSITION AND DIVERSITY

Joint occurrence of several species as a result of similar environmental preferences and tolerance limits, is a very useful criterion, applied with great success in the

recognition of life assemblages, at the species level for the Eden estuary fauna e.g. joint occurrence of Montacuta ferruginosa with Echinocardium cordatum (Fig. 3.1) or Retusa obtusa with Hydrobia ulvae (Figs. 3.3, 3.8). In the above, and many other cases, the dead shell fauna shows the same close associations of species that occur in the living fauna.

3. POPULATION DENSITY

The population density refers to the horizontal and vertical density of individuals of the same species. The horizontal density (number of specimens per m^2) was estimated for each species separately and is illustrated in Fig. 3.3 to Fig. 3.30. The highest population densities occur in most cases in the areas most suitable for the species (according to their life habits), and vice versa, the lowest densities in unfavourable areas, e.g. in Hydrobia (Fig. 3.3) the highest densities were found at the marginal areas of the upper and middle estuary where the optimal life conditions for the species are indeed met. In Mytilus the lowest population densities are confined in the high energy environments of the Eden estuary sandflats, where conditions are unfavourable for the species (strong currents, substrate), as well as in the marginal areas of the mudflats where the amount of food is insufficient (Fig. 3.15).

Population density is a useful criterion applied successfully to the Eden estuary fauna.

4. SURFACE CONDITION OF SHELLS.

Predation marks were examined in all dead shells and some species showed a marked percentage of borings e.g. Venus, Mytilus. These helped to evaluate the predator-prey interaction, e.g. Venus preyed upon by Natica alderi, and draw useful conclusions regarding the origin of fragmented shells otherwise believed to be a result of turbulence and transportation.

5. RATIO OF OPPOSITE VALVES

"An undisturbed deposit of shells containing unhinged shells should yield approximately equal numbers of opposing valves. The opposing valves should have dimensions that permit them to fit together" (Boucot, 1953).

Detailed observation of the opposing valves for every species in each sample revealed the ratio to be about 1 in most cases. For example in Mya arenaria, where the two valves differ in their hydrodynamic behaviour and thus the ratio of opposite valves is critical for life assemblage discrimination, the ratios of opposite valves for samples of sites in one transect from the head to the mouth of the Eden are shown in Table 4.1.

Table 4.1

Site	sample	ratio
A4	1st	1
	2nd	1
B4	1st	1
	2nd	0.5
D4	1st	1
	2nd	1
E4	1st	1
	2nd	1
F4	1st	0.33
	2nd	0.33
H4	1st	2
	2nd	1

Further, the high percentage of opposite valves fitting perfectly supports the criterion of opposite valves as being a most valuable one for recognition of life assemblages in the Eden estuary case.

UNSUCCESSFULLY APPLIED CRITERIA

1. SIZE FREQUENCY DISTRIBUTIONS.

In most cases the number of whole valves preserved was inadequate to give a meaningful histogram. Where the density of valves was enough the histograms that were drawn gave a variety ranging from left-skewed, normal, right-skewed to multimodal distribution. No attempt to interpret them according to Craig and Oertel's (1966) deterministic models was made, since their models apply to ideal closed systems where no interspecies competition, predation, migration, transportation and selective elimination of the remains of dead animals occur. Predation, migration and transportation are known to take place in the Eden estuary. Besides "as valves are frequently broken by impact and eventually a few typical forms remains but these in great number, the frequency distribution of preserved shells is entirely unrepresentative for the relative frequencies in the population of the living species" (Schäfter 1972).

So size-frequency distributions believed by many workers (Boucot (1953), Turney Perkins (1972)), as the strongest criterion of distinguishing life and death assemblages was not considered reliable in this study and was therefore rejected.

2. RATIO OF ARTICULATED TO DISARTICULATED VALVES

This is applicable to brachiopods which disarticulate less readily after death while "bivalves are prone to become unhinged after death" (Boucot 1953). The values of such ratios were very low to zero for the Eden bivalves but this is no proof of transportation. There is no absolute value to compare our ratios with. Therefore, the criterion was insignificant and was rejected.

3. RATIO OF WHOLE TO FRAGMENTED SHELLS

The ratios taken for the Eden estuary bivalves and gastropods varied a lot and did not add significantly to our information. Thin-shelled molluscs are easily fragmented in high-energy environments such as the outer estuary ones. It is rather their limited distribution that lead us to conclusions since these thin, small, light shells (e.g. Pecten, Thracia, Nurula, Anomia) would show a more general distribution in the presence of more rigorous transportation agents.

On the other hand, presence of whole, thin, fragile shells (Crassostrea, Ostrea, Hiatella) in high energy environment is a good indication of life assemblage. Generally the ratio of whole to fragmented shells was not an applicable criterion for recognition of life assemblages in the Eden estuary.

OTHER INDICATIONS

1. LIVE - DEAD POPULATIONS CORRELATION.

The number of species in each site varied from 5 to 31 for the dead populations and from 0 to 6 for the living ones.

In order to evaluate how accurately the death assemblages reflect the life assemblages from which they were derived, the live recorded species in each site are compared with the dead ones. Such comparison will give low correlations of dead to live populations if the inadequacy of sampling (for the live populations) is not considered.

However more reliable comparisons can be made with the living mollusca reported by Brown (1938), after extensive sampling throughout a year in a few sites representative of the different substrate types present in the Eden estuary. The species composition of the dead population of sites as close to Brown's as possible, is given in Table 4.2 and next to it the species composition of Brown's live populations and this study's results for the live populations of the same sites. It is clear from Table 4.2 that there is a very high correlation of dead to living populations with regard to the species composition of the same sites. In almost all cases (the dead species found in this study) were reported alive by Brown (1938), with the exception of Mya arenaria in station IV which was collected alive during this study and Macoma. Scrobicularia and Cardium of station VII, which were also found alive at the respective areas during this study.

Limopontia capitata and Chinon marginatus were not found alive or dead in any station during this survey, neither were they found in Bell's surveys (1978, 1979). Either the species have disappeared from the estuary due to unknown factors, or the recent surveys were not intensive enough as has been pointed out for this survey in CHAPTER 2.

2. SPECIES DIVERSITY.

In its initial use diversity meant nothing more than the total number of species in a sample or area and it has been used in this way by many ecologists. More recently number of individuals have been taken into account as well as number of species. In order to separate the two meanings, the former is now called "species diversity" and the second "dominance diversity" (Sanders, 1968).

When species diversity is plotted against all sampling sites a tendency for increase in number of species can be seen for both bivalves and gastropods, as one proceeds from the head of the estuary to the mouth (Fig. 4.1). The same tendency is noticed when species diversity for bivalves is plotted against sites for each W-E transect separately (Fig. 4.2). But things change if species diversity for gastropods is plotted against the same sites (Fig. 4.3). Here it seems that the maximum number of species occurs in the middle estuary and decreases towards the mouth of the Eden. This is in agreement with the diversity of living gastropods which shows the same tendency for reduction in number of species towards the mouth of the Eden, and which is justified by the fact that conditions are favourable for gastropods in the middle estuary mudflats (small stones, empty shells, substrate, algae to feed on etc.). On the other hand neither the substrate nor the food supply is suitable in exposed sandflats.

In plotting species diversity for all Mollusca against sites in the same W-E transects (Fig. 4.4) the increase in number of species towards the mouth of the Eden is clear again, presumably because there are more bivalves than gastropods.

Generally species diversity of the subfossil populations related to the living populations (See Table 4.2) and controlled by the same environmental factors (e.g. substrate food supply) as them, as indicated earlier, suggests that we are dealing with life assemblages since they are in agreement with Gunter's (1947) statement referring to the live animals that "as the distance covered by a salinity gradient is travelled from lower to higher, from the river mouths to the open seas, it is found that the number of species of animals increases:

DISCUSSION AND CONCLUSIONS.

All the information gained from the application of life-death assemblages discrimination criteria to the Eden estuary subfossil molluscan assemblages is summarized in Table 4.3. It is quite clear from the table that the majority of species (23 Bivalvia and 11 Gastropoda) represent with fidelity the life assemblages from which they are derived. However 10 species Mya truncata, Musculus discors, Arctica islandica, Astarte borealis, Crassostrea sp., Venerupis sp., Barnea candida, Gibbula cineraria, Acmaea tessulata and Patina pellucida are doubtful regarding their origin. A degree of transportation therefore does take place in the Eden estuary to some extent but it is not enough to obscure the faunal composition or the relative abundances of species in the samples. It is established here that for the Eden estuary the subfossil assemblages reflect quite accurately the life assemblages from which they are derived.

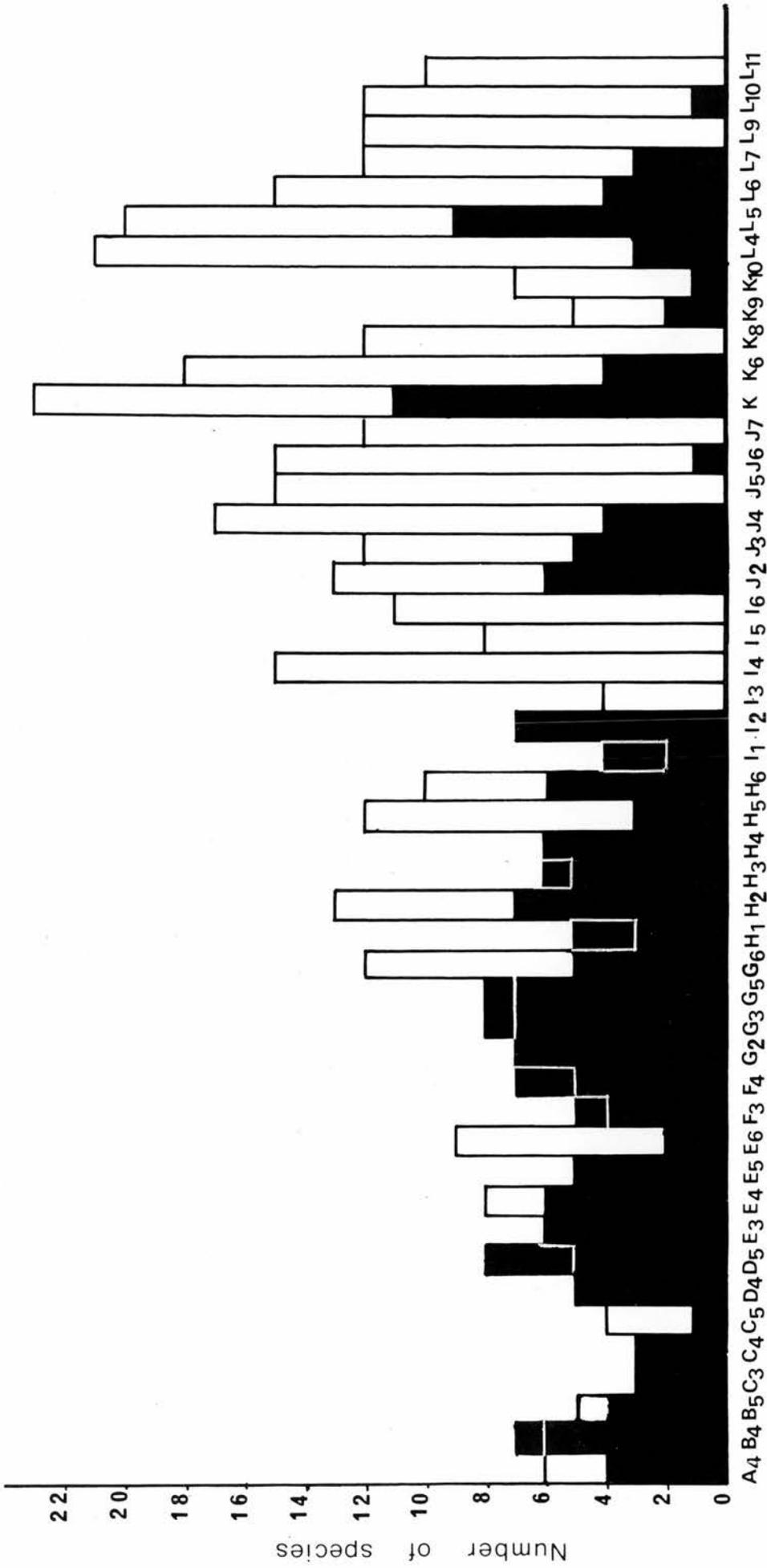
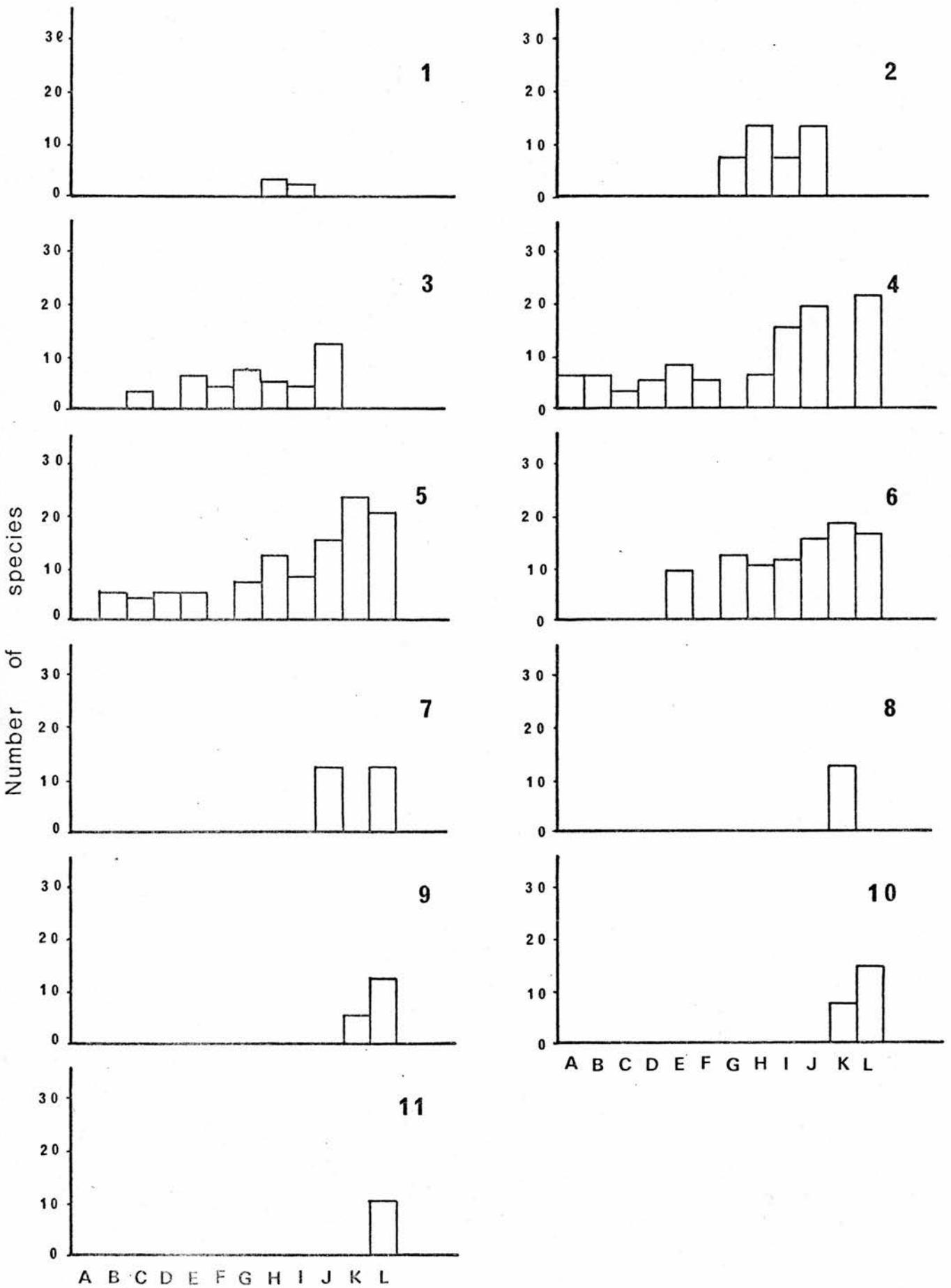
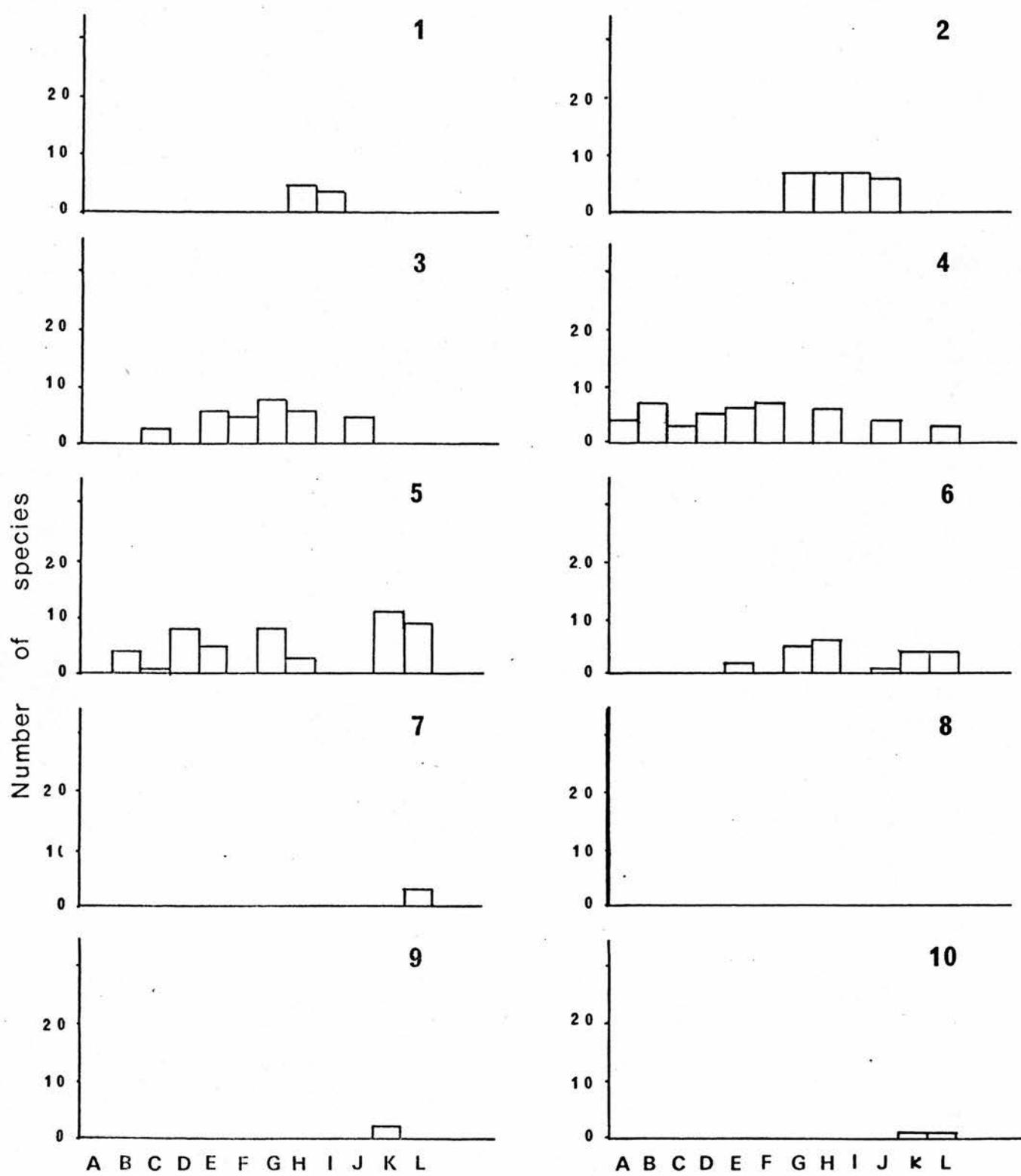


Fig. 4.1. Species diversity (based on dead populations) for bivalves (white) and gastropods (black) for all sampling sites, from head (A4) to the mouth (L11) of the Eden estuary. The white lines indicate sites where gastropods diversity exceeds the bivalves diversity.



