LIVE AND DEAD FAUNAS FROM CORALLINE ALGAL GRAVELS, CO. GALWAY

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ABSTRACT. A visual assessment, supported by multivariate statistical analysis, of the fauna from seventy-one benthic samples from Mannin Bay shows the existence of five communities, which are coincident with the sedimentary facies of the area. The Bank Community is found in algal banks constructed by the free-living corallines *Lithothamnium corallioides* and *Phymatolithon calcareum*. This community is characterized by a varied and abundant epifauna living on the algal thalli. The Muddy Algal Gravel Community also has a rich epifauna but has a more diverse burrowing infauna. The Clean Algal Gravel Community is found in high-energy areas and has a poorer epifauna but a specialized burrowing infauna. The Fine Sand Community is distinct from the algal gravel faunas, being composed of sand-living bivalves, echinoderms, and gastropods. The Mud Community is very poor in both species and numbers. The fauna from Mannin Bay is similar to communities described from coralline algal sediments of Ireland, Brittany, and the English Channel.

The post-mortem history of abrasion, encrustation, and boring of the skeletal material is described. The dead fauna is analysed to ascertain whether the previously defined communities are recognizable from the skeletal debris. Most of the dead molluscan species in a facies are exotic but the bulk of the individuals come from that facies. Exotic species are most dominant in the Clean Algal Gravel Facies and the Fine Sand Facies. Gastropods from the rocky substrates form the most abundant group of exotic species. The trophic nuclei of the benthic communities cannot be reconstructed from the dead fauna even though the live faunas are dominated by skeletal organisms. Multivariate statistical analysis shows that the living communities cannot be reconstructed from the dead fauna.

COMMUNITY analysis of macrobenthic organisms is now popular among palaeonto-logists as it provides a greater understanding of fossil assemblages, ancient environ-ments, biostratigraphy, and community evolution. However, the recognition of original life communities from fossil assemblages is difficult, and frequently has to be based on slender evidence. One of the main reasons for the difficulties lies in the paucity of studies on recent death assemblages and their relationships to the com-munities from which they are derived. Detailed studies of this problem in sublittoral environments comes from shallow coastal lagoons in California (Johnson 1965; Warme 1969; Petersen 1976), a Spanish estuary (Cadee 1968), and the Yucatan coast (Warme *et al.* 1976). The results from these studies show that death assemblages reflect, with varying degrees of accuracy, the composition of the living communities. Warme *et al.* (1976) go further and suggest that the death assemblages supply more information on the benthic communities than the results from one sampling pro-gramme. This is because of the temporal fluctuations in living populations and the time averaging effect of death assemblages. These results contrast markedly with studies from littoral environments (e.g. Wilson 1967), where major differences are found between live and dead populations.

The main aim of this paper is to describe the macrobenthic communities and death assemblages from a shallow marine environment in Co. Galway, Eire, where the death assemblages do not permit the reconstruction of the original trophic nuclei or
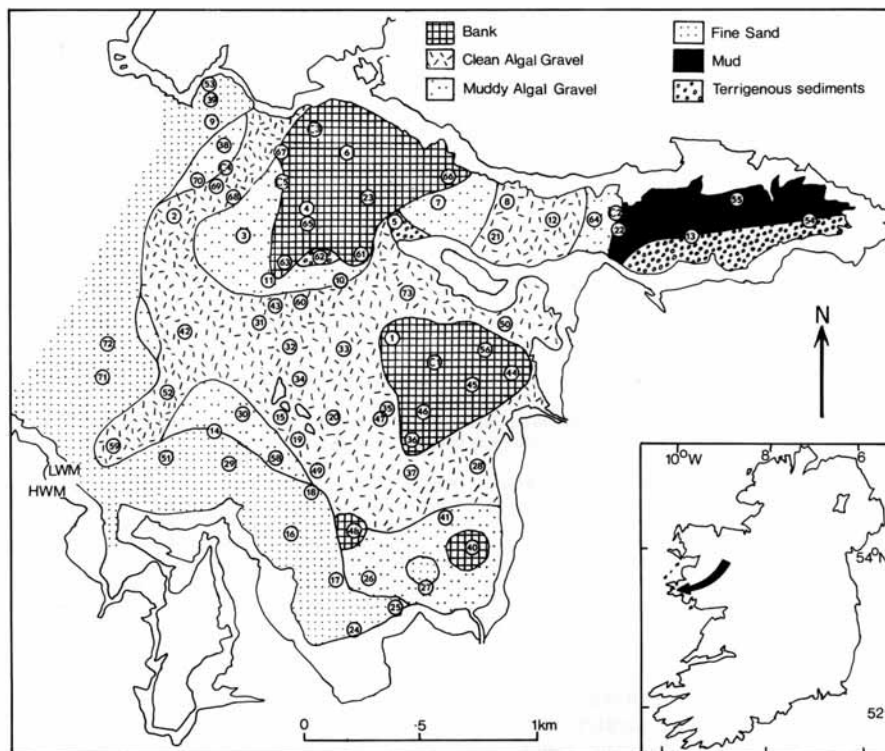
TEXT-FIG. 1. Location, sedimentary facies, and sample station numbers of Mannin Bay, Co. Galway, Eire.

communities. Mannin Bay (text-fig. 1) is moderately exposed to wave and tidal currents and therefore provides a comparison with the previous studies, many of which are from low energy environments.

The environment of the study area has been well documented by Lees *et al.* (1969), Buller (1969), Bosence (1976*a, b*, 1978) and Gunatilaka (1977). Most of the sediments of the inner part of Mannin Bay are coralline algal gravels (maerl) together with molluscan, echinoderm, foraminiferal, bryozoan, sponge, and ostracode debris. Five sedimentary facies have been described from the results of a detailed programme of scuba-collected samples and observations (Bosence 1976*b*). A Bank Facies is found in shallow water (1–8 m), reasonably sheltered areas and comprises an auto-chthonous build-up of the branching coralline algae *Lithothamnium corallioides* Crouan and *Phymatolithon calcareum* (Pallas) Adey and McKibbin (Pl. 51, fig. 1). The banks have a relief of up to 30 cm and cover areas up to half a kilometre square. A Clean Algal Gravel Facies is found in exposed areas and is formed of algal and

molluscan debris swept into wave ripples. A Muddy Algal Gravel Facies is found intermediate between the two previous facies and comprises algal and molluscan material with a sandy mud matrix. A Fine Sand Facies of mixed biogenic origin is found offshore and overlapping the algal gravels. A Mud Facies of both terrigenous and carbonate origin is found in the very sheltered creeks around the bay.

The biological production of calcium carbonate within each of the facies is to be described in a future publication.

METHODS

The area was sampled by scuba-diving at seventy-seven stations during the summer of 1972 (text-fig. 1). The fauna was sampled by excavating $50 \times 50 \times 30$ cm deep samples into strong polythene bags, sealed at the top, with a hole in the side and a 2 mm mesh net over the base. After sampling, the bags were floated to the surface with air introduced to the top of the bag and the sample was washed to remove the sand and mud-sized material. The small fauna (less than 2 mm) was collected in samples $12 \times 20 \times 10$ cm deep (i.e. one-tenth the area of the large sample). The sample area was photographed in colour and notes were taken on the ecology and taphonomy of the fauna and flora, together with substrate structures and textures. The samples were sorted by hand (a $\times 10$ lens was used for the small fauna). The live material was stored in formaldehyde solution neutralized in Hexamine. All dead material recognizable to specific and generic level was washed and dried. Because the study was mainly concerned with the carbonate-producing organisms the soft bodied macrofauna was not identified below family level. Specimens for SEM work were washed, dried, fractured, and coated with gold.

Duplicate sampling of a visually uniform substrate (stations at 1A, B, C, and D) showed that 60% of the live and 68% of the dead taxa found in one square metre were being sampled in the 50×50 cm samples. However, two species were making up 75% of the live individuals and four species account for 78% of the dead individuals, and these common species were being adequately sampled. Similarly, air-lift suction sampling (Keegan 1974) to depths of 100 cm in the substrate showed that all species were being sampled in the top 20 cm. Complete faunal lists from the samples are stored at the British Library, Boston Spa, Wetherby, Yorkshire, LS23 7BQ, U.K. as Supplementary Publication No. SUP 14012. 124 taxa were identified, comprising 6,687 live specimens and 100,680 dead specimens.

COMMUNITY ANALYSIS

Community descriptions

Observations made whilst diving, together with examination of species/stations data suggested that similar groupings of species were occurring in the same sedimentary facies. These qualitative observations were tested with multivariate statistical analyses (see below) which confirm that species can be grouped into recurring associations or communities. These communities correspond to previously defined sedimentary facies and are, therefore, named after the facies (cf. Jones 1950): Bank Community, Clean Algal Gravel Community, Muddy Algal Gravel Community, Find Sand Community, and Mud Community. The composition and synecology of these communities are described below.

Bank Community. The Bank Community (Table 1) contains the most abundant vagile epifauna of all the facies. The unattached corallines provide a sheltered three-dimensional structure in which food is supplied by the algae and by the debris trapped within the algal branches (Pl. 51, figs. 1, 2). This microenvironment allows the small-sized epifauna to live throughout the bank structure so that they are in effect infaunal (cf. 'subsurface epifauna' of Keegan 1974). Gastropods are common in this algal

TABLE 1. Composition and abundance of fauna in Bank Community (18 stations).

Taxa	Trophic group	Abundance (No. per 0·25 sq. m)		
		Mean	No. stations present	Maximum
VAGILE EPIFAUNA				
Bittium reticulatum	H	31·60	7	270
Xantho sp.	C/S	6·61	16	24
Porcellana longicornis	C/S	6·16	7	74
Gibbula cinerarea	H	6·00	3	93
Rissoa parva	H	3·88	2	40
Idotea sp.	S	2·22	2	30
Tricolia pullus	H	1·66	1	30
Portunus sp.	C/S	1·11	9	4
Gibbula magus	H	0·88	7	8
Chitonida	H	0·61	2	10
Nassarius incrassatus	C	0·44	3	6
Eupagurus sp.	C/S	0·11	2	1
Nassarius reticulatus	C	0·05	1	1
Galathea squamifera	C/S	0·05	1	1
Asterias rubens	C ⎫			
Marthasterias glacialis	C ⎬	observed present, not sampled		
SESSILE EPIFAUNA				
Musculus discors	SF	5·55	2	80
Anemonia sulcata	C/S	0·44	3	5
Halichondria sp.	SF	0·11	2	1
Chlamys varia	SF	0·05	1	1
Spirorbidae	SF ⎫			
Serpulidae	SF ⎬	observed present, not sampled		
Tubulipora phalangea	SF			
Other bryozoa	SF ⎭			
BURROWING INFAUNA				
Golfingia sp.	DF ⎫ comm.	2·94	11	16
Mysella bidentata	SF ⎬	2·77	2	40
Lucinoma borealis	SF	2·00	9	11
Nucula turgida	DF	0·94	5	9
Nereidae	C/S	0·88	7	6
Glyceridae	C	0·64	6	4
Venus verrucosa	SF	0·44	6	2
Amphitritidae	DF	0·38	4	4
Eunicidae	C/S	0·33	6	1
Parvicardium ovale	SF	0·27	1	5
Venerupis rhomboides	SF	0·22	2	3
Venerupis aurea	SF	0·22	3	2
Parvicardium exiguum	SF	0·16	2	2
Thyasira flexuosa	SF	0·11	1	2
Terribellidae	SF	0·11	1	2
Gouldia minimum	SF	0·05	1	1
Abra nitida	SF	0·05	1	1
Dosinia exoleta	SF	0·05	1	1
Nemertini	C	0·05	1	1
BORING INFAUNA				
Hiatella arctica	SF	0·55	1	10
Gastrochaena dubia	SF			
Polydora sp.	DF/SF ⎫	observed present, not sampled		
Cliona sp.	DF/SF ⎭			

Key: H = herbivore; C/S = carnivore/scavenger; DF = deposit feeder, SF = suspension feeder; comm. = commensals.

TABLE 2. Composition and abundance of fauna in Muddy Algal Gravel Community (11 stations).

Key as for Table 1.

Taxa	Trophic group	Abundance (No. per 0·25 sq. m)		
		Mean	No. stations present	Maximum
VAGILE EPIFAUNA				
Bittium reticulatum	H	53·64	5	230
Rissoa parva	H	4·54	1	50
Gibbula cinerarea	H	3·45	8	20
Mangelia sp.	C	2·72	1	30
Cingula semicostata	H	1·81	1	20
Xantho sp.	C/S	1·09	5	5
Eupagurus sp.	C/S	0·81	6	4
Idotea sp.	S	0·36	3	2
Diadora apertura	H	0·27	1	3
Portunus sp.	C/S	0·27	2	2
Patina pellucida	H	0·09	1	1
Chitonida	H	0·09	1	1
Natica	C	0·09	1	1
Nassarius incrassatus	C	0·09	1	1
Nassarius reticulatus	C	0·09	1	1
Maidae	C/S	0·09	1	1
Asterias rubens	C	observed present, not sampled		
Marthasterias glacialis	C			
SESSILE EPIFAUNA				
Anemonia sulcata	C/SF	1·00	5	5
Anomia ephippium	SF	0·09	1	1
Halichondria sp.	SF	0·09	1	1
Spirorbidae	SF	observed present, not sampled		
Serpulidae	SF			
Bryozoans	SF			
BURROWING INFAUNA				
Mysella bidentata	SF	7·27	2	50
Nucula turgida	DF	6·72	4	69
Lucinoma borealis	SF	6·36	10	28
Astarte triangularis	SF	3·63	2	10
Thyasira flexuosa	SF	2·18	2	23
Golfingia sp.	DF	1·82	5	6
Turritella communis	SF	1·45	2	15
Parvicardium exiguum	SF	1·36	4	10
Nereidae	C/S	1·36	4	43
Parvicardium ovale	SF	1·27	4	10
Venerupis rhomboides	SF	0·91	2	6
Venerupis aurea	SF	0·91	5	5
Tellina tenuis	SF	0·54	1	6
Glyceridae	C/S	0·54	4	3
Nemertini	C	0·54	5	4
Haminoe navicula	C	0·36	1	4
Venus pullastra	SF	0·27	1	3
Sabella pavonina	SF	0·27	2	2

[*Table continued overleaf.*]

[*Table 2 continued.*]

Taxa	Trophic group	Abundance (No. per 0·25 sq. m)		
		Mean	No. stations present	Maximum
Dosinia exoleta	SF	0·18	2	1
Venus verrucosa	SF	0·18	2	1
Dentalium sp.	DF	0·18	2	1
Venus fasciata	SF	0·09	1	1
Gouldia minimum	SF	0·09	1	1
Lutraria lutraria	SF	0·09	1	1
Abra alba	SF	0·09	1	1
Branchiomma vesiculosum	SF	0·09	1	1
Echinocyamus pusillus	DF	0·09	1	1
Leptosynapta inhaerens	DF	0·09	1	1
BORING INFAUNA				
Gastrochaena dubia	SF	0·09	1	1
Hiatella arctica	SF	0·09	1	1
Polydora sp.	SF ⎱	observed present, not sampled		
Cliona sp.	SF/DF ⎰			

lattice and may reach abundances of up to 93 *Gibbula cinerarea* and 270 *Bittium reticulatum* per 0·25 sq. m. Another common group are decapod crustacea which live on and within the bank. The small forms, exemplified by *Porcellana longicornis* and *Galathea squamifera*, can move within the lattice of the corallines but the larger xanthids and portunids either swim over the surface, nestle into crevices, or occupy rough burrows within the bank (Pl. 51, fig. 3).

The sessile epifauna comprises two crevice-dwelling byssate bivalves, *Musculus discors* and *Chlamys varia*, and various encrusting organisms. When found on the

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EXPLANATION OF PLATE 51

Fig. 1. Underwater photograph of the free-living coralline algae *Phymatolithon calcareum* (left) and *Lithothamnium corallioides* (right). Note epiphytes and *Halichondria* (upper right and lower left on *P. calcareum*) on corallines, ×1.

Fig. 2. SEM micrograph of surface of *Lithothamnium corallioides* illustrating rich diatom population, ×200.

Fig. 3. Underwater photograph of portunid crab burrow in margin of bank of *Lithothamnium corallioides*. Brown macrophyte *Dictyota dichotoma* growing on bank (upper left), ×⅓.

Fig. 4. Foraminifer encrusting surface of coralline, SEM, ×225.

Fig. 5. Foraminifer overgrown and buried within algal thallus, SEM, ×230.

Fig. 6. Dried specimen of *Halichondria* encrusting coralline. The sponge does not visibly alter the surface of the alga, SEM, ×200.

Fig. 7. *Pomatoceras triqueter* encrusting *Phymatolithon calcareum*, ×1·5.

Fig. 8. Underwater photograph of *Pomatoceras triqueter* encrusting live *Lithothamnium corallioides*, ×1·5.

Fig. 9. SEM micrograph of *Phymatolithon calcareum* bored by *Polydora*, ×15.

Fig. 10. SEM micrograph showing spreite in central partition of U-shaped boring of *Polydora*, ×400.

Fig. 11. SEM micrograph of opening of *Polydora* boring. The alga has reacted to the worm by building a callus around the boring, ×90.