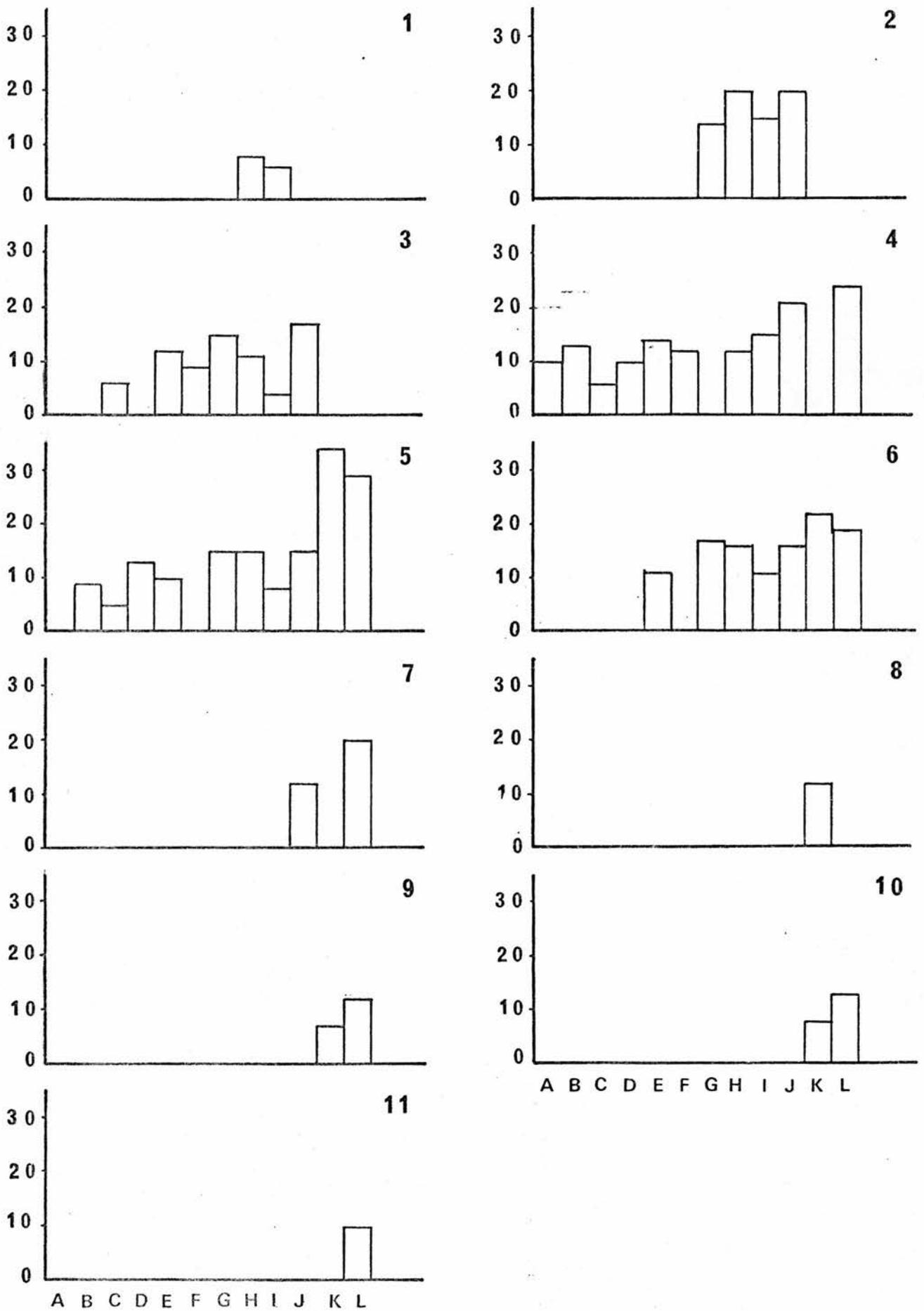
Sampling sites in W-E transects 1-11

Fig.4.2 Species diversity for the Eden bivalves along W-E transects. Only dead populations are considered.



Sampling sites in W-E transects 1-10

Fig.4.3 Species diversity for the Eden gastropods along W-E transects. No gastropods are recorded from transect 8. Only dead populations are considered.



Sampling sites in W-E transects 1-11

Fig.4.4 Species diversity for all Mollusca along W-E transects in the Eden estuary. Only dead populations are considered.

STATION III

R. Z. DEAD	BROWN'S LIVING	R. Z. LIVING
Cardium edule	present	present
Macoma balthica	present	present
Scrobicularia plana	present	present
Mya arenaria	present	present
Littorina saxatilis	present	present
Littorina littorea	present	present
Littorina littoralis	present	absent
Hydrobia ulvae	present	absent
Nucella lapillus	present	present
Mytilus edulis	present	present
-	Tellina tenuis	-
-	Buccinum undatum	-
-	Chinon marginatus	-
-	Limopontia capitata	-

STATION IV

R. Z. DEAD	BROWN'S LIVING	R. Z. LIVING
Cardium edule	present	present
Mytilus edulis	present	present
Macoma balthica	present	present
Scrobicularia plana	present	absent
Mya arenaria	absent	present
Hydrobia ulvae	present	absent
Littorina saxatilis	present	absent
Littorina littorea	present	absent
Littorina littoralis	present	absent
-	Chinon marginatus	-

STATION V

R. Z. DEAD	BROWN'S LIVING	R. Z. LIVING
Macoma balthica	present	present
Scrobicularia plana	present	present
Cardium edule	present	present
Mytilus edulis	present	present
Hydrobia ulvae	present	absent
Littorina littorea	present	present
Littorina saxatilis	present	present
-	Limopontia capitata	-

STATION VII

R. Z. DEAD	BROWN'S LIVING	R. Z. LIVING
Macoma balthica	absent	present
Scrobicularia plana	absent	present
Cardium edule	absent	present
Mytilus edulis	present	present
Hydrobia ulvae	present	absent
Potamopyrgus jenkinsi	absent	absent
Littorina saxatilis	present	present
Littorina littoralis	present	present
Littorina littorea	present	absent

T A B L E 4.2

Comparison of R.Z. dead molluscan species with Brown's living molluscs and R.Z. living molluscs at the same sites. Stations III, IV, V and VII are those of Brown(1938) and are shown on figure 2.1.

TABLE 4.3 (opposite)

Life-death assemblages discrimination criteria as applied to the Eden Mollusca populations.

- Column 1 + = both living and dead specimens present.
blank = dead shells only present.
- Column 2 + = presence of species is in accord with factors discussed on pages 21-50 such as salinity, substrate etc.
- = presence not in accord with these factors and suggesting transport from elsewhere of the dead shells.
- Column 3 Species marked with + are predators on other species commonly occurring in the estuary (pp. 26, 27, 28). Species marked with * are living symbiotically with another species in the estuary (p. 43).
- Column 4 + = maximum density of dead shells occurs in areas which would be expected to be favourable to living organisms in the estuary.
blank = insufficient data to draw any conclusions as to density of species distribution.
- Column 5 + = close positive correlation.
- = correlation deviates markedly from 1.
? = doubtful owing to insufficient information.
blank = does not apply.
- Column 6 + shells showing no evidence of appreciable transport; predation markings common.
- shells commonly show evidence of transport, e.g. breakage.

CRITERIA	LIVING	DISPER-	FAUNAL	POPULA-	RATIO	CONDI-
<u>SPECIES</u>	<u>DEAD</u>	<u>SION</u>	<u>COMPO-</u>	<u>TION</u>	<u>OF OP-</u>	<u>TION OF</u>
	<u>CORRE-</u>	<u>OF SUB-</u>	<u>SITION</u>	<u>DENSITY</u>	<u>POSITE</u>	<u>SHELLS</u>
	<u>LATION</u>	<u>FOSSILS</u>			<u>VALVES</u>	
<i>Macoma balthica</i>	+	+		+	+	+
<i>Scrobicularia plana</i>	+	+		+	+	+
<i>Cardium edule</i>	+	+		+	+	+
<i>Mya arenaria</i>	+	+		+	+	+
<i>Mytilus edulis</i>	+	+		+	+	+
<i>Solen-Ensis</i>	+	+		+	+	-
<i>Tellina fabula</i>		+		+	+	+
<i>Spisula-Mactra</i>		+		+	?	-
<i>Montacuta ferruginosa</i>		+	*	+	+	+
<i>Venus striatula</i>		+		+	+	+
<i>Dosinia sp.</i>		-			?	-
<i>Donax vittatus</i>	+	+		+	+	+
<i>Lutraria lutraria</i>	+	+		+	+	-
<i>Pecten sp.</i>		-			+	+
<i>Ostrea edulis</i>		+			?	+
<i>Thracia sp.</i>		+		+	?	-
<i>Abra alba</i>		+			?	-
<i>Anomia sp.</i>		+			+	+
<i>Nucula nucleus</i>		+		+	+	+
<i>Hiatella arctica</i>		-			+	+
<i>Gari fervensis</i>		+			?	+
<i>Corbula gibba</i>		+		+	?	+
<i>Mya truncata</i>	+	+		+	-	-
<i>Musculus discors</i>		+			-	-
<i>Arctica islandica</i>		-			+	-
<i>Astarte borealis</i>		-			-	-
<i>Crassostrea sp.</i>		+			-	-
<i>Venerupis sp.</i>		-			+	+
<i>Barnea candida</i>		-			-	-
<i>Tellina tenuis</i>	+	+		+	+	+
<hr/>						
<i>Hydrobia ulvae</i>	+	+		+		+
<i>Potamopyrgus jenkinsi</i>		+		+		+
<i>Littorina saxatilis</i>	+	+		+		+
<i>Littorina littorea</i>	+	+		+		+
<i>Littorina littoralis</i>	+	+		+		+
<i>Nucella lapillus</i>	+	+	+			+
<i>Tritonalia aciculata</i>		+				-
<i>Retusa obtusa</i>	+	+	+	+		+
<i>Natica alderi</i>		+	+	+		-
<i>Buccinum undatum</i>	+	+				-
<i>Gibbula cineraria</i>		-				-
<i>Patella sp.</i>		+		+		+
<i>Acmaea tessulata</i>		-				+
<i>Patina pellucida</i>		-				+

CHAPTER 5

CONTRIBUTION OF FAUNA TO SEDIMENT

CONTRIBUTION OF FAUNA TO SEDIMENT.

"Lamellibranch valves are amongst the most resistant organic hard parts in the sediments of the shallow sea. The enormous quantities of such remnants in recent sediments are not only due to the large population but even more to their strength and uncomplicated structure. Eventually they are destroyed, reduced to fragments and ground into fine grit (Schafer, 1972).

Ginsburg (1956) has demonstrated the large contribution that molluscs make to Florida Bay sediment. He found that molluscan debris made up 58 to 95 percent of the particles greater than $\frac{1}{8}$ mm.

Except under ideal conditions, there is no way to determine how many years' deposition a given sample represents, and we do not know the actual percentage of shells that is preserved in the record. Carefully controlled quantitative field observations at selected localities, carried out over a long period of time, is the only approach to this question.

"In the initial stages of disintegration there appears to be some selective breakdown of shells. The thin shelled bivalves tend to be broken more rapidly than gastropods or more heavily built bivalves" (Turney and Perkins, 1972). "Solution of calcium carbonate facilitates the mechanical destruction, especially in the last stages. Solution is more intensive the smaller the weight of the original fragment. Calcium-carbonate boring microorganisms also play a considerable role in the reduction of valves" (Schäfer, 1972).

Many investigators consider the boring thallophytes as the most important destroyers of empty marine shells, e.g. *Pia*, in Schäfer (1972). Wetzel (in Schäfer 1972) listed the

following common calcium-carbonate boring thallophytes:

green algae (mainly Phaeophila, Entocladia, Gomontia, Ostreobium), blue green algae (especially Hyella) and fungi (Ostracoblabe, Lithophytum).

In the Eden the following Chlorophyceae have been identified in the periostracum of mollusc shells: Gomontia polyrhiza in the periostracum of Cardium edule and Littorina littorea by D.E.G. Irvine, 1954), Ostreobium quekettii in the periostracum of Littorina littorea by D.E.G. Irvine (1954) and in the periostracum of Buccinum undatum by Blackler (1974). Tellamia contorta in the periostracum of Littorina littoralis, L. saxatilis, L. littorea and Nucella lapillus by Irvine (1954). Also in Cardium edule by Blackler and Tellamia intricata in the periostracum of Littorina littoralis, L. saxatilis and Nucella lapillus by Blackler (1974).

Carbonate-boring organisms also help to destroy the shells. Boring marks of mollusc predators are evidenced in many cases in the Eden. Those of Natica alderi clearly seen on Donax vittatus and Venus striatula fragmented valves. Birds predated on molluscs have been noticed in the Eden estuary mudflats by Johnston (in Bell-Johnston-Cobb, 1978) and are believed to reinforce the mechanical destruction of shells. "Gradual destruction by sand abrasion and sudden breakage by impact, play the most important roles in the mechanical destruction of Recent gastropod shells and Lamellibranch valves" Pratje, (1929).

Assuming that as Schäfer states the Lamellibranch (Bivalvia) valves end up as fine grit, and the same is valid for gastropod shells, an effort was made to relate the distribution of molluscs in terms of densities and biomass over

the Eden with the distribution of calcium carbonate content as given by Eastwood (1977).

Because different species of molluscs would contribute differently CaCO_3 to sediment, due to their size (i.e. Macoma and Mya), it was believed that biomass results were more suitable than densities results since they overcome the problem of what each species contributes. Biomass in this study is defined as the dry weight per m^2 . In this particular case biomass was estimated adding the dry weight of all molluscs found in the >2 mm part in the two samples and multiplying it by 26 to give total per m^2 . Considering the number of specimens, for bivalves the number of valves was divided by two and rounded upwards, if necessary, to reach a number of individuals which was then added to the number of gastropod shells as taken from the original data, to give final density per site.

The problem of relating the distribution of molluscs to the distribution of calcium carbonate (CaCO_3) is difficult and only general conclusions can be drawn.

Contrary to expectation, the distribution map based on biomass data and that based on densities of molluscs were very much alike as can be seen in Fig. 5.1 and Fig. 5.2. There appears to be some similarities of the above maps with the calcium carbonate content one, (Fig. 5.3), summarized below:

- 1) A low CaCO_3 content area in the North-Eastern margin of the Eden corresponds to a low biomass content and low density respectively.
- 2) A low CaCO_3 content area in the Southern margin of Kincapple Flat corresponds to a low biomass area but not to a low

density one.

- 3) A high CaCO_3 area around the edges of the Eden channel in the middle estuary corresponds roughly to a high biomass content and a high density of molluscs evidenced by the mussel banks and Cardium edule shell pavements.
- 4) A small area of high CaCO_3 content, in the Kincapple Flat reflects the high biomass content and high density respectively.
- 5) An extensive high CaCO_3 content area in the South bank of the outer estuary corresponds to a medium-high biomass content area and a medium high density area too.
- 6) Medium (1-3%) CaCO_3 content areas in the Kincapple Flat and upper estuary reflect roughly medium to high biomass and density areas.

There seems to be a marked relationship between the distribution of CaCO_3 in the Eden estuary and the density (or biomass) distribution of the dead molluscs suggesting that the latter play an important role in the contribution of CaCO_3 to sediment.

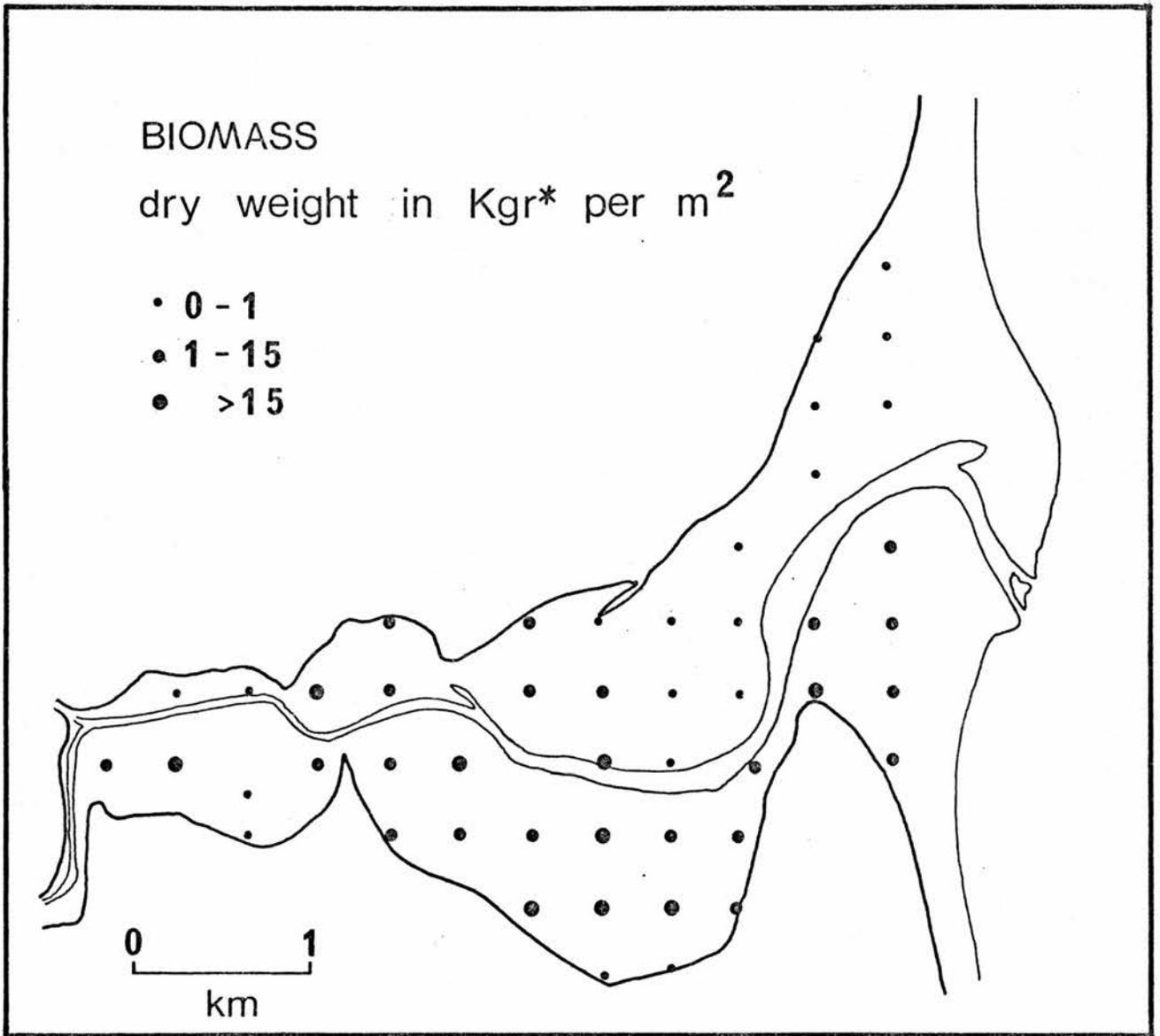


Fig.5.1 Distribution of biomass in the Eden estuary. The biomass is calculated from the dead Mollusca populations.

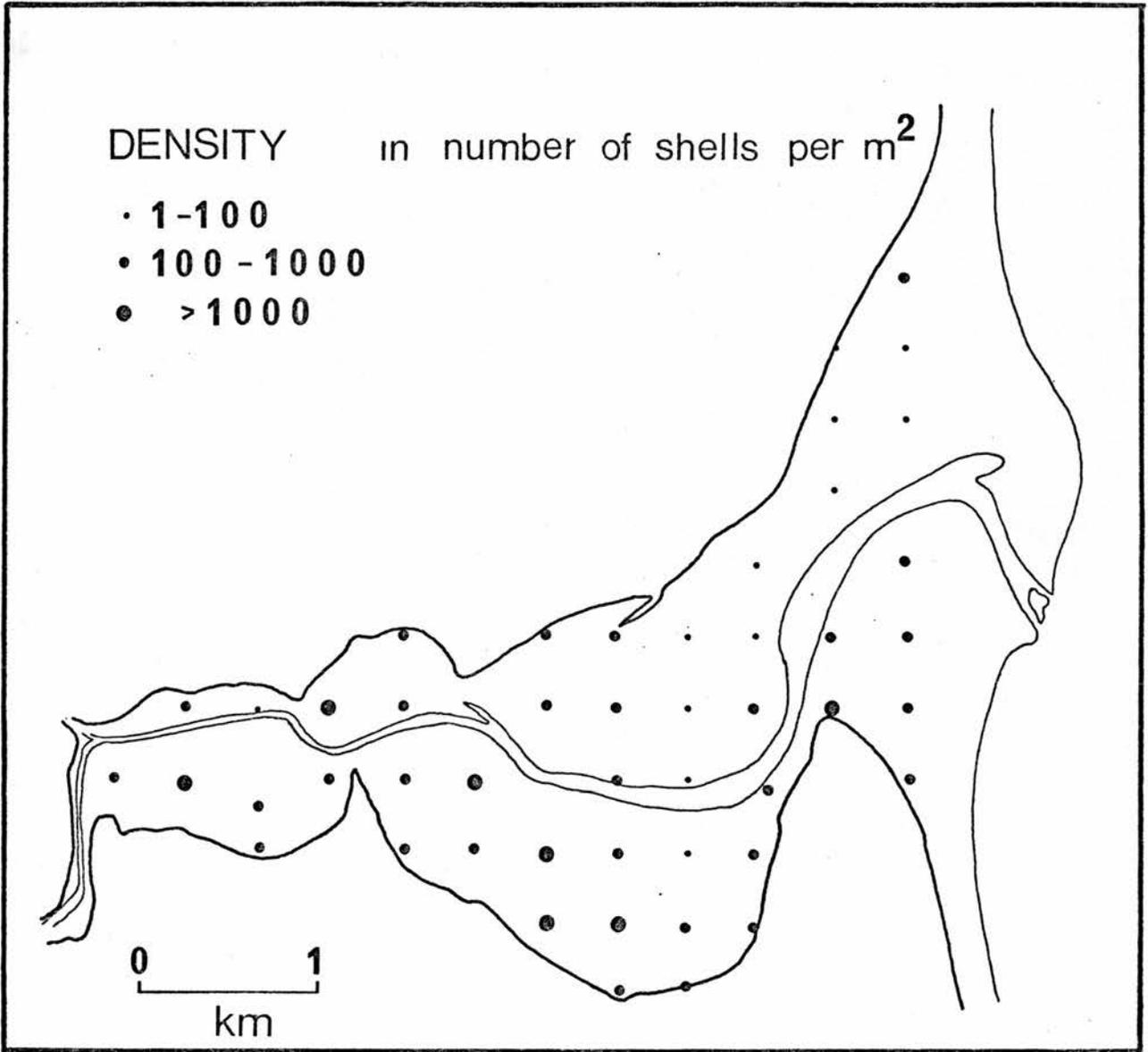


Fig.5.2 The distribution of molluscan density in the Eden estuary. All species at each site are taken into account.

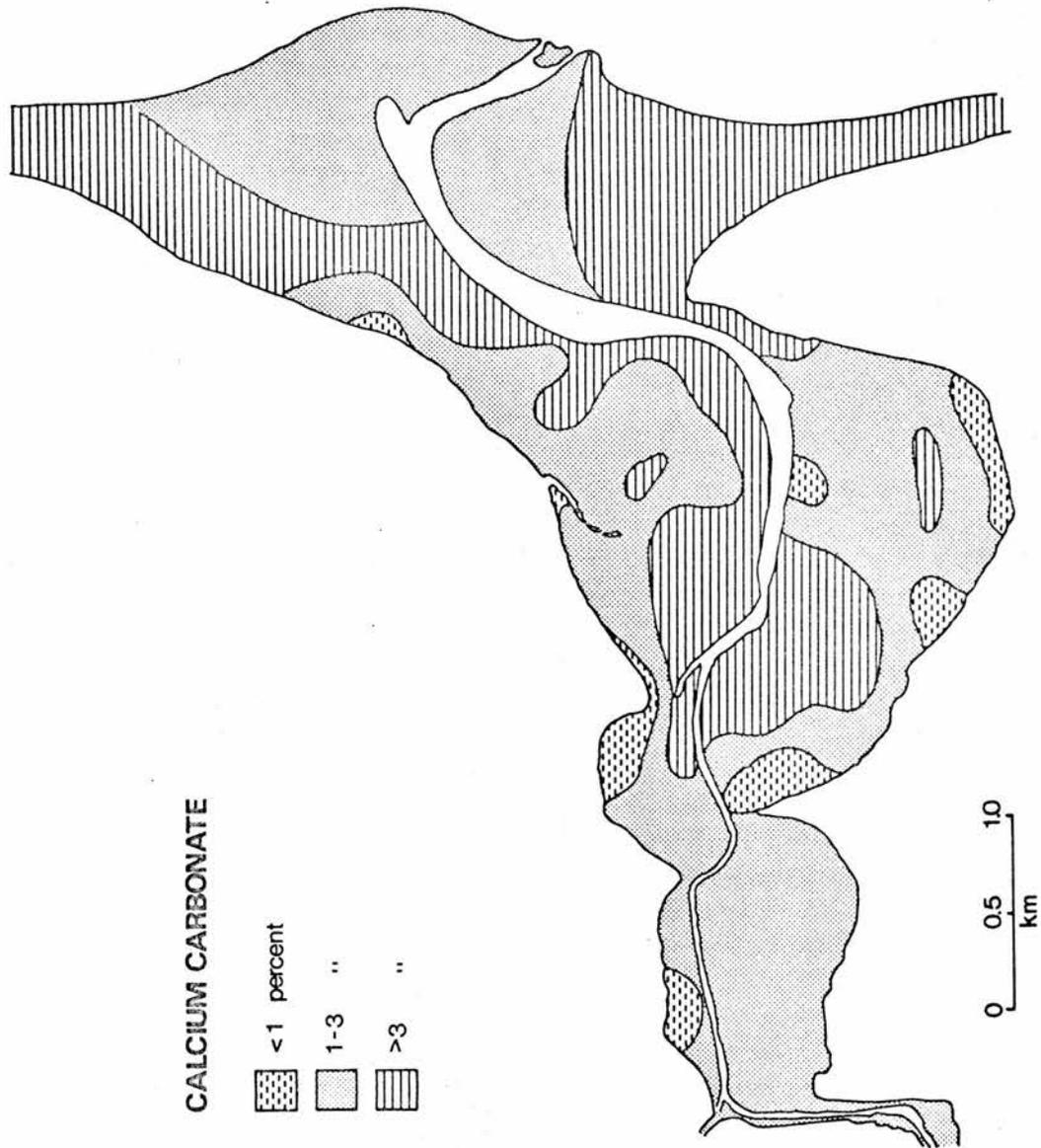


Fig.5.3 The distribution of CaCO_3 in the Eden estuary (after Eastwood, 1977)

PART II.

CHAPTER 6
INTRODUCTION
TO NUMERICAL TAXONOMY

GENERAL - PROBLEMS..

NUMERICAL TAXONOMY (Sneath and Sokal, 1962) is "the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities". In ecological and paleoecological studies the "taxonomic units" are ecological units (stations) and the "taxa" are biotopes, or respectively the taxonomic units are species and the taxa are biofacies.

Among the many definitions that have been given for biofacies and biotopes are the following:

"The zonation of some living populations, that is multispecies assemblages living in a specified area has been referred to as biofacies" (Phleger, Walton in Buzas, 1969).

"Ideally, biofacies is the total imprint of organogenic material and of traces of activities in a depositional unit formed under uniform conditions". In this sense, Schäfer (1972), considers biofacies as synonymous with biocoenosis.

"An individual biofacies is a unit compared with other biofacies units, only because the effects of a certain set of forces and conditions for a certain set of biocoenosis happened to coincide at a given place and time, producing a fossil result with uniform aspect or "face" (Buzas, 1969).

For work on Recent organisms, both living and subfossil, Kaesler's definition (1966) is most appropriate and it is in this sense that it is used in this study.

BIOFACIES is a group of organisms found together and presumably adapted to environmental conditions in their place of occurrence, such groups differing from contemporary assemblages found in different environments (Kaesler, 1966).

Transportation of subfossil material to environments different from those to which the organisms are adapted may complicate biofacies analysis. It was shown in PART I, that transportation and mixing of faunas is negligible in the Eden Estuary and that the subfossil assemblages are representative of the living assemblages.

From definitions given for biotopes again Kaesler's (1966) seems the most suitable in this study it being "an area of relatively uniform environmental conditions evidenced by a particular fauna found in the area and presumably adapted to environmental conditions existing there". Thus it is possible to speak of the Mollusca biotopes of the Eden estuary.

Kaesler (1966) was the first to apply quantitative techniques for ecological analysis and he noted three assumptions which are made in the kind of analysis attempted both by him and in this study:

- 1) Biofacies and biotopes exist in the study area
- 2) A sample adequately represents the population of organisms at the station
- 3) Biotopes are mappable".

Different combinations of alternative classificatory techniques lead to alternative classifications leaving one of the outstanding aims of numerical taxonomy (objectivity) open to the very criticism it seeks to avoid, the subjectivity element. In an attempt to delimit biofacies and biotopes in the Eden estuary a great range of classificatory techniques was used. Choices which were required at various stages included the following:

- (a) the form of data to be used, whether binary or quantitative
- (b) the need for data reduction
- (c) the selection of similarity/dissimilarity measure
- (d) the need for data standardization, and the method to be used
- (e) the type of cluster analysis to be employed
- (f) the best method for dendrogram partitioning.

(a) BINARY OR QUANTITATIVE DATA

There seems to be a divergence of opinions when it comes to deciding which type of data is to be preferred. The binary data are the least informative but the quantitative may be meaningless (when the dead populations are transported or mixed ones). When the only data available are species lists the problem does not arise. However, when the data is quantitative and a binary (presence-absence) technique is selected, the significance of the loss of information must be considered against the merits of the technique.

Franc and Remane (in Thorson, 1957) stated that "quantitative points of view have to be neglected when selecting biotic communities" but Thorson himself discussed the advantages of describing animal communities on a quantitative basis and concluded that "it seems a step backwards to abandon our quantitative methods". Kaesler (1966) suggested the use of presence-absence data in paleoecological work where the dead population is the best available estimate of the live population, and the use of quantitative data when the live population is considered.

In this study both types of data are used. The numerical

data (actual counts of animals) are believed to be more informative and meaningful since the dead populations reflect the live populations as discussed in CHAPTER 4. Nevertheless the binary data are used in order to test their validity in delimiting biofacies also delineated by numerical data

(b) DATA REDUCTION

A cut-off level was arbitrarily selected as the presence of a species in more than 3% of the samples. It also happened that all species (except Mya truncata) in the less than 3% category were doubtful as to their being representative of life assemblages in the areas of occurrence. Thus 6 species of Bivalves (Venerupis, Crassostrea, Astarte, Arctica, Musculus, Mya) and 3 species of Gastropods (Gibbula, Patina, Acmaea) were eliminated as being of poor ecological significance. To these Barnea candida was added firstly because the fragmented valves had definitely been transported, and secondly because there was no way of deciding how many individuals the collected fragments represented and were thus of no quantitative value, although Barnea occurred in nine samples.

(c) TYPE OF SIMILARITY/DISSIMILARITY COEFFICIENT

A) FOR BINARY DATA.

From the many coefficients of similarity/dissimilarity the ones used here are those of widespread use which have previously been employed in marine ecological studies (Kaesler (1966), Maddocks (1966), Mello and Buzas (1968), Michie (1978), Warne (1971) e.t.c.).

$$\text{Jaccard coef.} = \frac{a}{a+b+c}$$

$$\text{Matching coef.} = \frac{a+d}{a+b+c+d}$$

$$\text{Czekarowski coef.} = \frac{2a}{2a+b+c}$$

$$\text{Squared Euclidean Distance} = b + c$$

For biotopes analysis

- a is the number of species common to both sites A and B
 b is the number of species present in site A but absent from site B
 c is the number of species present in site B but absent from site A
 d is the number of species absent from both sites A and B,

For biofacies analysis

- a is the number of sites in which both species A and B are present
 b is the number of sites in which species A is present but species B absent
 c is the number of sites in which species B is present but species A absent
 d is the number of sites in which both species A and B are absent.

The Czekanowski coefficient is monotonic with the Jaccard coef. They both neglect co-absences (parameter d) and produce very similar results. However according to Clifford and Stephenson (1975) "the Jaccard coefficient is to be preferred when dealing with many conjoint presences because it will give a wider spread of values near the upper end of the range". According to the same author the Czekanowski coefficient is more attractive when there are relatively few conjoint presences. When conjoint absences are meaningful the Matching coef. is suggested by all taxonomists.

In Biotopes analysis, the Matching coef. has been employed by Kaesler (1966) with success, but with Maddocks' (1966) data it did not produce results interpretable ecologically. Mello and Duzas (1968) argue with Kaesler that the Matching coef. can be too sensitive to inadequate sampling and therefore suggest the use of the Jaccard coef. in biotopes analysis.

For BIOFACIES analysis Mello and Buzas (1968) concurred with Kaesler (1966) that negative matches should be excluded because "Perfect similarity between two species caused by negative matches alone would not justify grouping the species in the same biofacies.."

The squared Euclidean Distance coef. has not been tested with binary data in ecology, but because it is complementary to Matching coef., the results obtained with most methods are the same as those produced using the Matching coef. The squared Euclidean Distance does not take into account both conjoint presences and conjoint absences and stands therefore as intermediate between the two extremes, the Jaccard and the Matching coef.

All four coefficients above were used with binary data in order to test them for both biotopes and biofacies analysis.

B) FOR NUMERICAL DATA

The two most widely used measures of similarity/dissimilarity are tested in this study despite the conflicting opinions concerning their usage. The product moment correlation coefficient $\left(\frac{\sum_{i=1}^n (x_{ij} - \bar{x}_j) \cdot (x_{ik} - \bar{x}_k)}{\left[\sum_{i=1}^n (x_{ij} - \bar{x}_j)^2 \cdot (x_{ik} - \bar{x}_k)^2 \right]^{1/2}} \right)$ Appendix 1 takes into account the magnitude of mismatches between taxa for characters with more than two states. The Taxonomic Distance $\left(\sqrt{\frac{\sum_{l=1}^n (x_{ij} - x_{lk})^2}{n}} \right)$ see Appendix 1 or better still the Squared Euclidean Distance $\left(\frac{1}{n} \sum_{l=1}^n (x_{ij} - x_{lk})^2 \right)$ expresses degree of dissimilarity as distance in n-dimensional space. The two measures are closely related when data are standardized with a mean of zero and a standard deviation equal to 1.0. The D-coef. has been used in biotopes analysis successfully by Michie (1978),

while the r-coef. has been used by Kaesler (1966) in biofacies analysis unsuccessfully.

Objections to the use of the r-coef. come from:

- a) Kaesler (1966) who states that it may be used for biofacies analysis only if the populations are normally distributed and if the investigator has some means of ascertaining the ecologic meaning of each sample.
- b) Wishart (1978) who mentions that tests have suggested that r-coef. as a measure is unstable.
- c) Sokal and Sneath (1963) who note that doubt must prevail about the significance of the r-coef. in a Q-type (biotopes) study.
- d) Field (1970) who proposes that when 50% or more of the data entries are zero the r-coef. should be avoided.

Clifford and Stephenson (1975) suggest r-coef. for biofacies analysis where its ability to distinguish nil correlations from negative correlations gives it some advantage over some other coefficients of association. They also suggest it for a biotope analysis but with caution (when less than 50% of the data entries are zero).

All objections to D-coef. are concerned with the fact that it gives considerable weighting to abundant species. For this reason the calculation of D-coef. (or D^*) is preceded by a standardization of the original data.

(d) DATA STANDARDIZATION.

Standardization of data is advisable in order to reduce the size of each datum so that there is less difference between the data points, or otherwise to avoid taking biased results because of a few dominant species when using a similarity measure such as Euclidean Distance.

Most standardization methods may reduce large values but do not eliminate zeros. A typical method tested with ecological data (Michie, 1978) is one described by Noy-Meir (1973) as centering and normalization, and it is the one used here. Centering has the effect of eliminating zeros, while the problem of dominance can be diminished by normalizing. The data after standardization in this way ($\frac{x-\bar{x}}{Sx}$ where x , \bar{x} , Sx are the value, mean value and standard deviation of a given variable) appear to be normally distributed with a mean 0 and standard deviation 1.0. In our study species standardization was carried out prior to both site/site (biotopes) and species/species (biofacies) analysis, and site standardization prior to biofacies analysis.

(e) CHOICE OF CLUSTER METHOD.

Clustering of the similarity matrices was carried out using a number of the techniques described by Clifford and Stephenson (1975) and programmed by Wishart (1978), plus a W.P.G.A. (Weighted-Pair, Group Average) technique from a program written by Davis (1973) and modified for the present purposes. Because it was impractical to use all the 6 previously described similarity coefficients for all the clustering techniques, only the Squared Euclidean Distance based on numerical data was used with all of them. The rest (Jaccard, Czekanowski, Matching, Squared Euclidean Distance based on binary data and Correlation coefficient), were tried with N.N. (Nearest Neighbour), F.N. (Furthest Neighbour), W.P.G.A. and U.P.G.M.A. (Unweighted-Pair Group Method Average) clustering methods.

Selecting a particular clustering technique from the existing ones and having confidence that it is the best, is not

possible when the vast bibliography of papers on the subject is taken into account. The opinions of some of them are contradictory. For example Mojena (1976) comments: "N.N. was significantly inferior to all other methods. The performance of this method verifies its chaining tendencies and subsequent heterogeneity in the size of clusters". On the contrary Jardine and Gibson (1968) believe that the mathematical criteria that should be applied to classificatory strategies, virtually confine one to N.N. fusion. F.N. has fewer opponents. Mojena (1976) considers it as the best of the group (F.N., N.N., U.P.G.M.A., median and centroid) with regard to stability. Jardine and Sibson (1968) reject it as being ill-defined. Prichard and Anderson (1971) regard it as one of the most useful strategies used in their ecological studies of Scottish vegetation, and Wishart (1978) comments: "F.N. finds spherical clusters but is liable to produce irregular results because the similarity criterion is determined by only two individuals and does not measure group structure".

There are few reports of the use of the median, possibly because it is prone to produce inversions. Wishart (1978) noted that with distance, median tends to chain for large populations and the fusion coefficients are not monotonic.

Ward's method is, according to Wishart (1978) the best cluster method. It finds minimum variance spherical clusters, but is only valid with D-coef. Mojena (1976) reported that it gave a superior performance across all data sets. Matched t-tests showed very significant differences (<0.001) between Ward's and all other methods.

The most widely used clustering strategy for biofacies and biotopes analysis is W.P.G.A. It was first used by

Kaesler (1966) who was followed by Maddocks (1966), Mello and Buzas (1968), Warne (1969) and Michie (1978), as "having the highest cophenetic correlation coefficient when compared with U.P.G.M.A. as suggested by Sokal and Sneath (1963). The strategy is indeed suggested by Sokal and Sneath but it is the U.P.G.M.A. that gives the highest cophenetic correlation coefficient. What in fact Sokal and Sneath (1963, p. 189) say is that "unweighted methods have advantages but the weighted ones are to be preferred until such time as functions for intermediate weighting are developed.

Among the last reports on the performance of U.P.G.M.A. are Wishart's (1978) who states that it is reasonably well behaved and Clifford-Stephenson (1975) who notes "U.P.G.M.A. gives only moderately sharp clustering but has the advantage of being monotonic, little prone to misclassification and with little size group dependence. Being a weakly clustering strategy it has an important role to play in that it can be usefully employed to check for misclassifications resulting from the application of more intensely clustering programs".

(f) CHOICE OF PARTITIONING METHOD.

The final stage is to set up some criteria on how to partition a dendrogram, the end-product of a cluster analysis. For biotopes analysis so far, a criterion arbitrarily set by Kaesler (1966) and used both by him and Buzas-Mello (1968), was to draw a line so that the biotopes obtained are mappable. For biofacies analysis on the contrary the policy was to avoid drawing lines and to let the dendrograms stand alone as representation of similarity.

Recently Demirmen (1972) indicated criteria for the selection of groups but pointed out that the most meaningful partition in terms of the research aims is usually a subjective choice. After him Orford (1976) and Mojena (1976) made an attempt to set down mathematical criteria for deciding the optimal number of clusters to be obtained from a given dendrogram.

For the Eden estuary, biotopes and biofacies were selected using Orford's (1976) graphical constructions: These are:

- 1) A plot of the relative similarity value against the logarithm of the number of clusters, indicates groups that stand out from neighbouring classes. From these, the number of groups that are of practical use must be chosen.
- 2) A plot of the Redundancy against the logarithm of the number of clusters, indicates groups "where the entropy of the 1th level vector of sample number per cluster is maximized" (Orford, 1976).

Redundancy is a percentage obtained by $R = 100 (1 - H_r)$ where $H_r = H_a/H_m$ (relative information)

$$\text{Actual information } H_a = - \sum_{i=1}^n p_i \log_2 p_i$$

N = total number of clusters at the 1th linkage level

p_i = the probability of the sample number in the 1th cluster of the 1th linkage level.