PLATE 51
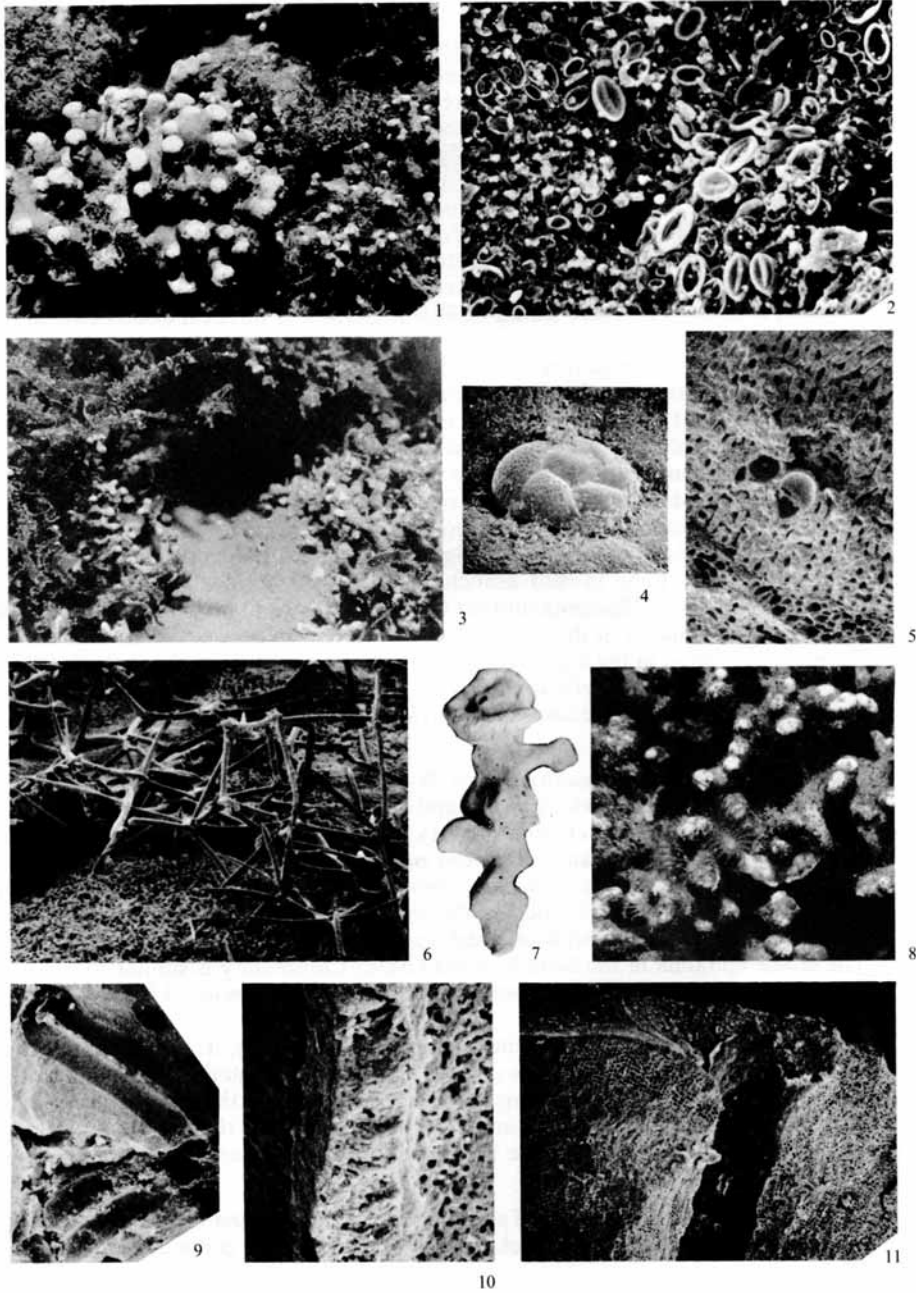
BOSENCE, algal gravel fauna

live corallines, the various encrusting forms show growth competition between the algal host and the encrusters. Bryozoans and foraminifers are seen to be overgrown by the corallines (Pl. 51, figs. 4, 5) whereas *Halichondria* (Pl. 51, figs. 1, 6), *Anemonia sulcata*, serpulids (Pl. 51, figs. 7, 8), and epiphytic algae (e.g. *Dictyota dichotoma*) overgrow the living corallines (Pl. 51, fig. 3).

The burrowing infauna lives below the level of matrix sedimentation (between 10 and 30 cm below bank surface) and is dominated by polychaetes, bivalves and the sipunculid *Golfingia*. Small-sized bivalves (e.g. *Nucula turgida*, *Lucinoma borealis*, and *Parvicardium* spp.) and polychaetes are able to burrow between the buried branches of the corallines but the large venerupid bivalves are thought to be stationary for most of their lives. There would be little predation or physical disturbance at this depth in the bank.

The infaunal boring organisms utilize the algal skeletons, and bivalve and gastropod shells as hard substrates. The most conspicuous borer into live algae is *Polydora* (Pl. 51, figs. 9–11). A growth reaction rim (Pl. 51, fig. 11) in fossil examples would indicate boring into the live as opposed to dead algal thalli. The U-shaped bores of *Polydora* are thought to be the result of both chemical and mechanical activity (Haigler 1969). Mechanical boring is suggested in this case because of the spreite present in the central portion of the boring (Pl. 51, fig. 10). Several species of un-identified filamentous red and green algae are common borers in the corallines (cf. Cabioch 1969) forming inward branching cylindrical borings 0·015–0·089 mm in diameter. The boring filaments support the large growths of filamentous algae found on the living corallines in the quieter areas of the bay (Bosence 1976*a*). The sponge *Cliona* is not found in the algal thalli but is abundant in large mollusc shells (Pl. 52, fig. 9). The bivalves *Hiatella arctica* and *Gastrochaena dubia* bore, or nestle very closely, as is more often the case with *Hiatella*, into the large coralline thalli and thick mollusc shells.

Muddy Algal Gravel Community (Table 2). The surface of the Muddy Algal Gravel Facies is a sandy mud on which lie live and dead corallines together with shell debris (Pl. 52, fig. 2). The vagile epifauna is very similar to that of the Bank Community except in the lower abundance of species present. Included are occasional patellids, *Diadora apertura* and *Patina pellucida*. These gastropods are capable of deeply scrap-ing the substrate for food whereas the more common trochiid gastropods have a radula which is only capable of brushing the surface (Fretter and Graham 1962). The sessile epifauna of the Muddy Algal Gravel Community is similar to the bank fauna except for the occasional presence of two byssate species of bivalve, *Anomia ephippium* and *Crenella* sp.

The substrate of this facies is similar to that of the lower, dead level of the algal banks except that the algal grains are not branching and interlocking. This renders the substrate easier for burrowing and may account for the greater diversity of burrowing infauna in this community in comparison with that of the Bank Com-munity (cf. Tables 1 and 2). The boring infauna is identical to that of the Bank Community.

Clean Algal Gravel Community (Table 3). The vagile epifauna of this community is not as abundant as that of the Bank or Muddy Algal Gravel communities because of

TABLE 3. Composition and abundance of fauna in Clean Algal Gravel Community (23 stations).

Key as for Table 1.

Taxa	Trophic group	Abundance (No. per 0·25 sq. m)		
		Mean	No. stations present	Maximum
VAGILE EPIFAUNA				
Bittium reticulatum	H	20·00	7	120
Idotea sp.	S	3·08	10	30
Cingula semicostata	H	2·61	1	60
Chitonida	H	2·30	6	20
Xantho sp.	C/S	1·30	12	7
Gibbula magus	H	0·83	4	10
Gibbula cinerarea	H	0·54	3	4
Nassarius reticulatus	C	0·48	2	10
Acmaea sp.	H	0·43	1	10
Tricolia pullus	H	0·43	1	10
Alvania punctura	H	0·43	1	10
Portunus sp.	C/S	0·35	6	2
Eupagurus sp.	C/S	0·17	3	2
Asterias rubens	C	0·04	1	1
Marthasterias glacialis	C	0·04	1	1
Porcellana longicornis	C/S	0·04	1	1
Trivia sp.	H	0·04	1	1
SESSILE EPIFAUNA				
Mytilus edulis	SF	0·43	1	10
Anemonia sulcata	C/SF	0·30	5	1
Spirorbidae	SF			
Serpulidae	SF	observed present, not sampled		
Bryozoans	SF			
BURROWING INFAUNA				
Astarte triangularis	SF	79·10	14	490
Lucinoma borealis	SF	1·99	8	26
Nucula turgida	DF	1·90	1	44
Golfingia sp.	DF	1·26	8	12
Venerupis aurea	SF	0·61	4	10
Echinocyamus pusillus	DF	0·52	2	10
Nereidae	C/S	0·52	9	3
Tellina tenuis	SF	0·48	2	10
Caecum sp.	SF	0·43	1	10
Mysella bidentata	SF	0·43	1	10
Crenella sp.	SF	0·43	1	10
Venerupis rhomboides	SF	0·39	6	4
Glyceridae	C/S	0·39	8	2
Dosinia exoleta	SF	0·35	7	2
Parvicardium ovale	SF	0·30	5	2
Eunicidae	C/S	0·26	5	2
Natica sp.	C	0·26	2	3
Gari tellinella	DF	0·22	2	3
Parvicardium exiguum	SF	0·17	2·	3