Maximum information $H_m = \log_2 N$ is the information obtained when all groups contain an equal number of observations.

It was hoped that as Gower (1969) stated: "if clusters are really distinct, any strategy worthy of use would find them".

CHAPTER 7

BIOFACIES ANALYSIS

GENERAL.

In the biofacies analyses (R-mode analysis) species are related one to the other on the basis of the samples in which they occur. Ideally, dendrograms resulting from clustering of R-mode similarities will reveal which species are responsible for the clusters of samples obtained in Q-mode (biotopes analysis).

Three sets of data were examined in this study:

- a) The dead molluscan assemblages referred to as R.Z. dead Mollusca
- b) The living molluscan assemblages from the same samples as above referred to as R.Z. living Mollusca
- c) The living molluscan assemblages from Bell's et al. (1978) collection in summer 1978 referred to as P. Bell living Mollusca.

Because it is impractical to give the results of all combinations of clustering techniques for each set of data, only the best (interpreted ecologically) will be discussed here plus the ones of techniques that have been considered as "standard" in the past.

R.Z. DEAD MOLLUSCA.

(1) Using numerical data

After standardization by species and calculation of the dissimilarity by Squared Euclidean Distance, most clustering techniques succeed in distinguishing clearly two groups, (mud-tolerant and sand-tolerant fauna). Unstandardized data and use of product-moment similarity coefficient (r-coef.), give similar results for most clustering techniques. Standardization by site of the original data matrix and use of r-coef. give a further better distinction into four groups for Furthest

Neighbour (F.N.) and Unweighted-Pair-Group-Method-Average (U.P.G.M.A.). The four groups level is selected as optimal clustering level using Orford's graphical techniques (Fig. 7.1). The computed dendrograms by r-coef./U.P.G.M.A. is shown in dendrogram 7.1 and the resulting biofacies (I-IV) in Table 7.1.

TABLE 7.1.

BIOFACIES DESIGNATED BY DENDROGRAM 7.1.

<u>MUD-TOLERANT FAUNA</u>		<u>SAND-TOLERANT FAUNA</u>	
<u>widely distributed</u>	<u>less common</u>	<u>widely distributed</u>	<u>less common</u>
Macoma balthica	Scrobicularia plana	Solen-Ensis	Mya arenaria
Cardium edule	Littorina saxatilis	Montacuta ferruginosa	Dosinia sp.
	Littorina littorea	Ostrea edulis	Gari fer- vensis
	Littorina littoralis	Anomia sp.	Patella sp.
	Mytilus edulis	Tellina fabula	Nucella lapillus
	Hydrobia ulvae	Venus striatula	Tritonalia aciculata
	Potamopyrgus jenkinsi	Tellina tenuis	Nucula nucleus
		Spisula-Mactra	Hiatella arctica
		Donax vittatus	Corbula gibba
		Abra alba	Buccinum undatum
		Thracia sp.	Lutraria lutraria
			Natica alderi
			Retusa obtusa
			Pecten sp.

(2) Using binary data

The standard Jaccard coefficient (Jac.-coef.) with Weighted-Pair Group-Average (W.P.G.A.) give meaningless results. This is in contrast to previous workers and suggests that co-absence of the two species in a site is surely of some importance. At a high similarity level the Jac-coef. groups Macoma and Tellina together. This is wrong when taking into account the actual counts of the two species. Macoma and Tellina do occur together to some extent but it can be seen in the original data matrix (Appendix 2), that where Macoma is abundant Tellina is rare and vice-versa. At a similarity level low enough to separate the Macoma and Tellina communities, as many as 18 groups can be distinguished - 6 interpretable ecologically and 12 single species groups-which in fact comprise species that have been found together and are known to live together. Dendrograms similar to Jac.-coef/W.P.G.A. are obtained with U.P.G.M.A, F.N. and N.N. from Jac.-coef. computed similarity matrices. Similarities calculated using Czekanowski coefficient (Czek.-coef.) also give similar results as the Jac.-coef. for W.P.G.A., U.P.G.A., N.N. and F.N. This is justified by the fact that both similarity coefficients based on presence-absence data neglect conjoint absences while stressing conjoint presences.

The best results with binary data are produced by Matching coefficient (Mat.-coef.) and its complement Squared Euclidean Distance (D-coef.). The pros and cons of the above two coefficients have been discussed earlier. The results are similar to those obtained by r-coef. based on numerical data and can be seen in Table 7.2, Dendrogram 7.2, Fig. 7.2. Also,

the several clustering techniques do not vary very much in their performance either with Mat-coef. or with D-coef. Thus dendrograms produced by Mat-coef. and D-coef. give the same four biofacies (2 mud-tolerant and 2 sand-tolerant ones) with F.N., W.P.G.A., U.P.G.M.A. and Ward's method. The four groups discriminated by Mat-coef./F.N., Mat-coef./U.P.G.M.A. and D-coef./U.P.G.M.A. are identical. Minor differences are present in the two sand-tolerant groups obtained by D-coef./F.N., D-coef./Ward's and Mat-coef./W.P.G.A. where as many as two species different at a time belong to either group. Only the results of the three identical dendrograms are given here.

TABLE 7.2.

BIOFACIES DESIGNATED BY DENDROGRAM OF FIG. 7.2.

<u>MUD-TOLERANT FAUNA</u>		<u>SAND-TOLERANT FAUNA</u>	
<u>widely distributed</u>	<u>less common</u>	<u>widely distributed</u>	<u>less common</u>
<i>Macoma balthica</i>	<i>Scrobicularia plana</i>	<i>Solen-Ensis</i>	<i>Montacuta ferruginosa</i>
<i>Cardium edule</i>	<i>Potamopyrgus jenkinsi</i>	<i>Lutraria lutraria</i>	<i>Abra alba</i>
<i>Mytilus edulis</i>	<i>Littorina littorea</i>	<i>Tellina fabula</i>	<i>Thracia sp.</i>
	<i>Hydrobia ulvae</i>	<i>Venus striatula</i>	<i>Pecten sp.</i>
	<i>Littorina saxatilis</i>	<i>Tellina tenuis</i>	<i>Anomia sp.</i>
	<i>Littorina littoralis</i>	<i>Donax vittatus</i>	<i>Ostrea edulis</i>
	<i>Mya arenaria</i>	<i>Spisula-Mactra</i>	<i>Dosinia sp.</i>
	<i>Nucella lapillus</i>		<i>Natica alderi</i>
	<i>Retusa obtusa</i>		<i>Hiatella arctica</i>
			<i>Tritonalia aciculata</i>
			<i>Nucula nucleus</i>
			<i>Gari fervensis</i>
			<i>Patella sp.</i>
			<i>Corbula gibba</i>
			<i>Buccinum undatum</i>

COMPARISONS OF BIOFACIES BASED ON BINARY AND NUMERICAL DATA

Binary data can give results as good as numerical data when the appropriate similarity coefficients are used. The clustering techniques do not vary widely in their performance. It is the similarity coefficient that most influences the grouping. The four groups discriminated in all cases are very similar for both numerical standardized by site data and binary data. The first two groups are what are referred to here as the mud-tolerant fauna and the other two as the sand-tolerant fauna.

Approximately the same species are present in the same groups. The first group, the mud-tolerant fauna, comprises Macoma and Cardium both widely distributed over the Eden mud flats. When binary data are considered Mytilus joins this group at a high similarity level. With numerical data though, Mytilus is classified with the second mud-tolerant group together with Scrobicularia, L. littoralis, L. littorea, L. saxatilis, Hydrobia and Potamopyrgus. Three more species - Retusa, Nucella and Mya - are placed in this group when binary similarity coefficients are calculated but in the sand-tolerant fauna when r-coef. is computed. Both classifications are correct because Mya, Nucella and Retusa are transitional species that can live together but are forced arbitrarily and variably to belong to one group.

Mutually exclusive biofacies is the serious drawback of the clustering procedures, since in nature biofacies are overlapping rather than mutually exclusive.

Unfortunately no comparisons can be made with molluscan biofacies defined by cluster analysis in other areas e.g. in the coastal Californian lagoon described by Warne, because of the different fauna evidenced. Similarly no comparisons with molluscan biofacies assigned by common sense (e.g. Petersen's or

Schäfer's) can be made because those are overlapping.

EVALUATION OF METHODS.

The Eden estuary dead Mollusca data are more sensitive to the various similarity coefficients than to the various clustering techniques. In general the same similarity matrix produces similar dendrograms regardless of the technique used. This means that extra care must be taken in selecting the appropriate similarity coefficient. The best choice, suggested by this study is the Matching-coef. for binary data and the r-coef. for numerical data. From the clustering methods the Nearest Neighbour (N.N.) was significantly inferior (ecologically interpretable) in its performance to the rest of the clustering techniques.

Although better discrimination of biofacies should be achieved using species densities because these kinds of data contain more information, in the present instance biofacies are as easily delineated using only presence-absence data, suggesting that data of this type contain enough information for recognition of biofacies provided that the appropriate cluster analysis techniques are used.

R.Z. LIVING MOLLUSCA.

The living fauna has two attributes that make it difficult to include every species in every sample from a habitat. These are: (1) patchiness or clumping of individuals of live populations and (2) rarity of some species in natural communities. For these reasons it is not likely that species lists and thereafter biofacies based on the live animals and separately on the empty shells will be identical. The validity

of biofacies is further obscured when the samples do not sufficiently represent the population of organisms at a habitat, i.e. when sampling is inadequate.

The living Mollusca are poorly represented in the Eden estuary samples collected in Summer '78. Thus the biofacies derived from data on occurrences of living forms are not meaningful and therefore not comparable to biofacies based on dead populations.

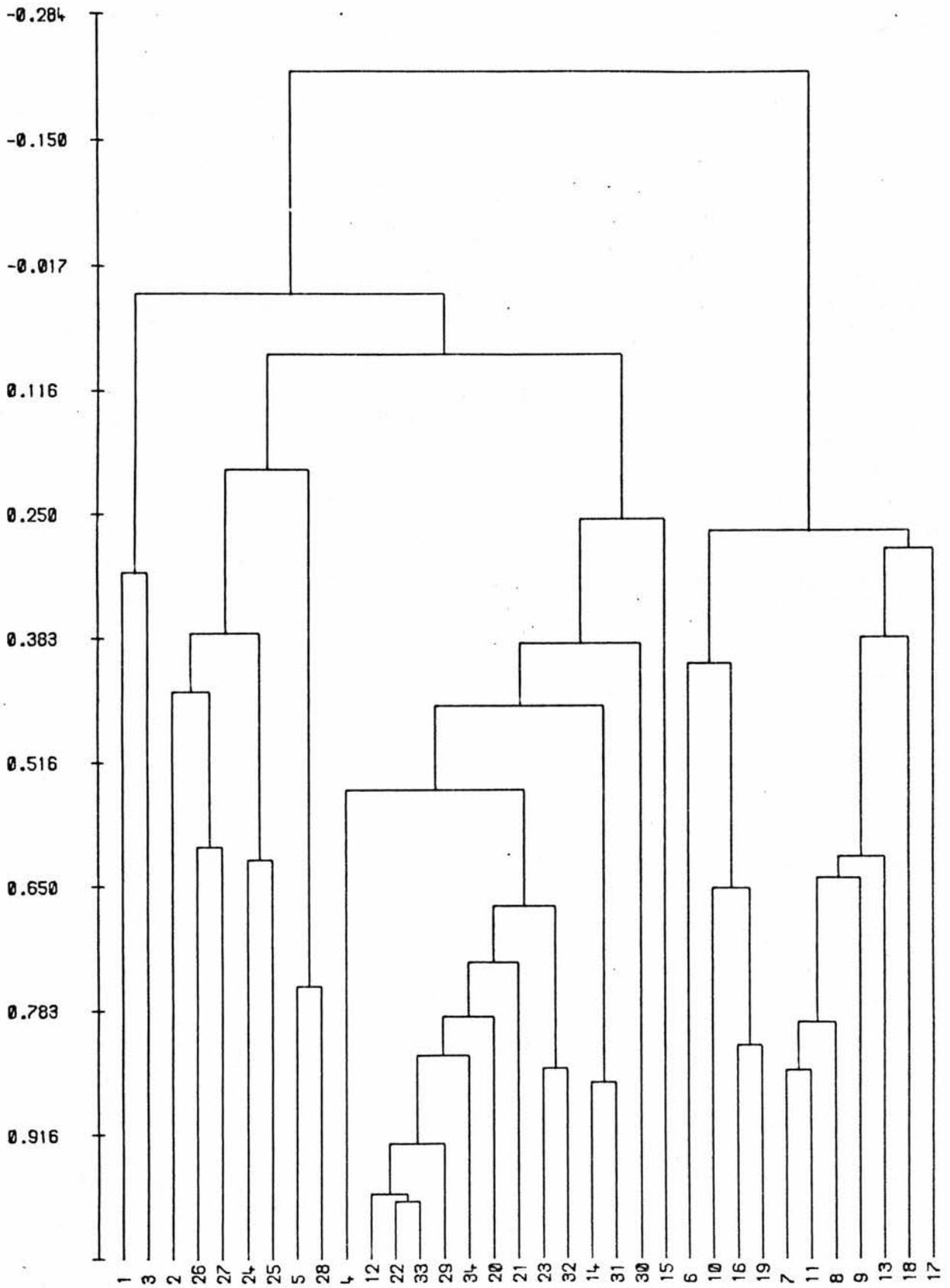
The only sand-tolerant species among the living molluscs is Tellina tenuis which is classified together with mud-tolerant fauna by most clustering techniques. The Jac.-coef. succeeds in separating the two groups not because it is superior to the others, but only because T. tenuis, being very scarce, joins the group at a very low similarity level.

P. BELL LIVING MOLLUSCA.

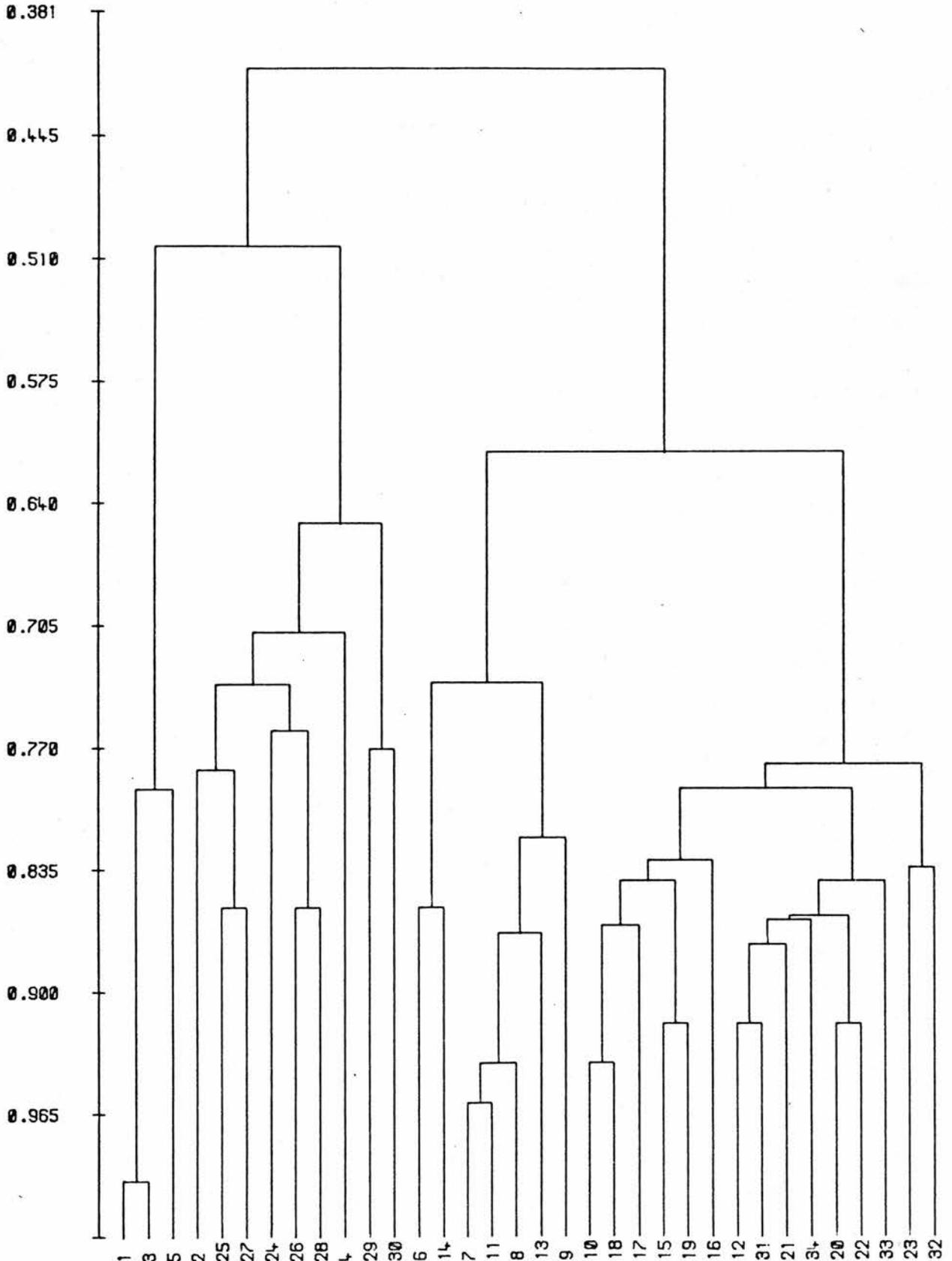
For the same reasons stated previously for the R.Z. living mollusca, the five species reported by Bell et al. (1978), all mud-tolerant, cannot be expected to give a clear picture of the environment in which they occur. However at the three-groups level, the two groups comprising Macoma-Cardium and Mytilus-Littorina are similar to the two mud-tolerant groups defined by R. Z. dead populations. These two groups are distinct in all dendrograms except those produced by Jac.-coef. and Czek.-coef. The close similarity of the two mud-tolerant groups derived from live and dead forms does not allow any conclusions because of the inadequacy of samples collected by Bell.

CONCLUSIONS

1. Lack of objective criteria to decide a priori which of the classificatory techniques is best, demands that different combinations of alternative techniques be used. From the resulting classifications the one that makes more sense ecologically, or leads to a more meaningful environmental interpretation, can be considered more valid.
2. Empirically tested "best" techniques do not guarantee the best results with all types of data. Thus the Jac.-coef. with W.P.G.A. is not the best selection in all cases, when biofacies are desired. In this biofacies analysis the Jac.-coef. and its monotonic Czek.-coef. produced the least meaningful results ecologically for all three sets of data.
3. The choice of similarity coefficient is critical to the resulting classifications. All three sets of data were insensitive to clustering techniques but very sensitive to the similarity coefficients used.
4. Binary data contain enough information for the recognition of biofacies provided that the appropriate coefficient is used.
5. Unless a sample adequately represents the population of organisms at a station, the biofacies designated are of doubtful validity.



Dendrogram 7.1 Dendrogram for biofacies analysis of the R.Z. dead molluscan populations using the r-coef., raw numerical data and U.P.G.M.A. Values along Y-axis are fusion coefficients. Numbers along X-axis correspond to species 1-34 of Appendix 2.1.



Dendrogram 7.2 Dendrogram for biofacies analysis of the R.Z. dead molluscan populations using the Mat.-coef., binary data and U.P.G.M.A. Values along Y-axis are fusion coefficients. Numbers in X-axis correspond to species 1-34 of Appendix 2.1.