[*Table continued overleaf.*]

[*Table 3 continued.*]

Taxa	Trophic group	Abundance (No. per 0·25 sq. m)		
		Mean	No. stations present	Maximum
Venerupis pullastra	SF	0·17	1	3
Nemertini	C	0·17	2	3
Aphroditidae	C/DF	0·17	1	4
Amphitritidae	DF	0·17	1	4
Leptosynapta inhaerens	DF	0·17	3	2
Venus fasciata	SF	0·13	3	1
Thyasira flexuosa	SF	0·08	2	1
Dentalium sp.	DF	0·08	2	1
Branchiomma vesiculosum	SF	0·08	2	1
Venus verrucosa	SF	0·04	1	1
Lanice conchilega	SF	0·04	1	1
Pseudococcumis mixta	SF			

BORING INFAUNA

Polydora sp.	SF	observed present not sampled		
Cliona sp.	SF/DF			

the unstable nature of the substrate. The gravel is commonly swept into ripples with ripple crests which are inhospitable to small members of the epifauna. Most of the epifauna is, therefore, found in the ripple troughs associated with the live coralline algae, coarse shell debris and clusters of grains held together by weed. Similarly, the sessile epifauna is found mainly in the ripple troughs attached to the shells and corallines. The burrowing infauna is dominated by bivalves and polychaetes. Because the grain size is smaller, and the algal branches are not interlocking, it is probably easier for the large bivalves to burrow in this sediment than in the Bank Facies. The bivalve fauna differs from that of the Bank and Muddy Algal Gravel communities in the lower abundances of the mud-inhabiting *Nucula turgida* and the thin-shelled lucinoids *Thyasira flexuosa* and *Lucinoma borealis*. These are replaced by the small *Astarte triangularis* which may reach numbers up to 490 per 0·25 sq. m. When compared to the Bank Community there are more thick-shelled veneracean bivalves and three species of the Tellinacea appear. The polychaete fauna includes the tube builders *Lanice conchilega* (Pl. 52, fig. 3) and *Branchiomma vesiculosum*, which use the algal debris for tube construction. There is also an amphitritid polychaete which forms a loose tube with algae, foraminifers, and shells.

The boring infauna is confined to the large grains found in the ripple troughs, in particular large bivalve shells and rhodoliths.

Fine Sand Community (Table 4). The mobile surface of this substrate does not normally provide niches for a diverse epifauna. However, an epifauna is found on local accumulations of shell debris and local cover of *Zostera marina* and sea weeds. No species are unique to this community and the diversity and abundances of the vagile epifauna is less than the coralline algal faunas. The sessile epifauna is, as with

TABLE 4. Composition and abundance of fauna in Fine Sand Community (12 stations).

Key as for Table 1.

Taxa	Trophic group	Abundance (No. per 0·25 sq. m)		
		Mean	No. stations present	Maximum
VAGILE EPIFAUNA				
Bittium reticulatum	H	17·50	5	180
Gibbula cinerarea	H	9·25	5	100
Idotea sp.	S	5·00	1	60
Nassarius incrassatus	C	1·83	3	20
Eupagurus sp.	C/S	1·33	4	8
Xantho sp.	C/S	0·58	4	3
Nassarius reticulatus	C	0·25	2	2
Buccinum undatum	C	0·08	1	1
Natica sp.	C	0·08	1	1
Mangelia sp.	C	0·08	1	1
Gibbula magus	H	0·08	1	1
SESSILE EPIFAUNA				
Musculus discors	SF	1·67	1	20
Anemonia sulcata	C/SF	0·92	3	5
Spirorbidae	SF ⎫			
Serpulidae	SF ⎬ observed present, not sampled			
Bryozoans	SF ⎭			
BURROWING INFAUNA				
Thyasira flexuosa	SF	14·50	6	10
Mysella bidentata	SF	6·66	2	70
Acrocnida brachiata	SF	2·58	2	30
Lucinoma borealis	SF	2·08	6	10
Abra alba	DF	1·83	3	15
Turritella communis	SF	1·75	4	14
Sabella pavonina	SF	1·50	3	15
Montacuta ferruginosa	SF	0·83	1	10
Abra prismatica	DF	0·83	1	10
Nereidae	C/S	0·67	6	2
Tellina tenuis	DF	0·5	3	3
Dentalium sp.	DF	0·5	2	4
Venerupis aurea	SF	0·42	3	2
Maldanidae	DF	0·42	1	5
Echinocardium caudatum	DF	0·42	1	3
Parvicardium ovale	SF	0·33	2	2
Owenia sp.	DF	0·33	2	3
Golfingia sp.	DF	0·33	1	4
Parvicardium exiguum	SF	0·17	2	1
Tellina fabula	DF	0·17	2	1
Leptosynapta inhaerens	DF	0·17	2	1
Glyceridae	C/S	0·08	1	1
Ensis sp.	SF	0·08	1	1
Venerupis rhomboides	SF	0·08	1	1
Venerupis pullastra	SF	0·08	1	1
Venus verrucosa	SF	0·08	1	1
Gari tellinella	DF	0·08	1	1
Branchiomma vesiculosum	SF	0·08	1	1
BORING INFAUNA				
Polydora sp.	SF ⎫			
Cliona sp.	SF ⎭ observed present, not sampled			

the vagile epifauna, only found on weed or encrusting shell debris on the sediment surface. The sediment is too fine-grained, mobile, and does not provide cover to protect encrusting or vagile organisms. The burrowing infauna of this substrate contains diverse and locally very abundant species of suspension feeders, deposit feeders, and carnivores. The fauna is clearly distinct from that of the algal gravels and contains species of bivalves, gastropods, polychaetes, and echinoderms commonly associated with sandy substrates (see below). The sand substrate does not support a boring macrofauna but the common carbonate grain borers are found in the shell debris on the sediment surface.

Mud Community (Table 5). The Mud Community was only sampled at four stations and the numbers of ecological groups are low, as are the species and their abundances. There are no species, apart from *Priapulus*, which are specially adapted for life in muddy substrates. The mud appears to be inhabited by species from neighbouring facies which can tolerate fine sediment deposition.

TABLE 5. Composition and abundance of fauna in Mud Community (4 stations).

Key as for Table 1.

| Taxa	Trophic group	Abundance (No. per 0·25 sq. m)		
		Mean	No. stations present	Maximum
VAGILE EPIFAUNA				
Bittium reticulatum	H	10·00	1	40
Littorina littorea	H	2·50	1	10
Gibbula magus	H	0·75	1	3
Xantho sp.	C/S	0·75	1	3
BURROWING INFAUNA				
Parvicardium exiguum	SF	2·75	2	10
Mysella bidentata	SF	2·50	1	10
Lucinoma borealis	SF	2·00	2	7
Venerupis aurea	SF	1·50	1	6
Lanice conchilega	SF/DF	1·00	2	3
Nereidae	C/S	1·00	3	2
Priapulus sp.	DF	0·25	1	1
Eunicidae	C/S	0·25	1	1
Glyceridae	C/S	0·25	1	1

Quantitative community analysis

The results from regional benthic surveys produce very large matrices of data from which species may or may not be grouped into recurring groups or communities. The data may be assessed qualitatively, as for example by Keegan (1973) for 2000 samples containing about 200 species, and Dorjes (1972) for 103 samples contain-

ing 268 species. In attempting to establish discrete faunal groupings from data of this size, clearly decisions are subjective and errors may be made. If objective grouping of the data is made then the communities have more value for comparative purposes and for investigating the relationships between faunal groups and sedimentary facies. Two multivariate statistical techniques are now widely used for grouping samples on the basis of their fauna. They are both Q-mode analyses which group objects (stations) on the basis of their variables (fauna), as opposed to R-mode analyses which group related variables. The techniques are cluster analysis which classifies groups of similar stations, and principal components analysis or ordination, which can be used to show the differences and similarities between stations. Both these methods are used here for the live and dead faunas and the results are compared. Full descriptions of these methods can be obtained from Sneath and Sokal (1973, p. 214) and Davis (1973, p. 456).