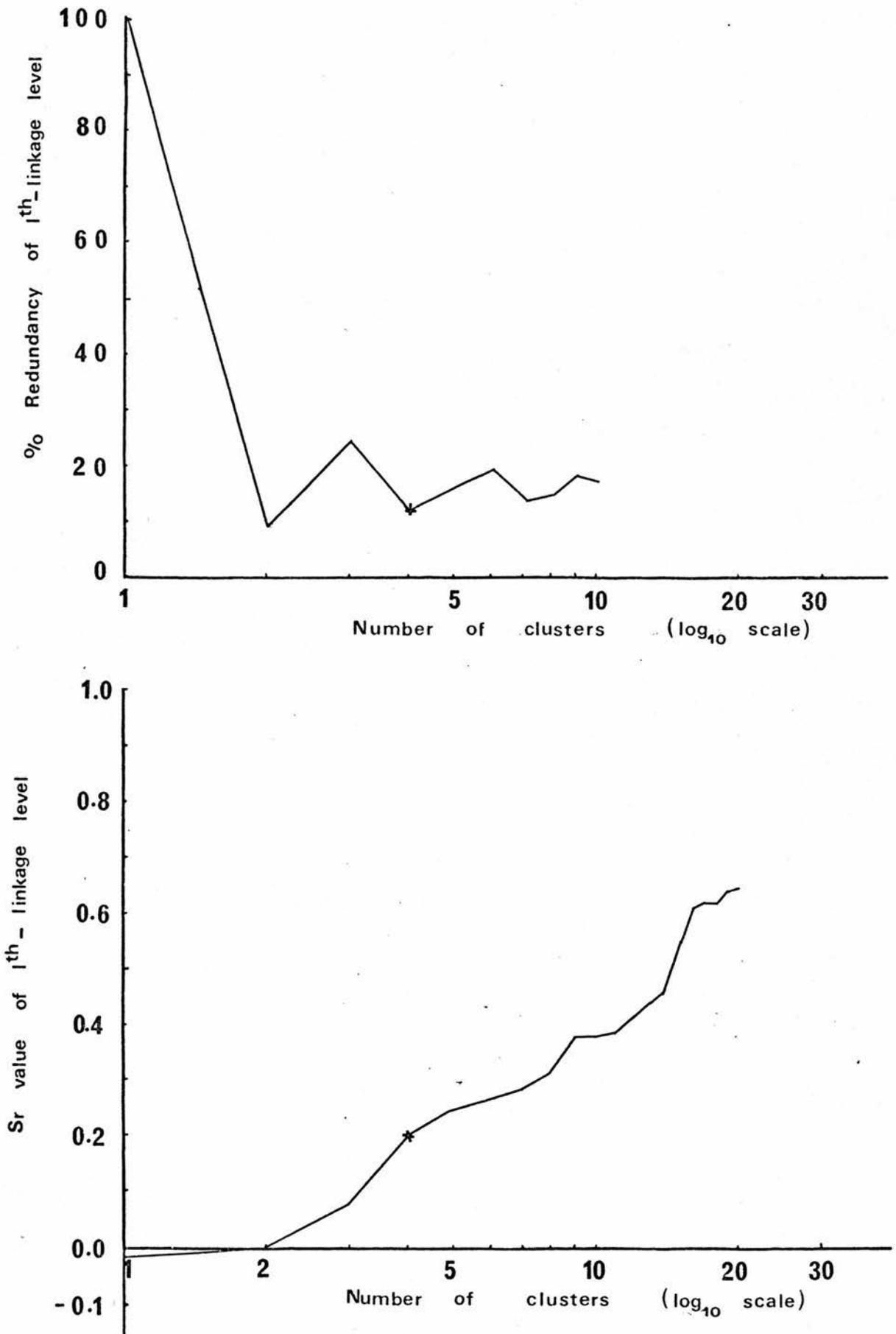


Fig.7.1 Structure of Dendrogram 7.1 in terms of (a) Redundancy associated with 1-th linkage level and (b) Sr value of 1-th linkage level associated with number of clusters, justifying the "cut off" at the 4 clusters level (cross on figure).

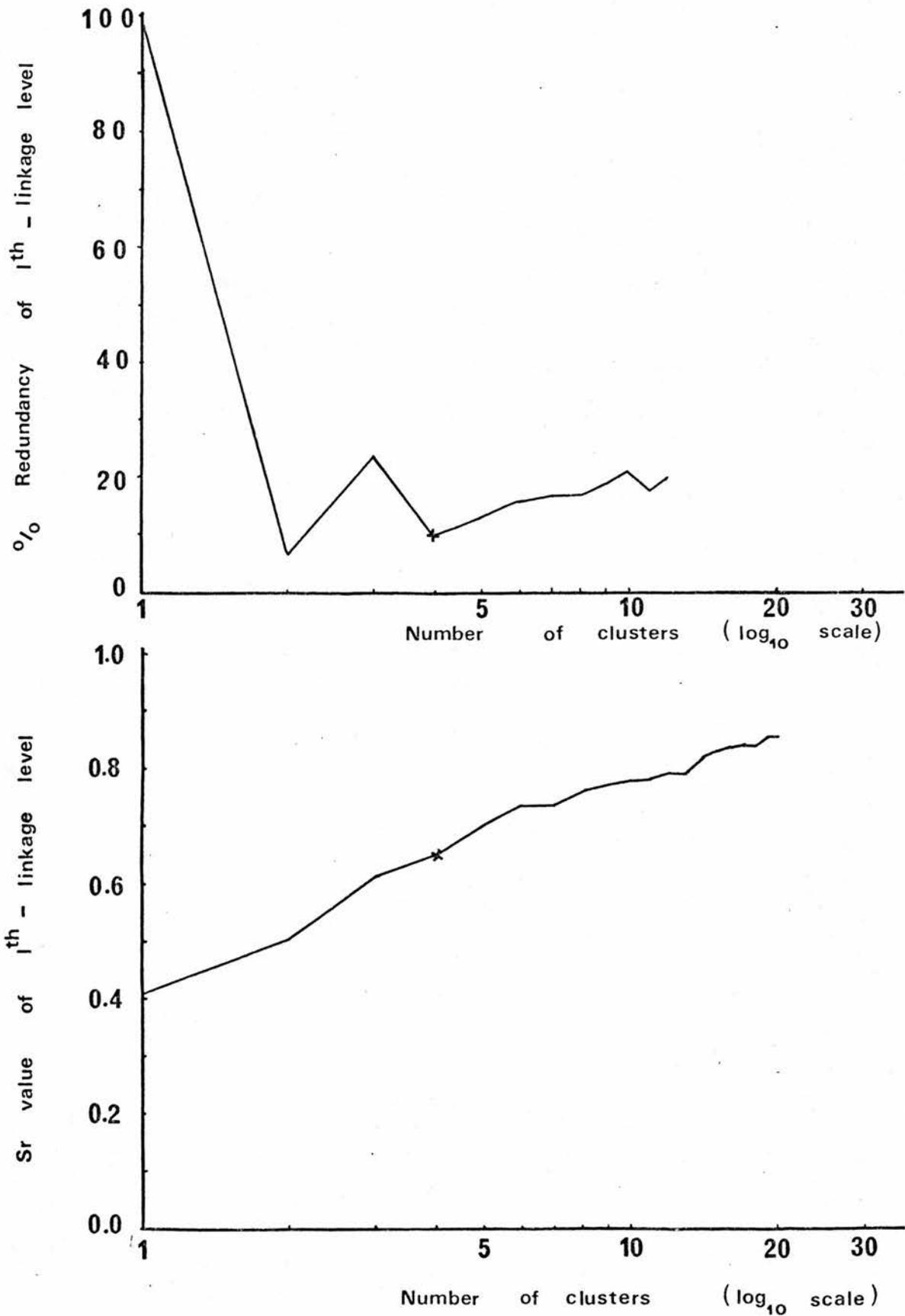


Fig.7.2 Structure of Dendrogram 7.2 in terms of (a) Redundancy associated with l-th linkage level and (b) Sr value of l-th linkage level associated with number of clusters, justifying the "cut off" at the 4 clusters level (cross on figure).

CHAPTER 8
BIOTOPES ANALYSIS.

Three sets of data are examined here. Samples are related one to the other on the basis of (a) the R.Z. dead Mollusca (b) the R.Z. living Mollusca and (c) the P. Bell living Mollusca.

R.Z. DEAD MOLLUSCAN BIOTOPES

A plethora of different classifications results from the sensitivity of data to both similarity/dissimilarity coefficients and clustering methods when defining biotopes. Sites rich in species diversity join larger clusters at very low similarity levels thus giving many single site groups; while poor sites are clustered with equally poor sites by other methods irrespective of the fauna present, resulting in meaningless classifications. However, a few combinations of the clustering techniques at the two groups level can distinguish successfully a muddy from a sandy biotope. Furthermore some methods can quite satisfactorily separate three or four biotopes corresponding to natural patterns. Only the methods leading to the best classifications (more meaningful environmental interpretation) will be discussed here and those considered as "standard" in the past. Selection of biotopes from the dendrograms is arbitrary with single site groups (due to either poor or extremely rich sites) omitted, instead of objective partitioning which produced too many single site groups.

(1) Using binary data.

The Jac.-coef. and its monotonic Czek.-coef. with W.P.G.A. at the two groups level distinguish clearly the sand and mud flats but fail at higher similarity level. The U.P.G.M.A. computed from Jaccard and Czek.-coef. matrices succeed further in distinguishing two sand biotopes North and South of the channel at the mouth of the estuary.

Sand and mud flats is the closest meaningful classification the Mat.-coef. and D-coef. lead to with U.P.G.M.A. The Mat.-coef. with W.P.G.A. can however discriminate four meaningful biotopes - two in the sand flats and two in the mud flats - when different similarity levels are considered (Dendrogram 8.1). The four biotopes are shown in Fig. 8.1 and will be discussed in detail later.

(2) Using numerical data

The r-coef. matrix calculated from standardized-by-species data and clustered by U.P.G.M.A. generates three biotopes - one in the sand flats and two in the mud flats - resembling the faunally uniform areas inspected during field observations. The r-coef. and D^{*}-coef. of standardized-by-site data and clustered by W.P.G.A. produce identical results at the four group level (dendrogram 8.2, Fig. 8.2) being:

- (a) the Edenside Flat and the marginal areas of the Kincaple Flat.
- (b) Mytilus edulis banks and their immediate surroundings
- (c) transitional sites at the borders of mud and sand flats and
- (d) the sand flats.

Four different biotopes are determined from dendrograms constructed by Lance and Williams and Ward's method of D-coef. calculated from standardized-by-species data. Yet in this "best" classification a few poor sites on the Edenside and Kincaple Flats are misclassified. Only the results of Ward's clustering method are given here in dendrogram 8.3 and are illustrated in Fig. 8.3. The resultant biotopes are:
Biotope I located mainly on the North bank of the Eden channel in the mouth of the estuary with a few sites in the middle

estuary. The poor sites of Edenside Flat are placed here simply because of the blind objectivity of the method where poor sites are clustered together at high similarity levels.

Biotope II occupies the Southern sand flat at the mouth of the Eden

Biotope III extends over the Edenside Flat and marginal areas of the Kincaple Flat and

Biotope IV includes the Mytilus edulis banks and the area surrounding them in the middle estuary

EVALUATION OF METHODS

The biotopes illustrated in the dendrograms depend as much on the clustering method as on the similarity/dissimilarity measure used. For numerical data the type of standardization (by sites or by species) is also critical to the resulting dendrogram.

As for biofacies, it can be seen here that binary data contain enough information to give a clear picture of the area but caution must prevail in the selection of the techniques to be used. The Mat.-coef./W.P.G.A. combination produces biotopes in full agreement with the biotopes obtained by the D-coef. of standardized-by-species data when clustered by Ward's or Lance and Williams method. Among binary similarity measures the Mat.-coef. gives the best fit to expected biotopes (according to field observations). This is in agreement with Kaesler's (1966) conclusions that "Dendrograms computed from \mathcal{Q} -matrices of simple Matching Coefficients are suitable for defining quantitative biotopes".

With numerical data, standardization-by-species,

computation of Squared Euclidean Distance and clustering by Ward's or Lance-Williams method, is the best combination leading to successfully defined biotopes. The results of this study are in disagreement with Michie's (1978) suggestion for standardization by sites and clustering with W.P.G.A. of D-coef. They are in agreement with Field (1970): "when 50% or more of the data entries are zero the r-coef. should be avoided" and with Sokal and Sneath (1963) that "doubt must prevail about the significance of r-coef. for a Q-type study.

Among the clustering methods Ward's was marginally better than Lance and Williams but both proved successful for the D-coef. matrix. The rest (N.N., F.N., U.P.G.M.A., Centroid, Median, McQuitty's) were inferior in their performance.

R.Z. LIVING MOLLUSCAN BIOTOPES.

It is not likely that biotopes identical to those previously defined will be obtained from R.Z. living Mollusca data considering (a) the low species diversity on which they are based (10 species against 34 of dead Mollusca) (b) the low population densities (c) that sites with no living Mollusca are excluded from the study leaving thus fewer sites to be compared (35 against 48 sites with dead Mollusca) and (d) the inadequacy of data (due to sampling). Yet limited conclusions can and must be drawn from such data.

(1) Using binary data

The Jac.-coef. produces similar results for W.P.G.A. and U.P.G.M.A. but with the latter giving more meaningful ecological patterns. The Mat.-coef. gives better results and

shows only minor differences between dendrograms obtained by W.P.G.A. and U.P.G.M.A. Both binary coefficients separate clearly the two mud biotopes (III and IV) produced by numerical coefficients based on dead Mollusca and corresponding to natural patterns observed during field observations, plus one or two sandy biotopes (I and II) similar to the ones produced by dead Mollusca (dendrogram 8.4, Fig. 8.4).

(2) Using numerical data

The biotopes derived by D-coef. and r-coef. of standardized-by-site data and clustered by W.P.G.A. are identical to those produced by the same methods but based on dead Mollusca.

All other dendrograms either generate biotopes which are not mappable, or show one main cluster and many single site groups or illustrate classifications which do not reflect any natural pattern.

EVALUATION OF METHODS.

Despite the inadequacy of data biotopes illustrated by the dead Mollusca can also be distinguished clearly by the living Mollusca.

The Matching coefficient is superior in its performance to all binary coefficients used with few differences shown between dendrograms computed by W.P.G.A. and U.P.G.M.A. clustering method.

The numerical coefficients fail to recognize the four biotopes possibly due to low population densities of the few species present in the sites. Yet the D-coef. and r-coef. matrices of standardized-by-site data, clustered by W.P.G.A. method succeed in discriminating successfully at least the two

muddy biotopes (III and IV).

P. BELL LIVING MOLLUSCAN BIOTOPES.

The five molluscan species reported as living in the Eden estuary by P. Bell are not sufficient to illustrate the differences between the biotopes they are sampled from. None of the combinations of clustering techniques examined give mappable, meaningful biotopes. Had the data been adequate the two muddy biotopes III and IV should have been conspicuous as well as biotope I as a zone between Sanctuary Spit and the flood-tidal delta. Biotope II could not have been detected since Bell's sampling stations cover only the upper and middle estuary.

STABILITY OF CLUSTERS.

One of the primary aims of Numerical Taxonomy is reproducibility of results. A means of testing the stability of the obtained clusters, used by Stephens & Dawson (1977), involves randomly splitting the complete sample set into two subsets and repeating the clustering process. Partition of the results of dendrograms takes place at the same number of clusters as for the complete set. The clusters produced by each subset are then compared with those of the complete set by cluster mean matching (comparison of the mean for all variables).

Testing the stability of dead Mollusca biotopes in the Eden estuary, the samples are split into two subsets so that each subset contains one sample from each site. Had the two samples in each site been identical, identical biotopes would have been generated. In reality, no two samples are ever identical and therefore identical biotopes are not expected.

In fact using the "best behaved" combination of D-coef., standardization by species and clustering by Ward's method very similar results are obtained.

The mean of each variable in each biotope for the complete set (X_{TOT}) and the two subsets (X_A, X_B), is given in Table 8.1. When plotting the logarithm of the mean of each variable for the complete set and the two subsets (X_{TOT}, X_A, X_B) against the variables of each biotope the results are speculative. The plots for the two subsets for each biotope I-IV, show a close fit to the plot designed by the complete set (Fig. 8.5 a-d), indicative of the stability of clusters. Indeed, four biotopes are determined by both subsets two in the sand flats and two in the mud flats, similar to the biotopes determined by the complete set.

COMPARISON OF BIOTOPES WITH EASTWOOD'S TEXTURAL FACIES.

Four "textural facies" (groups of sediments with distinct textural attributes) were identified by the application of D-coef. and Ward's clustering method by Eastwood (1977), to the raw weight percentage grain size data obtained by sieve and pipette analysis. The same number of biotopes are recognized by the application of the same cluster analysis to the R.Z. dead Mollusca numerical data. Furthermore the distribution of the biotopes is in good agreement with the distribution of the textural facies (compare Fig. 8.3 to Fig. 1.5). In any case identical results could not be expected considering that Eastwood's analysis is based on 145 sites against the 48 of this study and should therefore lead to a more detailed representation of the existing textural facies.

Biotope I coincides in its distribution with Eastwood's textural facies I in the middle and lower estuary. However, in the Edenside Flat the dearth of molluscan species leads to misclassification as discussed earlier. The distribution of biotope II is consistent with that of textural facies II. Biotope IV has not been detected in the Edenside Flat. This is believed to be because no samples coincide with textural facies IV distribution there. Biotope IV was positively recognized as a parallel zone immediately next to the Eden channel during field observations. Biotope III, consisting of very few sites, is analogous to textural facies III which is widely distributed over the Edenside and Kincapple Flats. The reason for the discrepancy is that poor sites are grouped together with poor sites of sand flats (biotope I), while rich sites are excluded because they form individual clusters such as site H 2.

In general the distribution of biotopes (I-IV) corresponds to the distribution of textural facies (I-IV) pointing out the role of the substrate in the distribution of Mollusca. The fact that the same cluster analysis combination based on independent variables (Fauna and Sediment Size distribution) leads to similar results is also encouraging in emphasizing the objectivity of the methods used and the stability of the clusters generated.

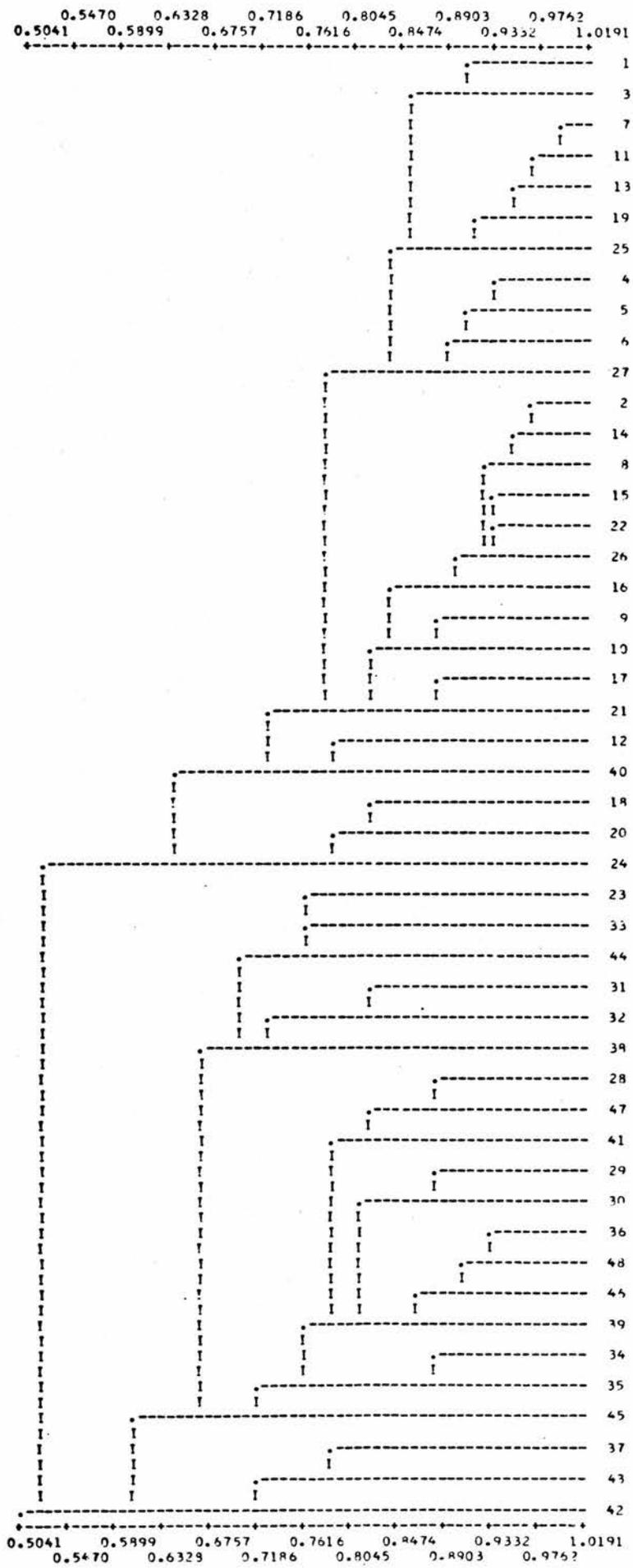
DISCUSSION - CONCLUSIONS.

The assignment of biotopes from the dendrograms is subjective as explained earlier because of the many resultant single site groups. Field observations of uniform faunas and substrates are considered to be a guide to successful interpretation of the dendrograms and the best fits are adopted as meaningful biotopes.

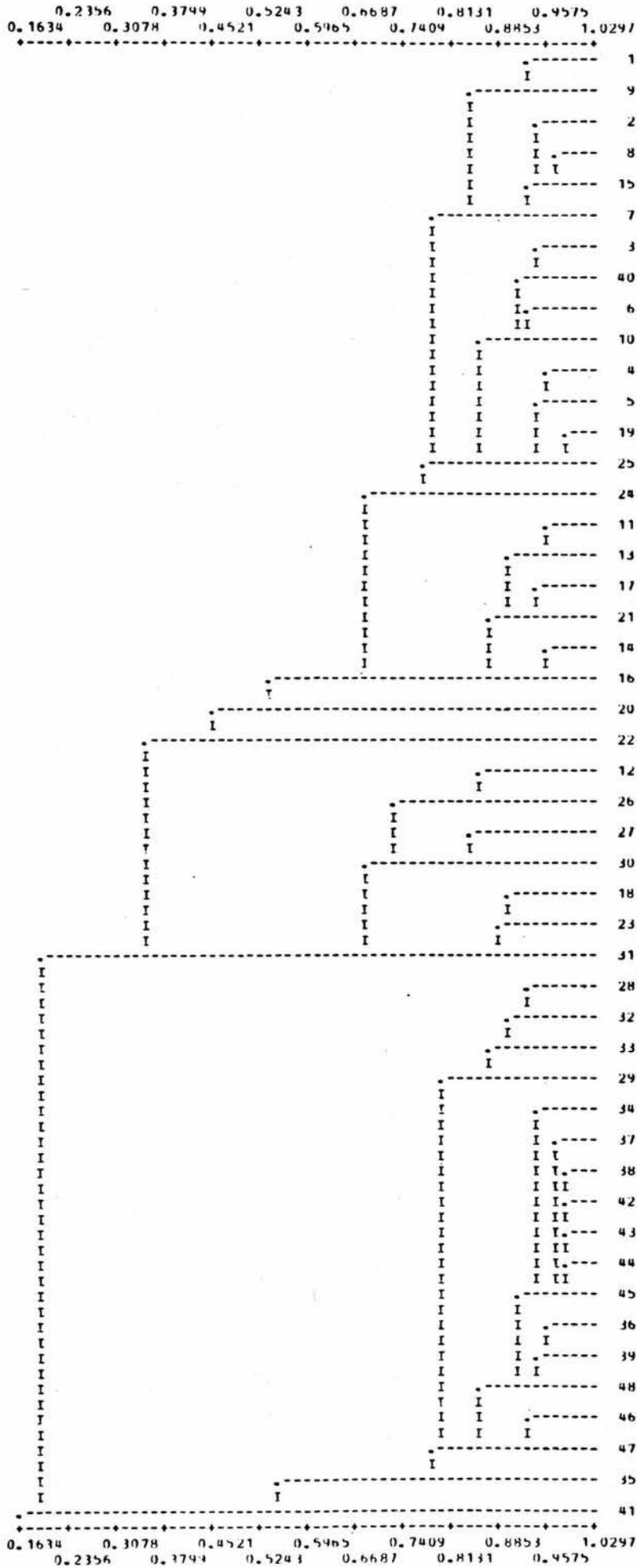
Ideally, as mentioned earlier, the R-mode analysis will show which groups of species are responsible for the Q-mode clusters the major ones of which have been interpreted here to represent biotopes. In Table 8.2 the species of dead Mollusca are listed in the order they occur in the output of the Mat.-coef./W.P.G.A. dendrogram. Opposite the species there is a chart giving the number of occurrences and percentages represented by the species in each biotope. The latter is termed sample constancy C and is defined as the percentage of samples from a biotope in which a species occurs. There are four main clusters of species (biofacies I-IV), in the original dendrogram which can also be distinguished in Table 7.1. It is obvious that Biofacies I is common throughout the four biotopes. Biofacies II occurs most commonly in biotopes II and IV but is clearly responsible for biotope IV. Biofacies III contains species which contribute almost exclusively to biotopes III and IV but at higher percentages in biotope II. Biofacies IV comprises species most common in biotopes I and II. The R-mode analysis in this case does indicate which group of species are responsible for the major Q-mode clusters.

Thorson (1957) stated that "the bottom communities are so sensitive that they may tell us more about the substratum than the substratum, treated according to recent methods, may tell us about the animals. The bottom animals can give a much finer analysis of the bottom than we can, and therefore are to be regarded as the best starting point for ecological studies". The recent development and widespread application of Numerical Taxonomy techniques promise a successful objective classification whichever way the analysis takes place. The textural facies

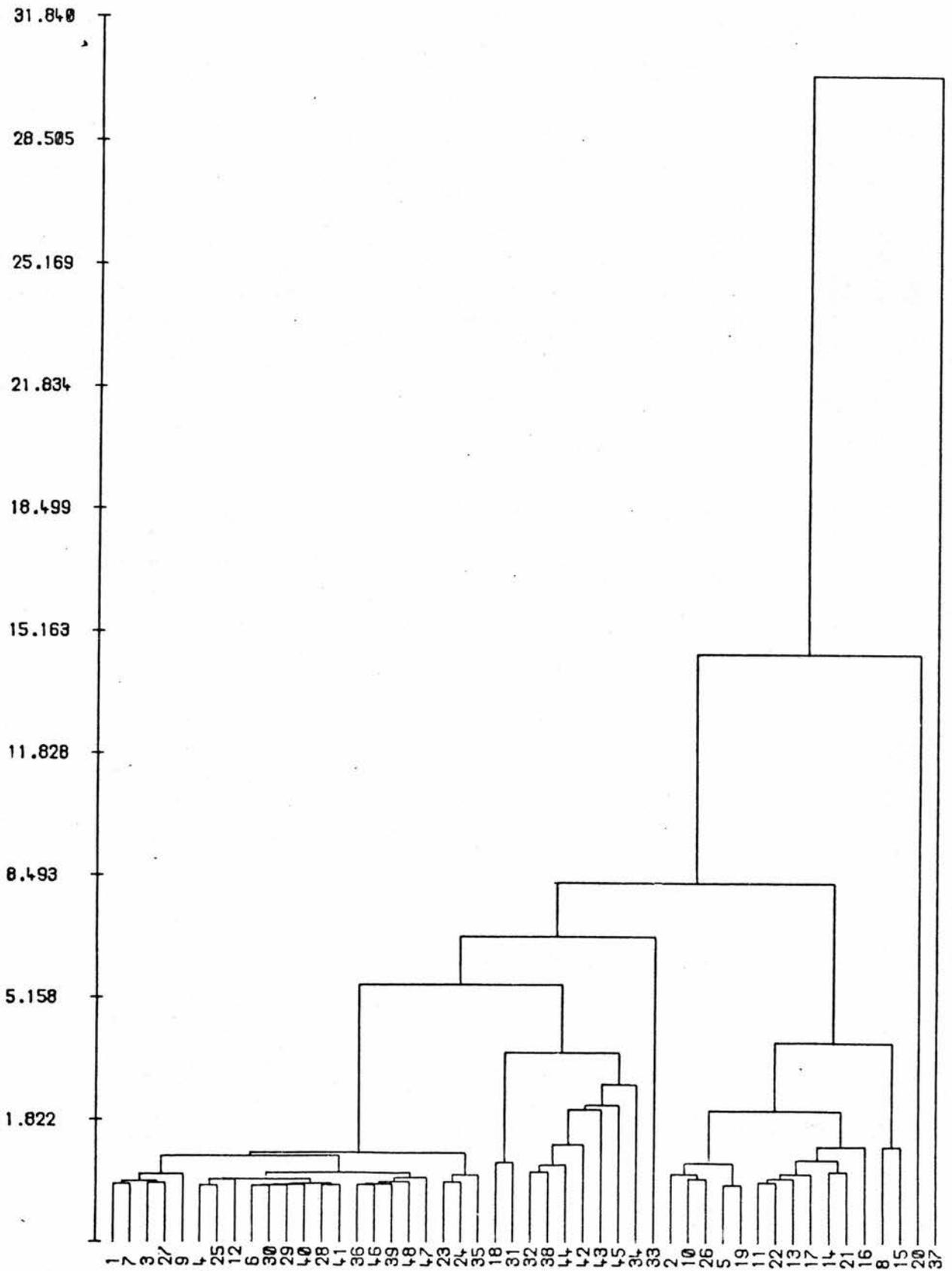
identified by Eastwood (1977) are consistent with the biotopes defined in this study. This means that sedimentary analysis can determine "areas of uniform environmental conditions" as successfully as biotopes analysis can. Thus the term biotope is extended to include the substrate or better emphasize the substrate instead of being vague about environmental conditions. It is encouraging that the biotopes of this study are so closely related to Eastwood's textural facies suggesting that the main factor determining the distribution of Mollusca in the Eden estuary is the grain size of the substrate. No analysis based on salinity, temperature or other distribution factors has been attempted and therefore no conclusions can be drawn regarding their role as "environmental conditions" in the biotopes already designated. It is also suggested that although direct relationships of the subfossil assemblages to the indigenous living population are attenuated, palaeoecological interpretation of a subfossil assemblage can be made most efficiently by direct comparison of subfossil distribution patterns with external ecological and physical parameters of the area (e.g. sediment size distribution). Yet valuable, limited conclusions can be drawn from the similar biotope patterns produced by the living and subfossil Mollusca. It is very unlikely that this would happen unless 1) the transportation of dead shells is negligible 2) transportation is systematic affecting all samples equally. All other lines of evidence indicate that the shells in the Eden estuary are not transported away from their proper habitats after death and the results of this study are another positive step to this suggestion.



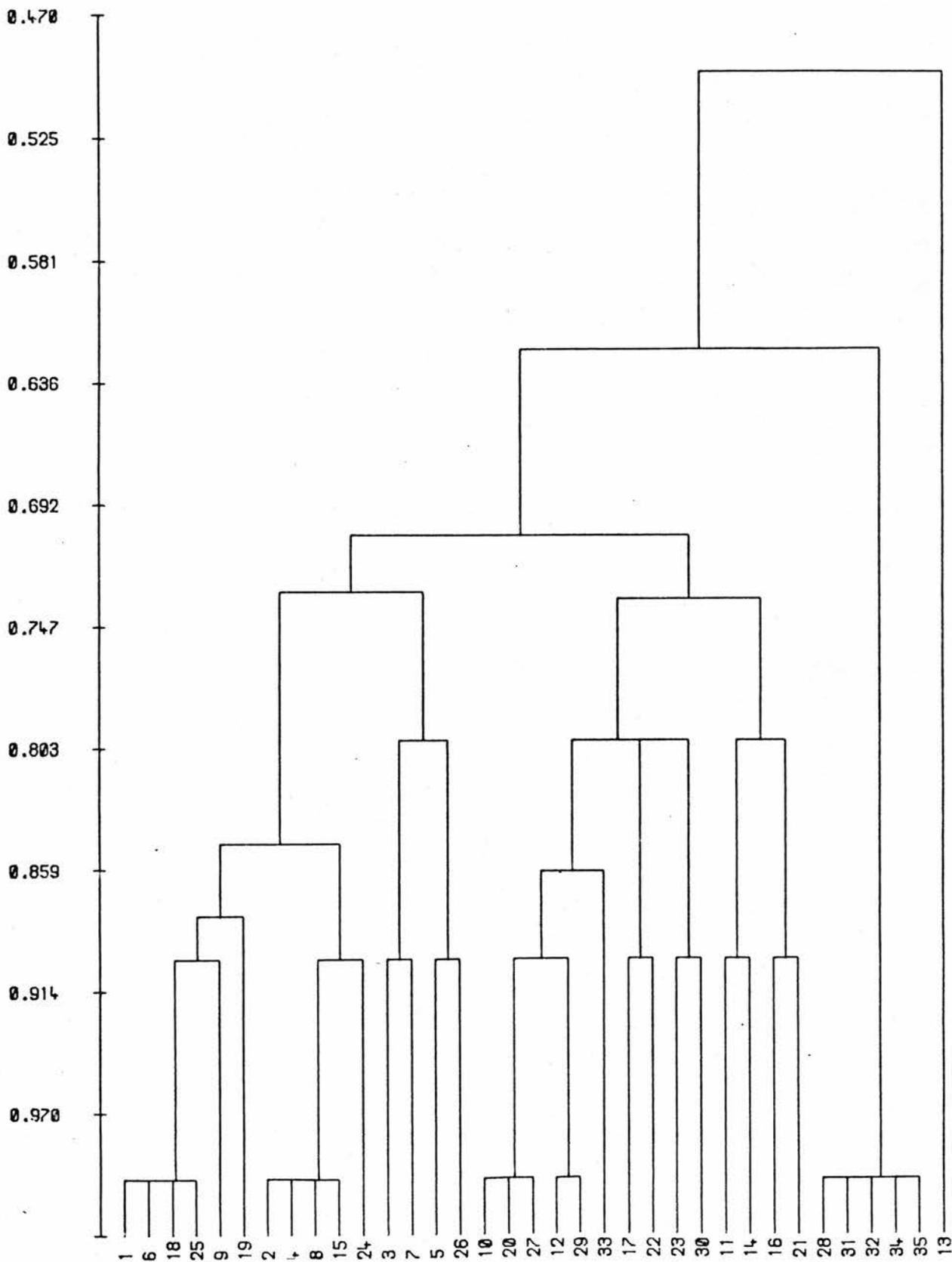
Dendrogram 8.1 Dendrogram for biotopes analysis of the R.Z. dead Mollusca using the Mat.-coef., binary data and W.P.G.A. Values along X-axis are fusion coefficients. Numbers along Y-axis correspond to sampling sites of Appendix 2.1.



Dendrogram 8.2 Dendrogram for biotopes analysis of the R.Z. dead Mollusca using the r-coef. with standardized-by-site numerical data and W.P.G.A. Values along X-axis are fusion coefficients. Numbers along Y-axis correspond to sampling sites of Appendix 2.1.



Dendrogram 8.3 Dendrogram for biotopes analysis of the R.Z. dead Mollusca, using the D-coef. with standardized-by-species numerical data and Ward's clustering method. Values along Y-axis are fusion coefficients. Numbers along X-axis correspond to sites 1-48 of Appendix 2.1.



Dendrogram 8.4 Dendrogram for biotopes analysis of the R.Z. living Mollusca, using the Mat.-coef. with binary data and U.P.G.M.A. Values along Y-axis are fusion coefficients. Numbers along X-axis correspond to sites 1-35 of Appendix 2.2.

- BIOTOPE I
- ◇ BIOTOPE II
- ▼ BIOTOPE III
- BIOTOPE IV

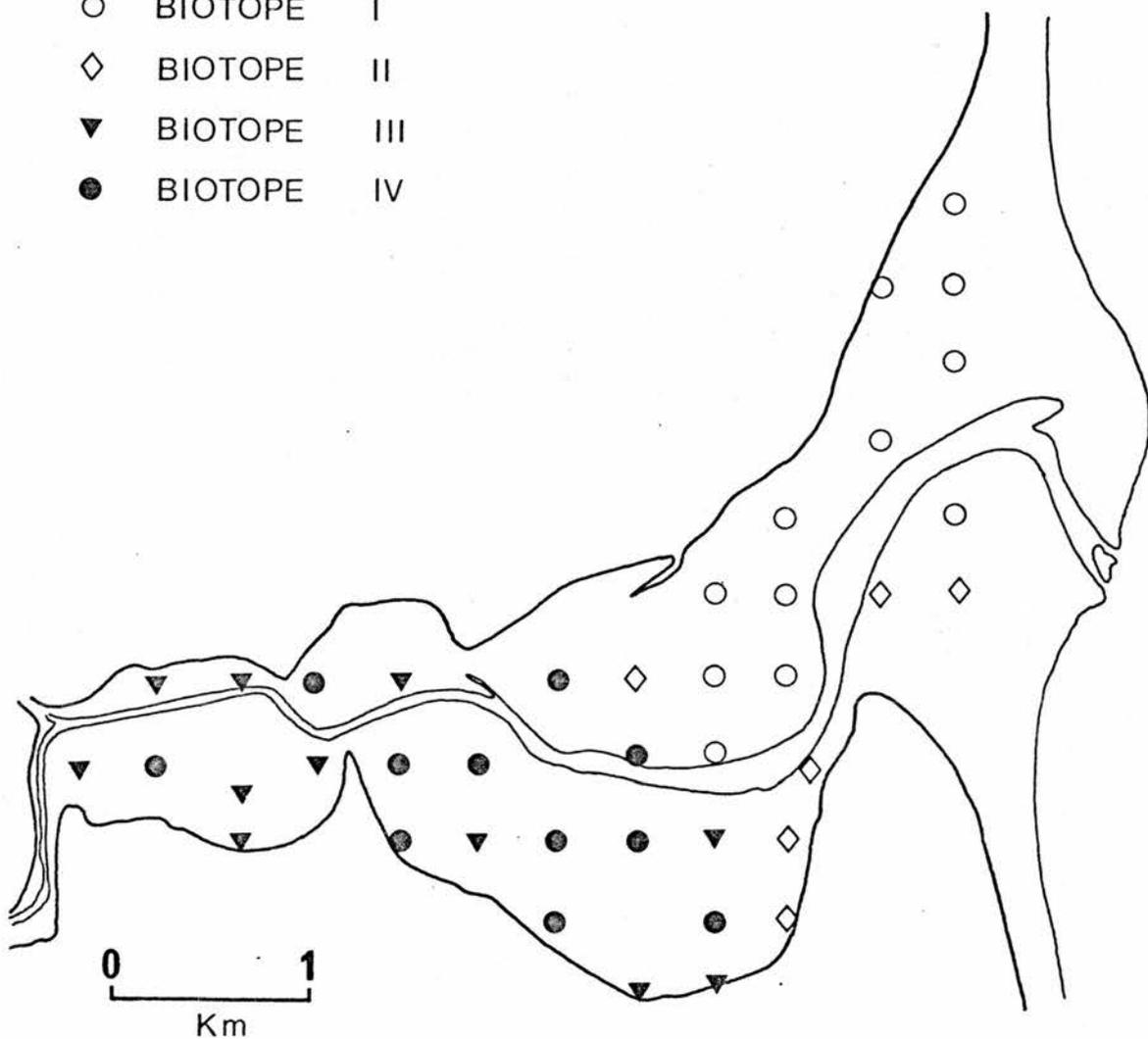


Fig. 8.1 Areal representation of Q-mode clusters (biotopes) obtained by Dendrogram 8.1 for the R.Z. dead Mollusca.

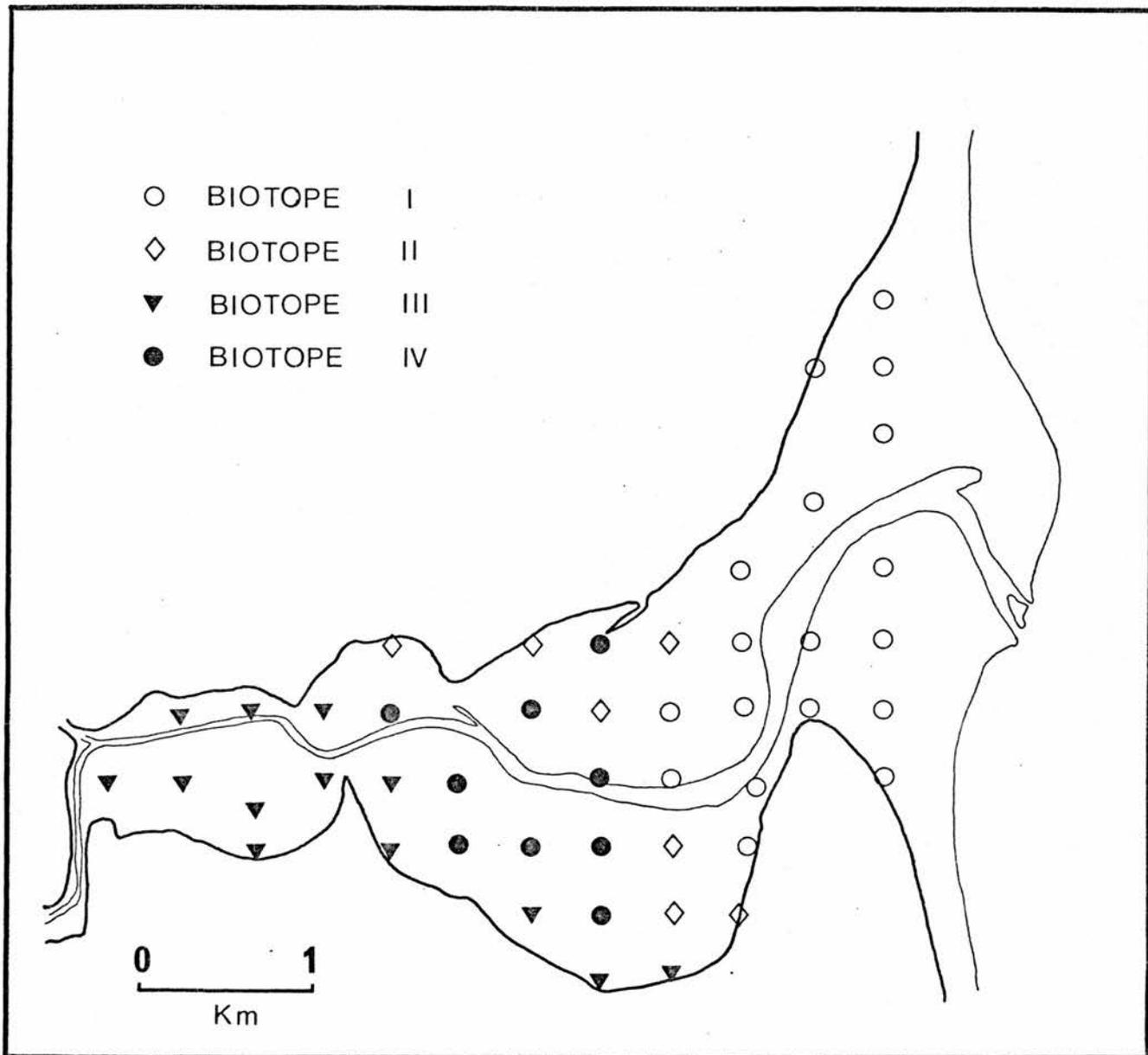


Fig. 8.2 Areal representation of Q-mode clusters (biotopes) obtained by Dendrogram 8.2 for the R.Z. dead Mollusca.