Methods. A non-parametric cluster analysis was selected as it analyses data on a presence–absence basis (Bonham-Carter 1967). This is particularly useful for the analysis of fossil assemblages where species abundances are difficult to obtain (Buzas 1972). The Jaccard coefficient of association was used to measure the similarity of the samples as it ignores the frequency of mismatches. This is important when comparing samples with large numbers of absences of species as samples may be considered similar because they have the same species absences. In the clustering procedure the groups were 'unweighted' (Sneath and Sokal 1973, p. 228). The analyses are presented as dendrograms with samples scaled against their coefficients of association (text-figs. 2, 4). The clusters of the live fauna are chosen at level of association of about 0·2 which is considerably higher than would be obtained from a clustering of the same data if it was randomly arranged (randomness level = 0·04). The clusters of the dead fauna are chosen at a level of association of 0·4 and have a randomness level of 0·1 (text-fig. 4). The principal-components analysis was modified from Wahlstedt and Davis (1968). Species which occurred in less than two stations were removed because of the large number of zeros in the matrix. For the live fauna this left a matrix of 51 taxa occurring at 71 stations, and for the dead fauna 59 species of molluses were analysed from 71 stations. The abundance data (x) were transformed to $\log_{10}(x+1)$ in accordance with other workers (e.g. Hughes and Thomas 1971) to make the data less skewed. Originally the first five eigenvectors were plotted for the live and dead faunas as they account for 60% and just over 50% of the total variation of the data respectively (Bosence 1976*b*). The similarities between the samples can be seen from their proximity when plotted with respect to the eigenvectors. Samples which consistently plot close to one another have similar faunas and samples which are always separate have dissimilar faunas. The eigenvectors one, three, and four provide the best separation of the stations on the basis of their live fauna. The analysis of the dead fauna shows the best separations of the stations when plotted with respect to eigenvalues one, two, and three (text-figs. 3, 5). The eigenvalues and their contributions are shown in Tables 6 and 8.

Cluster analysis. The cluster analysis, which is based on species presence or absence, shows a general low level of association between the samples. At the 0·2 level of association about one half of the stations are clustered in groups (text-fig. 2) which in the main correspond to the previously defined sedimentary facies. Stations from the Bank Facies are clustered in Group 4. Group 2, although containing the majority of samples from the Muddy Algal Gravel Facies contains a number of samples from neighbouring facies. Most of these stations are located near the boundary of the Muddy Algal Gravel Facies and this suggests a mixing of faunas at facies boundaries. The Clean Algal Gravel Facies stations are separated into three groups. Samples taken on Mannin Platform comprise Groups 3 and 5 whilst the more offshore stations make up Group 6. The Fine Sand stations are similarly divided into the offshore stations (Group 8) and the stations from Mannin Platform which are classified with the Clean and Muddy Algal Gravel Facies stations. Group 1 contains stations from terrigenous and intertidal stations. Stations from the Mud Facies do not form a cluster.

From this classification of stations based on species presence or absence there is some correspondence between fauna and sedimentary facies. However, the classification does not show an exact grouping of samples which can be equated with the previously defined sedimentary facies.
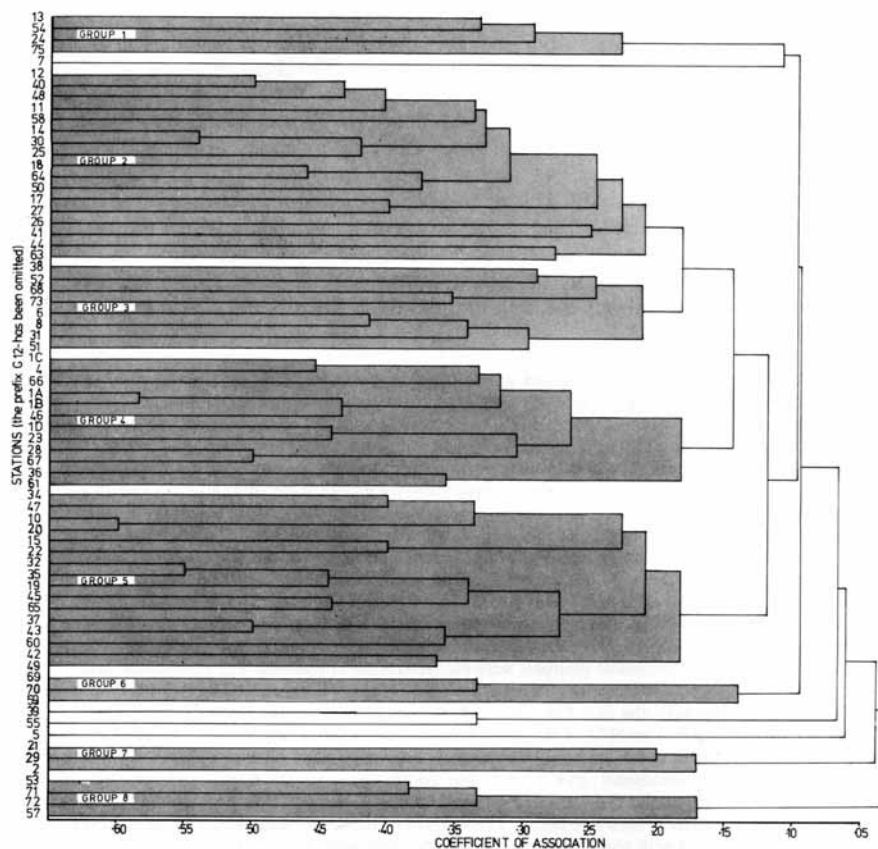
TEXT-FIG. 2. Dendrogram illustrating clustering of stations by cluster analysis of live fauna.

Principal-components analysis. This analysis is more sophisticated than the previous analysis in that the stations are compared by species abundances. The eigenvalues obtained from an analysis of the live fauna are shown in Table 6. Text-fig. 3 shows the original samples plotted with respect to the eigenvectors one, three, and four.

Stations from the Clean Algal Gravel Facies plot as a separate group due to variation in eigenvector one. The species contributing most of the loading to this vector is *Astarte triangularis* (Table 3), a species particularly common in this sedimentary facies. Another distinct group of stations are those from the offshore area of the Fine Sand Facies. The inshore Fine Sand Facies stations show more similarity with the fauna of the adjacent algal gravel stations. The Fine Sand Facies stations are mainly separated by eigenvector two, the main variation of which is controlled by the occurrences of the sand-living species *Echinocardium cordatum*, *Acrocnida brachiata*, and tellinid bivalves. Stations from the Bank Facies, in the main, plot in a separate area and the stations are separated by eigenvectors one and three. Eigenvector three is mainly defined by nereid polychaetes and xanthid and portunid crabs. Stations from the Muddy Algal Gravel

TABLE 6. First five eigenvalues and eigenvectors from principal-components analysis of live fauna.

	one	two	three	four	five
Eigenvalues	0·99	0·59	0·31	0·24	0·23
Percentage of total contribution per eigenvalue	25·01	15·01	7·80	6·10	5·91
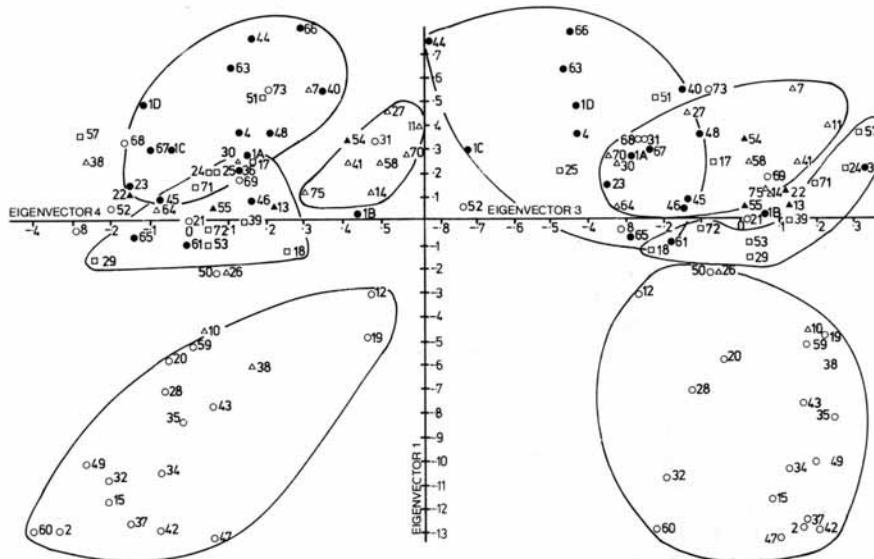
TEXT-FIG. 3. Live fauna from stations 1–73 plotted with respect to eigenvectors one, three, and four. *Key:*
● Bank Facies, △ Muddy Algal Gravel Facies, ○ Clean Algal Gravel Facies, □ Fine Sand Facies, ▲ Mud Facies.

Facies and inshore Fine Sand Facies generally have a scattered distribution in the centre of the field. Stations from the Mud Facies consistently plot together.

The principal-components analysis therefore supports the results suggested by the cluster analysis and shows a reasonably good correlation of sedimentary facies and the distribution of macrobenthic animals. The most distinct sedimentary facies and communities are the Bank, Clean Algal Gravel, and the offshore Fine Sand. The Muddy Algal Gravel, some Clean Algal Gravel, and the inshore Fine Sand facies have more similar faunas.

From this analysis of species abundances the fauna can be shown to be grouped into recurring associations or communities and this confirms the results of the initial qualitative work.

Discussion

The fauna of each of the algal communities is similar, but in detail differences can be seen in the abundances of certain groups and the presence or absence of species which appear particularly sensitive. The Bank Community has the most diverse and

abundant epifauna and boring infauna. The Muddy Algal Gravel Community has a similar epifauna but the species abundances are lower. However, the burrowing infauna is richer in species and their abundances: in particular, the nuculacean, lucinacean, veneracean, and tellinacean bivalves and polychaetes. The Clean Algal Gravel Community is the most distinct algal gravel community but is most similar to the Muddy Algal Gravel Community with the exception of the nuculacean and lucinacean bivalves. These are replaced by the abundant *Astarte triangularis*. Most other species are present, but with lower abundances, in this exposed environment. The Fine Sand Community is clearly distinct, particularly offshore, both in respect of its poor epifauna and the composition and abundance of the infauna.

Keegan (1974) has described similar faunas from the coralline algal sediments in near-by Kilkerrin and Galway Bays. The Bank Community is closely comparable with the fauna of Keegan's 'sublittoral living maerl'. In particular the varied epifauna and low numbers of infaunal burrowers are common to the two regions. The Clean Algal Gravel Community is similar to, but less diverse than, Keegan's 'maerl debris unstable sediment' fauna. Keegan does not describe facies similar to the Muddy Algal Gravel or the Fine Sand. In general the area studied by Keegan yielded much higher species abundances than did Mannin Bay. This is unlikely to be the result of the different sampling procedures as these were compared in the two areas (see Methods, above). In some cases the high abundances in Galway and Kilkerrin Bays may be related to larval retention in these enclosed areas (Keegan 1974). The difference in abundance of fauna between these two areas is not thought to be permanent but probably reflects a short-term population fluctuation in Mannin Bay. Evidence for this comes, for example, from the presence of abundant large dead shells of *Venerupis rhomboides* in the Mannin Bay gravels. In the live populations this species is only represented by occasional juveniles.

The results from Mannin Bay are similar to those of Cabioch (1968) from Brittany; in particular the Bank Community which, again, has the characteristic rich epifauna. Cabioch considers the maerl fauna to be basically a *Venus fasciata* Community (Ford 1923) with the addition of a rich epifauna. The similarities of the maerl and sand faunas to Ford's communities can also be seen when a comparison is made with the fauna from the sands and gravels of the English Channel (Jones 1950; Holme 1966; Howell and Shelton 1970).

Coralline algal banks are also known from subtropical areas (e.g. Rodriguez Bank, Florida Bay), and their sedimentology has been described by Turmel and Swanson (1971, 1976). However, as far as I am aware, no detailed description of the fauna has been published. Turmel and Swanson (1971) describe the fauna as being diverse and abundant, particularly with regard to epifaunal organisms which live within the '*Goniolithon* forest' on Rodriguez Bank.

Similarly, no detailed palaeoecological studies have been published on Tertiary coralline agal limestones. Pedley (1976) lists abundant molluscs, echinoids, crustaceans, brachipods, calcareous sponges, and foraminifera from the coralline algal bioherms of Malta. Bualuk and Radwanski (1968) describe the fauna from rhodoliths in the Lithothamnium Limestone from the southern Holy Cross mountains in Poland. They list diverse gastropods, bivalves, bryozoa, cirrepedes, starfish, and echinoids from sands with abundant corallines. Shalekova (1964) mentions

diverse faunas associated with lower Tertiary bioherms in western and central Slovakia.

From this previous work it can be seen that diverse faunas are found in subtropical and ancient coralline algal banks. However, more work is required before useful comparisons can be made or community evolution be discussed.

ANALYSIS OF DEATH ASSEMBLAGES

A persistent problem in palaeontology is the difficulty of establishing the relationships of fossil assemblages to living communities. Apart from the occasional organism preserved in growth position the majority of fossil assemblages contain a biota which has been transported and abraded to a greater or lesser degree. One approach to this problem is to analyse the relation between live and dead assemblages in recent environments. Apart from post-mortem transport there are several ecological factors causing differences between live and dead faunal assemblages. These causes include the patchiness in distribution of live benthic faunas which is well exemplified in this study (Tables 1–5). In addition, several authors have shown that the abundance or presence of species can change with time even if there are no apparent changes taking place in the environment (Fischer 1931; Moore 1933; Birkett 1953; Holme 1966). The importance of these temporal changes in the fauna can be assessed by either long-term sampling programmes (Cadee 1968) or by comparison with the fauna in similar neighbouring areas as is done in this study. Furthermore, rare species may be inadequately sampled. In Mannin Bay only 60% of the species of an area are being recovered (see Methods, above). Finally, when habitats are changing the dead fauna of an area will be composed of a mixture of faunas from different environments. On a large scale the sedimentary facies of Mannin Bay appear to be stable and have been shown to be related to present-day physical processes except for the onlapping of the Fine Sand Facies. In this area a mixed live fauna has been described (above) and a mixed dead fauna would be expected. On a smaller scale habitats may change, for example during storms the margins of the algal banks are eroded. This would result in mixing of dead populations at the margins of communities.

Notes on the taphonomy of the major invertebrate groups

Bivalvia. The most easily recognizable mode of death of the bivalves is from predation by naticid gastropods which are occasionally found living in the area (Pl. 52, fig. 4). However, gastropod predation is only rarely seen and is far less important than predation by the asteroids *Marthasterias glacialis* and *Asterias rubens*, which leave no direct evidence of their activity in the fossil record. Indirect evidence is in the form of asteroid plates and digging traces (Pl. 52, fig. 1); the later would only rarely be preserved in the coarse open algal sediments. Other predation on bivalves is by skates (Rajidae) which excavate saucer-like depressions to obtain infaunal bivalves. After the soft parts are eaten the fractured shells are seen scattered in the depression. In summary, only occasionally are damaged shells found and the majority of the specimens which have recently died show no evidence of predation. This is the converse of that found by Wilson (1967) on tidal flats where bird predation is high.

The individual valves of the dead bivalves are usually disarticulated, but they may stay attached for a long period. Initially the shells are held together by the ligament, dentition, and suction in closely fitting valves. In forms with closely fitting dentitions and margins (e.g. *Nucula*) the valves are held together until the shell is considerably abraded (cf. Boyd and Newell 1972). The joined valves of bivalves are frequently covered by encrusters which grow over the shell commissure to seal the valves together (Pl. 52, fig. 7). These observations suggest that attached valves should not be used indiscriminately as indicators of transport in fossil assemblages.

The post-mortem history of bivalve shells depends to a large extent on their size. Large shells (greater than about 2 cm diameter, e.g. some Mytilacea, Ostracea, Pectinacea, some Cardiacea, Veneracea, Mactracea, and Solenacea) are frequently bored, encrusted, abraded, and fractured, whereas small shells (less than about 2 cm diameter, e.g. some Mytilacea, Astartacea, Lucinacea, Erycinacea, some Cardiacea, and Tellinacea) are not encrusted and bored at the macroscopic level, but are abraded and fractured. This is thought to be because the larger shells are less frequently transported than the small shells and can, therefore, be colonized and bored. In addition the large shells will be on the sea bed longer than the small shells as they will take a longer time to be broken down. This size division of the bored shells is suggested by Boekschoten (1966) for *Venus striatula* in the North Sea. In shallow waters the shells are never bored but shells dredged from deeper, quieter waters show evidence of boring.

Larger shells are found mainly in the hydrodynamically stable convex up-position in the high energy Clean Algal Gravel Facies judging from the face value of photographs and underwater observations. This is also the case for the buried shall layer found 35 cm below the sediment surface at a station just to the south of Ardillaun (73, text-fig. 1). This convex up-orientation leads to a differentiation of the encrusting organism (Pl. 2, figs. 9, 10). The lower concave surface is commonly encrusted by serpulids, spirorbids, bryozoa, and barnacles, whereas the upper convex surface is encrusted and bored by epilithic corallines, filamentous algae, and sponges. Ryland (1970, p. 79) states that bryozoa are abundant on the concave surfaces of shells and

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EXPLANATION OF PLATE 52

Fig. 1. Underwater photograph of *Asterias rubens* excavating algal gravel with tube feet for bivalve (*Venerupis aurea*), ×1/8.