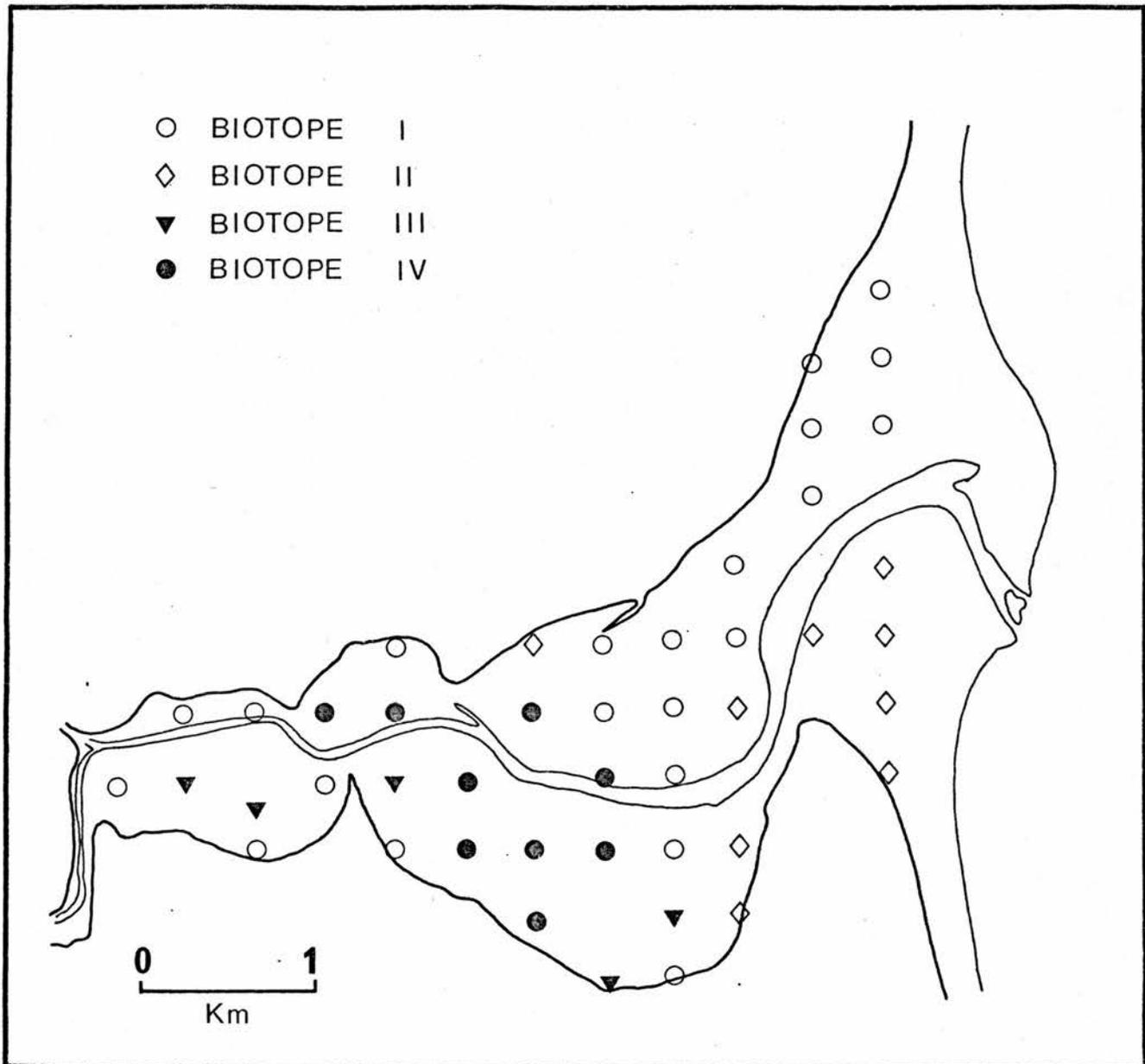


Fig. 8.3 Areal representation of Q-mode clusters (biotopes) obtained by Dendrogram 8.3 for the R.Z. dead Mollusca.

- BIOTOPE I
- ▼ BIOTOPE III
- BIOTOPE IV

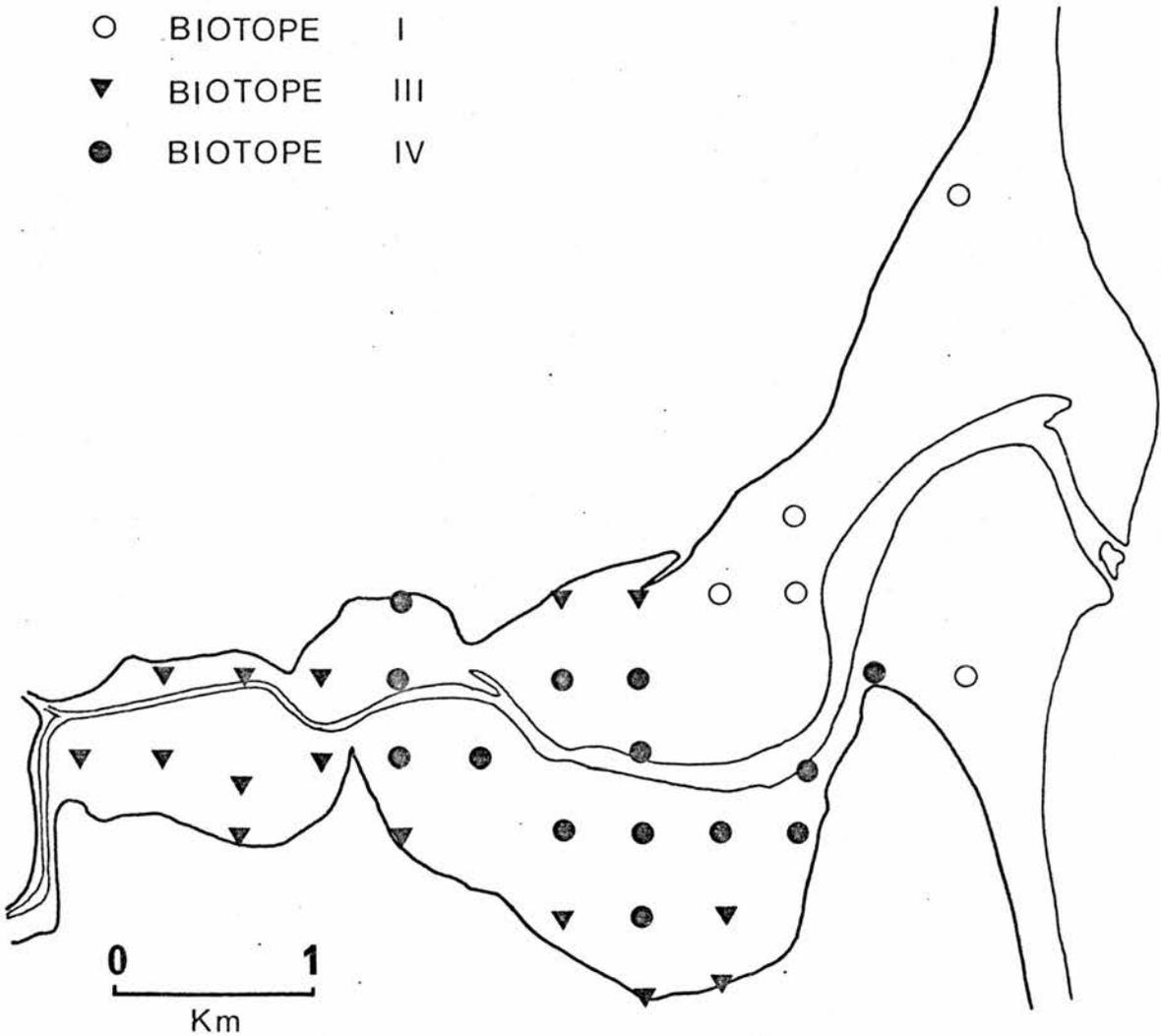


Fig. 8.4 Areal representation of Q-mode clusters (biotopes) obtained by Dendrogram '8.4 for the R.Z. living Molluska. Biotope II (a sandy one) is not detected from the R.Z. living molluscan populations.

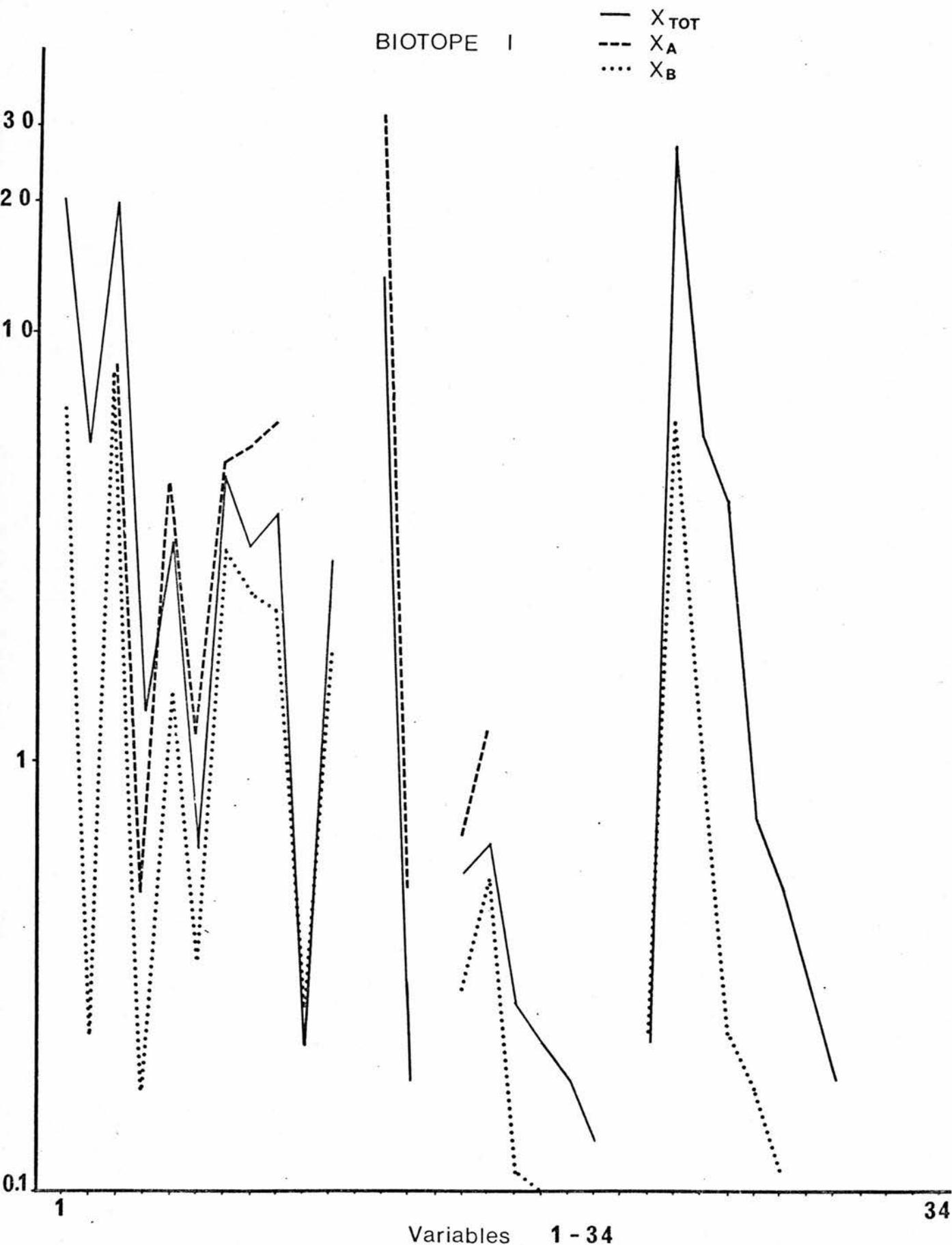


Fig. 8.5a Stability of Biotope I. Plot of means (in log unit) of each variable (1-34) for total sample set and each of two subsets (A & B) indicating close correspondence between set and subsets. This is taken to reflect a basic reproducible structure in the data. The data used are tabulated in Table 8.1.

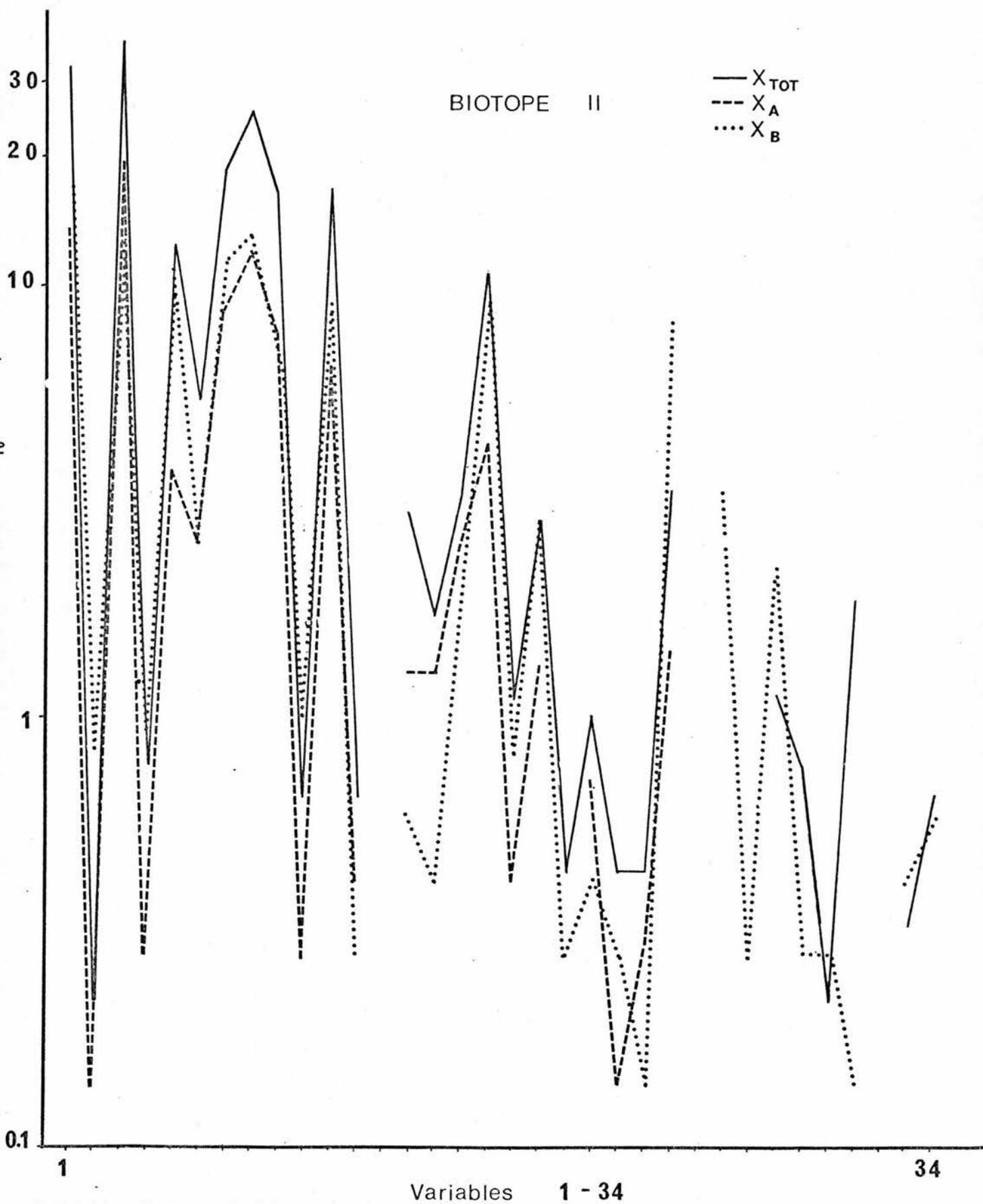


Fig. 8.5b Stability of Biotope II. Plot of means (in log unit) of each variable (1-34) for total sample set and each of two subsets (A & B) indicating close correspondence between set and subsets. This is taken to reflect a basic reproducible structure in the data. The data used are tabulated in Table 8.1.

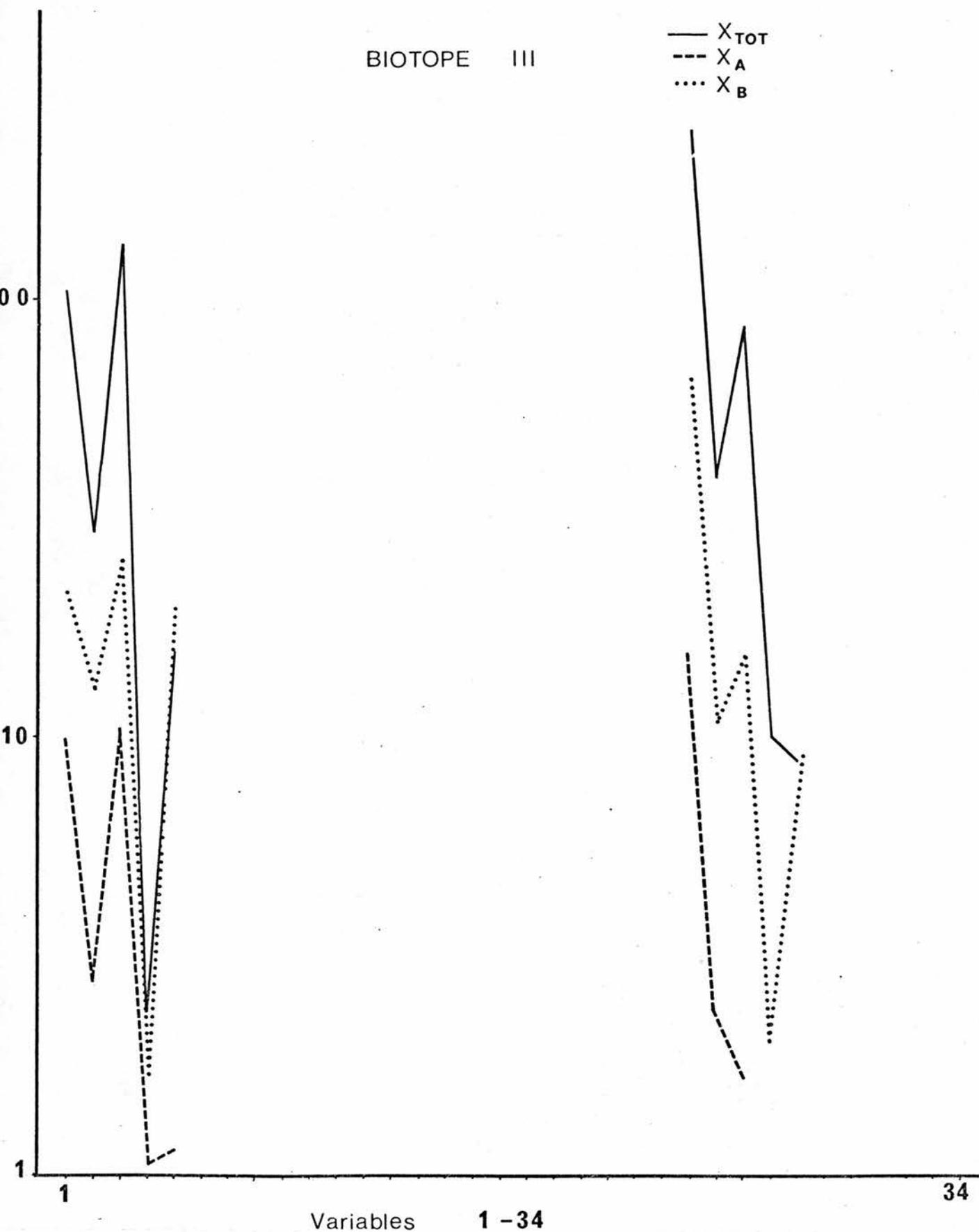


Fig. 8.5c Stability of Biotope III. Plot of means (in log unit) of each variable (1-34) for total sample set and each of two subsets (A & B) indicating close correspondence between set and subsets. This is taken to reflect a basic reproducible structure in the data. The data used are tabulated in Table 8.1.