Fig. 2. Underwater photograph of *Venus verrucaria* burrowing into muddy algal gravel, ×1.

Fig. 3. Underwater photograph of *Lanice conchilega* with tube and fan constructed of algal and mollusc grains in clean algal gravel, ×1.

Fig. 4. *Venerupis rhomboides* encrusted by corallines and a serpulid worm growing over the commissure, ×1.

Fig. 5. Fractured specimens of *Littorina littorea*. Crab predation is suggested for the three right-hand specimens but the others may have been fractured during transport, ×1.

Fig. 6. *Nucula turgida* (upper left), *Gibbula cinerarea* (upper right), and *Turritella communis* bored by naticid gastropods, ×1.

Fig. 7. Specimens of *Bittium reticulatum* showing abrasion of outer whorls, ×1.

Fig. 8. Heavily encrusted and bored specimen of *Buccinum undatum*, ×1.

Fig. 9. Upper convex surfaces of bivalves encrusted mainly by corallines and filamentous algae and bored by sponges, ×0·5.

Fig. 10. Lower concave surfaces of bivalves in fig. 9 encrusted mainly by serpulids and bryozoa, ×0·5.

PLATE 52
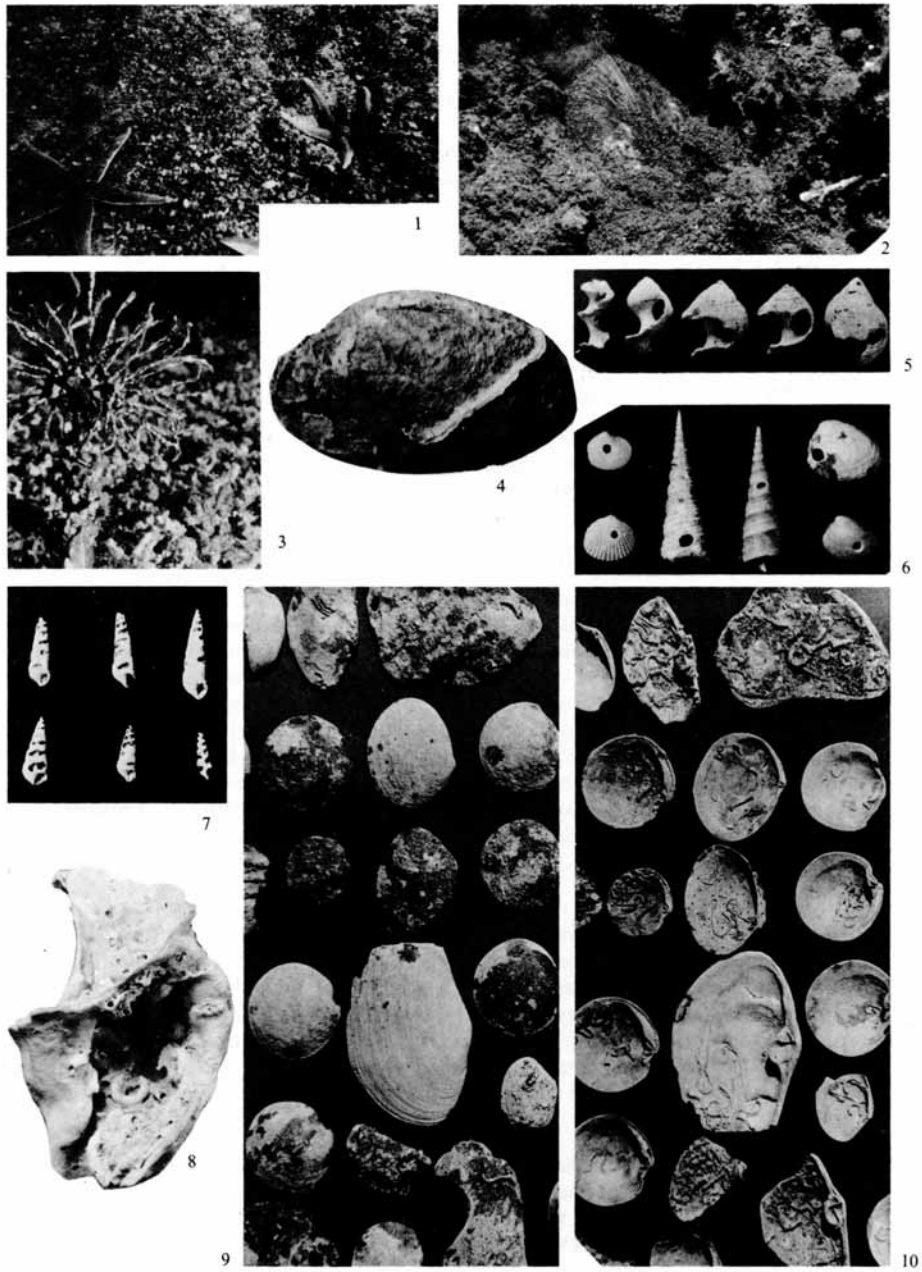
BOSENCE, algal gravel fauna

that in current swept areas the shells are convex down with the bryozoa inside. He suggests that settlement may occur on the inside of the shells because of the strong currents on the outer, upper surface. This separation of epifauna on the lower, and epiflora on the upper, more brightly lit, surfaces has been reported from settlement plates by Dybern (1967), Sentz-Braconnot (1968), and Bosence (in press). There are many factors which may cause this separation of encrusting organisms. Positive geotropism and negative phototropism have been shown for the larvae of rock-encrusting spirorbids by de Silva (1962). He considers that the larvae are led away from the bright areas which algae inhabit. The upper surfaces of the shells in Mannin would have more light and would, therefore, likely to be attractive to the algae. Once the algae are established the encrusting organisms would prefer the clean surfaces away from the algae.

This separation of the epiflora and fauna is likely to be preserved and would indicate small breaks in sedimentation or omission surfaces.

Gastropoda. Only rarely do the shells of gastropods show evidence of the way in which they died. The sedentary infaunal *Turritella communis* is sometimes found bored by naticid gastropods together with some bored *Gibbula cinerarea* (Pl. 52, fig. 4). *Asterias rubens* and *Marthasterias glacialis* have been observed preying on gastropods and have been seen with up to six snails at a time in their enfolded arms. The recognition and possible extent of crab predation on gastropods is difficult to interpret from shell fracture. Boekschoten (1967) has shown how crabs break away the outer whorl to eat gastropods and this is seen in Mannin Bay. However, this outer section of the shell is the weakest part and would be the first to fracture by physical processes as is suggested for some of the littorinids in Pl. 2, fig. 5. The post-mortem history of gastropods, as with bivalves, is related to the original shell size. The large shells (greater than about 1 cm high: e.g. some Patellidae, Trochidae, Littorinidae, Turritellidae, Buccinidae (Pl. 52, fig. 8), and Nassidae) show boring and encrusting in addition to some physical abrasion and fracturing. Small gastropods (less than about 1 cm high: e.g. Acmaeaidae, Turbinidae, Rissoidae, Cerithiidae, Triphoridae and Conidae) show only abrasion and fracturing (Pl. 52, fig. 6). As argued for the bivalves this division is considered to be the result of the small shells being transported more often than the large shells.

Polychaeta. Potential polychaete macrofossils are the agglutinated tubes of the terribellids, amphitritids, maldanids, *Pectinaria* and *Chaetopterus*, the calcified tubes of serpulids, and the burrows of nereid, glycerid, and eunicid worms. The agglutinated tubes would normally be preserved in their subvertical life position. But they are frequently eroded and may be buried with their tubes parallel to the bedding (e.g. Goldring 1964). The calcareous tubed polychaetes are mainly found encrusting shell debris and would be buried with the shell, or fractured off and buried as sedimentary grains.

Crustacea. Decapod crustacea and, in particular, the more heavily calcified Brachiuridae, are abundant in the coralline algal gravels. As the exoskeleton is renewed many times in their life it would be expected that these would be common in the sediment. However, this is not found to be the case in Mannin Bay where only the

occasional worn tips of chelae are found. The major cause of this is the extensive decalcification of the cuticle which occurs prior to ecdysis (Robertson 1941) leaving soft exoskeleton which soon decays. Major predators of the smaller decapods are members of the family Rajidae. Stomach contents of *Raja clavata* have shown up to fourteen small crabs per fish.