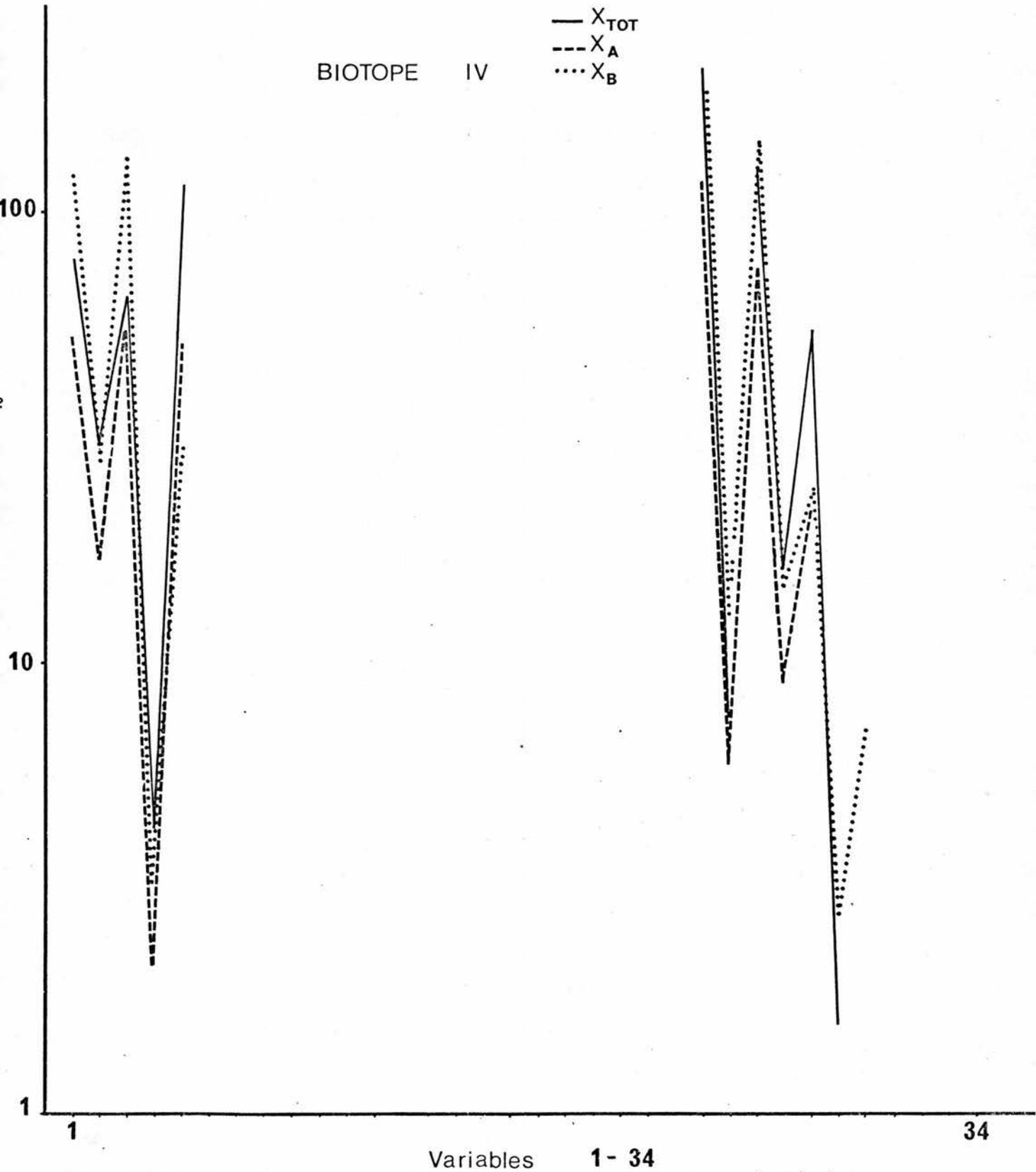


Fig. 8.5d Stability of Biotope IV. Plot of means (in log unit) of each variable (1-34) for total sample set and each of two subsets (A & B) indicating close correspondence between set and subsets. This is taken to reflect a basic reproducible structure in the data. The data used are tabulated in Table 8.1.

BIOTOPES

BIOFACIES		I		II		III		IV	
		N	C	N	C	N	C	N	C
I	Macoma	12	92%	6	100%	11	100%	11	100%
	Cardium	11	92%	6	100%	11	100%	11	100%
	Mytilus	12	100%	4	67%	6	55%	11	100%
II	Scrobicularia	1	8%	0		9	82%	10	91%
	Potamopyrgus	0		0		9	82%	9	82%
	L. littorea	0		0		6	55%	11	100%
	Hydrobia	2	17%	4	67%	10	91%	11	100%
	L. saxatilis	0		4	67%	8	73%	11	100%
	L. littoralis	0		3	50%	5	45%	11	100%
	Mya arenaria	1	8%	3	50%	5	45%	11	100%
	Nucella	0		6	100%	0		7	64%
	Retusa	0		1	17%	1	9%	9	82%
	Solen-Ensis	6	50%	6	100%	1	9%	1	9%
	III	Lutraria	3	25%	6	100%	0		0
Montacuta		3	25%	2	33%	0		0	
Abra abra		6	50%	2	33%	0		0	
Pecten		3	25%	1	17%	0		0	
Anomia		3	25%	2	33%	0		0	
Ostrea		5	42%	6	100%	0		0	
Thracia		5	42%	4	67%	0		0	
Docinia		1	8%	1	17%	0		0	
Natica		1	8%	2	33%	0		1	9%
Hiatella		2	17%	1	17%	0		0	
Nucula		3	25%	1	17%	0		0	
IV	Gari	0		1	17%	0		0	
	Patella	1	8%	1	17%	0		2	18%
	Tritonalia	1	8%	2	33%	0		2	18%
	Corbula	1	8%	1	17%	0		2	18%
	Buccinum	1	8%	2	33%	0		0	
	T. fabula	12	100%	6	100%	0		1	9%
	Venus	12	100%	6	100%	1	9%	1	9%
	T. tenuis	12	100%	6	100%	0		0	
	Donax	12	100%	6	100%	0		4	36%
	Spisula-Mactra	10	83%	6	100%	0		5	45%

TABLE 8.2.

Number of occurrences (N) and sample constancy (C) of species of dead molluscs (biofacies I-IV) for the biotopes I-IV of Fig. 8.1.

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APPENDIX 1.
NUMERICAL COEFFICIENTS.

1. Product moment similarity coefficient (r - coef.).

$$r = \frac{\sum_{i=1}^n (x_{ij} - \bar{x}_j) \cdot (x_{ik} - \bar{x}_k)}{\sqrt{\sum_{i=1}^n (x_{ij} - \bar{x}_j)^2 \cdot (x_{ik} - \bar{x}_k)^2}}$$

2. Taxonomic Distance (D*-coef.).

$$D^* = \sqrt{\sum_{i=1}^n \frac{(x_{ij} - x_{ik})^2}{n}}$$

3. Squared Euclidean Distance (D-coef.).

$$D = \frac{1}{n} \sum_{i=1}^n (x_{ij} - x_{ik})^2$$

In the foregoing equations we interpret the following symbols to mean: n the number of observations, j, k the observed variables, x the value for each variable and finally \bar{x} the mean value for each variable.

APPENDIX 2.1.

R.Z. DEAD MOLLUSCA

SAMPLING SITES 1-7

SPECIES 1-34		A4	B4	B5	C3	C4	C5	D4
		1	2	3	4	5	6	7
<i>Macoma balthica</i>	1	72	289	23	13	22	2	52
<i>Scrobicularia plana</i>	2	28	76	21	6	11	2	56
<i>Cardium edule</i>	3	31	208	21	2	28	4	70
<i>Mya arenaria</i>	4	3	5	8	-	-	-	6
<i>Mytilus edulis</i>	5	1	14	-	-	-	1	17
<i>Solen-Ensis</i>	6	1	-	-	-	-	-	-
<i>Tellina fabula</i>	7	-	-	-	-	-	-	-
<i>Tellina tenuis</i>	8	-	-	-	-	-	-	-
<i>Spisula-Mactra</i>	9	-	1	-	-	-	-	-
<i>Montacuta ferruginosa</i>	10	-	-	-	-	-	-	-
<i>Venus stratula</i>	11	-	-	1	-	-	-	-
<i>Dosinia sp.</i>	12	-	-	-	-	-	-	-
<i>Donax vittatus</i>	13	-	-	-	-	-	-	-
<i>Lutraria lutraria</i>	14	-	-	-	-	-	-	-
<i>Pecten sp.</i>	15	-	-	-	-	-	-	-
<i>Ostrea edulis</i>	16	-	-	-	-	-	-	-
<i>Thracia sp.</i>	17	-	-	-	-	-	-	-
<i>Abra alba</i>	18	-	-	-	-	-	-	-
<i>Anomia sp.</i>	19	-	-	-	-	-	-	-
<i>Nucula nucleus</i>	20	-	-	-	-	-	-	-
<i>Hiatella arctica</i>	21	-	-	-	-	-	-	-
<i>Gari fervensis</i>	22	-	-	-	-	-	-	-
<i>Corbula gibba</i>	23	-	-	-	-	-	-	-
<i>Hydrobia ulvae</i>	24	90	417	77	58	104	6	106
<i>Potamopyrgus jenkinsi</i>	25	20	44	10	22	48	0	21
<i>Littorina saxatilis</i>	26	16	283	6	5	-	-	45
<i>Littorina littorea</i>	27	4	20	3	-	-	-	5
<i>Littorina littoralis</i>	28	-	10	-	-	-	-	5
<i>Nucella lapillus</i>	29	-	1	-	-	-	-	-
<i>Retusa obtusa</i>	30	-	6	-	-	1	-	-
<i>Natica alderi</i>	31	-	-	-	-	-	-	-
<i>Buccinum undatum</i>	32	-	-	-	-	-	-	-
<i>Patella sp.</i>	33	-	-	-	-	-	-	-
<i>Tritonalia aciculata</i>	34	-	-	-	-	-	-	-

APPENDIX 2.1 Continued

SAMPLING SITES 17 - 25

SPECIES	G5	G6	H1	H2	H3	H4	H5	H6	I1
1 - 34	17	18	19	20	21	22	23	24	25
1	58	47	5	568	76	10	65	35	15
2	21	2	-	206	80	5	-	5	-
3	28	94	5	1215	49	55	71	12	2
4	3	1	-	13	2	6	2	1	-
5	73	2	4	55	178	103	-	-	-
6	-	2	-	1	-	-	4	1	-
7	-	3	-	11	-	-	14	16	-
8	-	2	-	9	-	-	2	6	-
9	1	13	-	2	-	-	7	-	-
10	-	-	-	-	-	-	-	-	-
11	-	7	-	12	-	-	16	5	-
12	-	-	-	-	-	-	-	-	-
13	1	38	-	71	-	1	68	32	-
14	-	7	-	2	-	-	2	-	-
15	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	2	-	-
17	-	-	-	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-
21	-	-	-	-	-	-	-	-	-
22	-	-	-	-	-	-	-	-	-
23	-	-	-	-	-	-	-	1	-
24	72	11	285	693	251	47	4	60	89
25	-	-	49	66	-	1	-	4	20
26	46	9	8	1893	120	20	-	2	2
27	9	-	5	45	6	8	-	-	-
28	26	2	3	392	97	53	-	3	1
29	-	-	-	14	-	3	1	1	-
30	1	-	-	40	-	-	-	2	-
31	-	5	-	-	-	-	-	-	-
32	-	1	-	-	-	-	1	1	-
33	1	-	-	-	-	-	-	-	-
34	1	-	-	-	1	-	-	-	-

APPENDIX 2.1 Continued

SAMPLING SITES 26 -34

SPECIES	I2	I3	I4	I5	I6	J2	J3	J4	J5
1 - 34	26	27	28	29	30	31	32	33	34
1	105	2	2	4	2	19	28	30	10
2	46	1	-	-	1	-	-	-	-
3	287	64	8	8	13	49	43	49	19
4	2	4	-	1	-	-	-	3	-
5	55	-	2	1	2	4	-	9	7
6	-	-	-	-	-	5	6	11	3
7	-	-	5	3	5	3	19	66	20
8	-	-	5	8	4	6	15	60	23
9	1	-	3	-	-	15	14	15	6
10	-	-	1	-	-	-	-	13	-
11	-	-	2	2	1	10	16	42	9
12	-	-	-	-	-	1	-	-	-
13	9	-	12	10	4	50	75	122	73
14	-	-	-	-	-	13	2	1	1
15	-	-	1	-	-	-	-	-	12
16	-	-	1	-	1	2	6	9	1
17	-	-	1	-	2	-	10	48	-
18	-	-	1	-	-	-	-	5	2
19	-	-	-	-	-	-	-	16	2
20	-	-	-	-	-	-	-	-	-
21	-	-	-	-	-	1	-	-	-
22	-	-	-	-	-	-	-	-	-
23	-	-	-	-	-	-	2	-	-
24	146	-	-	-	-	4	8	-	-
25	25	-	-	-	-	-	-	-	-
26	99	-	-	-	-	1	2	-	-
27	17	-	-	-	-	-	-	-	-
28	29	-	-	-	-	5	2	1	-
29	2	-	-	-	-	1	2	1	-
30	5	-	-	-	-	-	-	3	-
31	-	-	-	-	-	6	3	-	-
32	-	-	-	-	-	-	-	3	-
33	-	-	-	-	-	-	-	-	-
34	-	-	-	-	-	3	-	-	-

APPENDIX 2.1 Continued

SAMPLING SITES 35 - 43

SPECIES	J6	J7	K5	K6	K8	K9	K10	L4	L5
1 - 34	35	36	37	38	39	40	41	42	43
1	3	5	169	22	8	4	-	16	47
2	-	-	-	-	-	-	-	-	-
3	6	6	135	13	7	4	-	19	55
4	-	-	2	-	-	-	-	2	2
5	3	6	29	16	4	-	1	17	41
6	2	2	37	6	2	-	-	3	12
7	8	4	115	21	7	1	4	29	34
8	5	7	104	30	7	-	2	39	64
9	5	6	68	16	10	1	2	17	40
10	2	-	8	1	-	-	-	1	4
11	5	4	86	13	7	-	2	15	41
12	-	-	3	-	-	-	-	-	2
13	11	23	770	223	27	1	2	235	578
14	-	-	4	2	1	-	-	1	-
15	1	-	-	-	-	-	-	2	1
16	6	-	14	7	-	-	-	7	6
17	-	3	89	20	-	-	-	13	18
18	2	-	8	2	-	-	1	2	3
19	4	-	33	-	1	-	-	9	14
20	-	1	8	1	-	-	-	-	3
21	-	-	10	-	1	-	-	6	2
22	-	-	5	1	-	-	-	2	1
23	1	-	9	-	-	-	-	2	-
24	-	-	7	2	-	16	3	1	4
25	-	-	2	-	-	-	-	-	-
26	-	-	-	6	-	-	-	-	1
27	-	-	2	-	-	-	-	-	-
28	-	-	4	-	-	-	-	-	1
29	-	-	2	1	-	-	-	-	2
30	-	-	4	-	-	-	-	1	1
31	-	-	8	-	-	-	-	-	2
32	1	-	-	-	-	-	-	-	-
33	-	-	1	-	-	-	-	-	-
34	-	-	8	1	-	1	-	-	1

APPENDIX 2.1 Continued

SAMPLING SITES 44 - 48

SPECIES	L6	L7	L9	L10	L11
1 - 34	44	45	46	47	48
1	40	47	2	5	9
2	-	-	-	0	-
3	20	21	3	4	4
4	2	-	-	-	-
5	18	9	5	9	12
6	4	9	2	-	-
7	20	18	13	12	6
8	27	23	9	11	4
9	15	16	8	13	21
10	-	-	-	2	-
11	21	16	4	4	4
12	-	3	-	-	-
13	238	273	19	26	53
14	1	-	1	-	-
15	1	-	-	-	-
16	1	-	2	-	-
17	14	22	-	8	-
18	-	1	-	2	-
19	1	-	-	-	-
20	-	-	1	-	2
21	-	-	-	2	-
22	-	-	-	-	-
23	-	-	-	-	-
24	-	-	-	2	-
25	-	-	-	-	-
26	1	-	-	-	-
27	-	-	-	-	-
28	-	-	-	-	-
29	1	-	-	-	-
30	-	-	-	-	-
31	-	1	-	-	-
32	-	-	-	-	-
33	1	2	-	-	-
34	-	1	-	-	-

APPENDIX 2.2.

R.Z. LIVING MOLLUSCA.

SAMPLING SITES	LIVING SPECIES	Macoma	Scrobicularia	Cardium	Mya arenaria	Mytilus edulis	Tellina tenuis	Hydrobia ulvae	Retusa obtusa	Littorina	Littorina
		balthica	plana	edule						littoralis	saxatilis
		1	2	3	4	5	6	7	8	9	10
A4	1	7	-	-	-	-	-	53	-	-	-
B4	2	3	1	-	-	-	-	5	-	-	-
B5	3	16	2	2	2	-	-	37	-	-	-
C3	4	6	1	-	-	-	-	101	-	-	-
C4	5	5	4	10	-	-	-	227	1	-	-
C5	6	3	-	-	-	-	-	4	-	-	-
D4	7	11	7	19	1	1	-	323	-	-	-
D5	8	8	1	-	-	-	-	1	-	-	-
E3	9	3	-	-	1	-	-	151	-	-	-
E4	10	9	-	3	-	-	-	-	-	-	-
E5	11	1	-	-	-	6	-	-	-	-	-
E6	12	6	-	4	-	-	-	1	-	-	-
F3	13	1	2	1	-	110	-	-	-	6	1
F4	14	3	1	-	-	38	-	-	-	-	-
G2	15	13	3	-	-	-	-	80	-	-	-
G3	16	10	-	3	1	1	-	-	-	-	-
G5	17	9	2	-	-	-	-	-	-	-	-
G6	18	7	-	-	-	-	-	8	-	-	-
H1	19	4	-	-	-	1	-	63	-	-	-
H2	20	8	-	9	-	-	-	-	-	-	-
H3	21	7	-	3	-	38	-	-	-	-	-
H4	22	5	1	2	-	-	-	-	-	-	-
H5	23	-	1	7	-	-	-	-	-	-	-
H6	24	-	1	-	-	-	-	64	-	-	-
I1	25	11	-	-	-	-	-	11	-	-	-
I2	26	13	2	4	-	-	-	21	-	-	-
I3	27	2	-	278	-	-	-	-	-	-	-
I6	28	-	-	-	-	-	1	-	-	-	-
J3	29	4	-	1	-	-	-	22	-	-	-
J4	30	-	-	1	-	-	-	-	-	-	-
J6	31	-	-	-	-	-	3	-	-	-	-
J7	32	-	-	-	-	-	3	-	-	-	-
K5	33	3	-	1	-	-	1	-	-	-	-
L5	34	-	-	-	-	-	3	-	-	-	-
L11	35	-	-	-	-	-	1	-	-	-	-