Occurrences and relative abundances of species and individuals of molluscs

Molluscan species and individuals are here classified as: (*a*) only occurring live in a facies; (*b*) only occurring dead in a facies; and (*c*) occurring live and dead (Table 7). From this classification it can be seen that there are about twice as many dead species as there are live species in a facies. The dead individuals are up to three orders of magnitude more abundant than the live individuals. In most facies exotic species are more abundant than live and dead only species. However, the greatest numbers of occurrences of dead species and individuals from a facies are from species which live within that facies. Occurrences of exotic species are the next most abundant group, followed by very few species and individuals of molluscs which occur living in a facies but are not found dead. If the non-molluscan members of the fauna had been included within this study then this last group would have been much more important. In summary, although there may be large numbers of exotic species in a facies, their occurrences are lower and the numbers of individuals are lower still. The exotic species are characterized by low occurrences (often one specimen) of a large number of species. The smallest numbers of exotic shells are found in the lower energy Bank and Muddy Algal Gravel facies. The high-energy Clean Algal Gravel Facies has a large proportion of exotic species (56·4%) and individuals (23·8%). The largest single identifiable ecological group present in the exotic species are prosobranch gastropods which usually inhabit weed-covered rocky substrates (Patellidae, Littorinidae, Rissoidae). These species are thought to be transported in from the adjacent rocky

TABLE 7. Occurrences of mollusc species and individuals in sedimentary facies.

	Facies				
	Bank	Muddy Algal Gravel	Clean Algal Gravel	Fine Sand	Mud
No. of stations	18	11	23	12	4
Species					
% dead species exotic to facies	46·3	49·1	56·4	67·6	76·0
Occurrences of live only species	2 (0·8%)	3 (0·9%)	8 (1·8%)	7 (3%)	0—
Occurrences of dead only species (exotic)	73 (27·7%)	97 (28·9%)	145 (32·6%)	119 (50·6%)	34 (64·1%)
Occurrences of live and dead species	188 (71·5%)	236 (70·2%)	292 (65·6%)	109 (46·4%)	19 (35·9%)
TOTAL species occurrences	263	336	445	235	53
Individuals					
Occurrences of live only individuals	3—	11—	35 (0·1%)	20 (0·1%)	0—
Occurrences of dead only individuals (exotic)	842 (4·9%)	1625 (4·8%)	9039 (23·8%)	5590 (39·5%)	419 (10·9%)
Occurrences of live and dead individuals	16260 (95·1%)	32170 (95·2%)	28845 (76·1%)	8556 (60·4%)	3435 (89·1%)
TOTAL individuals	17105	33806	37919	14166	3854

areas or floated in on weed dislodged during storms (Cadee 1968, p. 88). In addition, the exotic species in the Clean Algal Gravel Facies includes bivalves which are known to inhabit adjacent facies which may well have been transported in. Some of the exotic species in the Clean Algal Gravel Facies are known from similar facies in adjacent bays (Keegan 1974) and it is probable that they once lived in Mannin Bay. A persistent exotic species in the algal gravels is the common oyster (*Ostrea edulis*) which used to be cultivated in this region. It is only rarely found live today.

The Fine Sand Facies also has a high proportion of exotic species (67·6%) and individuals (39·4%) which includes the gastropods from rocky areas. Another identifiable group are six species of tellinid bivalves which are known to inhabit sand substrates (Keegan 1974; Tebble 1966). It seems likely that these species are either only occasionally inhabiting this facies or that they are living in the sediment but in too low numbers to be sampled in the live populations. Other exotic species of the sand are found living in the adjacent coralline algal gravels and are thought to be mixed with the sand fauna as the Fine Sand Facies is overlapping the algal facies.

TABLE 8. First five eigenvalues and eigenvectors from principal-components analysis of dead fauna.

	one	two	three	four	five
Eigenvalues	1·71	1·17	0·99	0·72	0·59
Percentage of total contribution per eigenvalue	16·79	11·51	9·70	7·07	5·79

The low diversity fauna found in the Mud Facies is not reflected in the dead faunas. A high percentage of exotic species (76%) is found which is made up of a small number of individuals (10·9%). These exotic species are largely accounted for by specimens from the rocky areas, with the addition of molluscs from the algal gravels which may have been transported into Mannin Creek.

The numbers of species which occur only living in a facies is very small and the numbers of individuals of the species is very low. An examination of the species involved shows that they are nearly all either thin-shelled bivalves (lucinids and tellinids) or that they are very thin-shelled gastropods (*Haminoea navicula* and *Natica*). After death these thin-shelled forms would be expected to break down quickly and so be unrecognizable in the dead material.

In summary, the dead molluscan fauna bears a complex relationship to the live fauna. Most of the dead species in a facies are exotic but the bulk of the individuals come from that facies. The higher-energy facies have the greatest numbers of exotic shells. The largest single identifiable group of exotic shells are gastropods from near-by rocky areas; others are thought to have been transported in or to have formerly lived in the area.

Reconstruction of trophic nuclei from the dead fauna

This analysis attempts to reconstruct the original trophic nuclei of the benthic communities using the dead material from each facies (Table 9). The six most abundant species of a death assemblage are taken to represent the trophic nucleus. If the more

commonly accepted definition of a trophic nucleus is used (species making up 80%
of the fauna; Neyman 1967) for the dead material, the nuclei would be made up of the
same three species (*Bittium reticulatum*, *Rissoa parva*, and *Gibbula magus*) for the
coralline algal and Fine Sand faunas (Table 9).

TABLE 9. A comparison of actual and reconstructed trophic nuclei.

Species	Actual Trophic group	Actual Cum. % abndce.	Species	Reconstructed Trophic group	Reconstructed Cum. % abndce.
BANK COMMUNITY TROPHIC NUCLEUS					
Bittium reticulatum	H	37·5	*Bittium reticulatum*	H	72·9
Xantho sp.	C/S	45·3	*Rissoa parva*	H	85·4
Porcellana longicornis	C/S	52·5	*Gibbula cinerarea*	H	88·8
Gibbula cinerarea	H	59·5	*Tricolia pullus*	H	90·7
Musculus discors	SF	66·0	*Parvicardium exiguum*	SF	92·1
Rissoa parva	H	70·5	(E) *Acmaea* sp.	H	93·6
CLEAN ALGAL GRAVEL COMMUNITY TROPHIC NUCLEUS					
Astarte triangularis	SF	62·1	*Bittium reticulatum*	H	55·7
Bittium reticulatum	H	77·8	(E) *Rissoa parva*	H	77·5
Idotea sp.	S	80·2	*Gibbula cinerarea*	H	83·7
Lucinoma borealis	SF	82·4	*Astarte triangularis*	SF	88·0
Cingula semicostata	H	84·4	*Tricolia pullus*	H	91·1
Chitonida	H	86·2	*Gibbula magus*	H	92·2
MUDDY ALGAL GRAVEL COMMUNITY TROPHIC NUCLEUS					
Bittium reticulatum	H	49·0	*Bittium reticulatum*	H	77·8
Mysella bidentata	SF	55·6	*Rissoa parva*	H	83·2
Nucula turgida	DF	61·7	*Gibbula cinerarea*	H	86·8
Lucinoma borealis	SF	67·5	*Parvicardium exiguum*	SF	88·5
Rissoa parva	H	71·6	*Acmaea* sp.	H	91·2
FINE SAND COMMUNITY TROPHIC NUCLEUS					
Bittium reticulatum	H	23·2	*Bittium reticulatum*	H	43·8
Thyasira flexuosa	SF	42·4	(E) *Rissoa parva*	H	72·8
Gibbula cinerarea	H	54·7	*Gibbula cinerarea*	H	78·7
Mysella bidentata	SF	63·5	*Turritella communis*	SF	82·3
Idotea sp.	S	70·1	(E) *Rissoa lilacina*	H	84·8
Acrocnida brachiata	SF	73·5	*Thyasira flexuosa*	SF	86·7
MUD COMMUNITY TROPHIC NUCLEUS					
Bittium reticulatum	H	39·2	*Bittium reticulatum*	H	82·5
Parvicardium exiguum	SF	49·9	(E) *Littorina littoralis*	H	86·9
Mysella bidentata	SF	59·7	*Littorina littorea*	H	90·3
Littorina littorea	H	69·5	(E) *Gibbula cinerarea*	H	92·4
Lucinoma borealis	SF	77·3	(E) *Rissoa parva*	H	94·2
Venus aurea	SF	83·1	*Parvicardium exiguum*	SF	95·5

Key: H = herbivore; C/S = carnivore/scavenger; SF = suspension feeder; DF = deposit feeder; (E) = exotic
to community.

The results from this analysis show that the correct composition and order of abundance of the species making up the trophic nuclei cannot be reconstructed from the dead fauna. Apart from the ubiquitous *B. reticulatum*, which is the commonest live and dead organism, three of the six most abundant organisms in the dead material are not present in the six commonest live species. In addition, up to one-third of the organisms in the 'dead trophic nuclei' are exotic. The reconstructed trophic nuclei
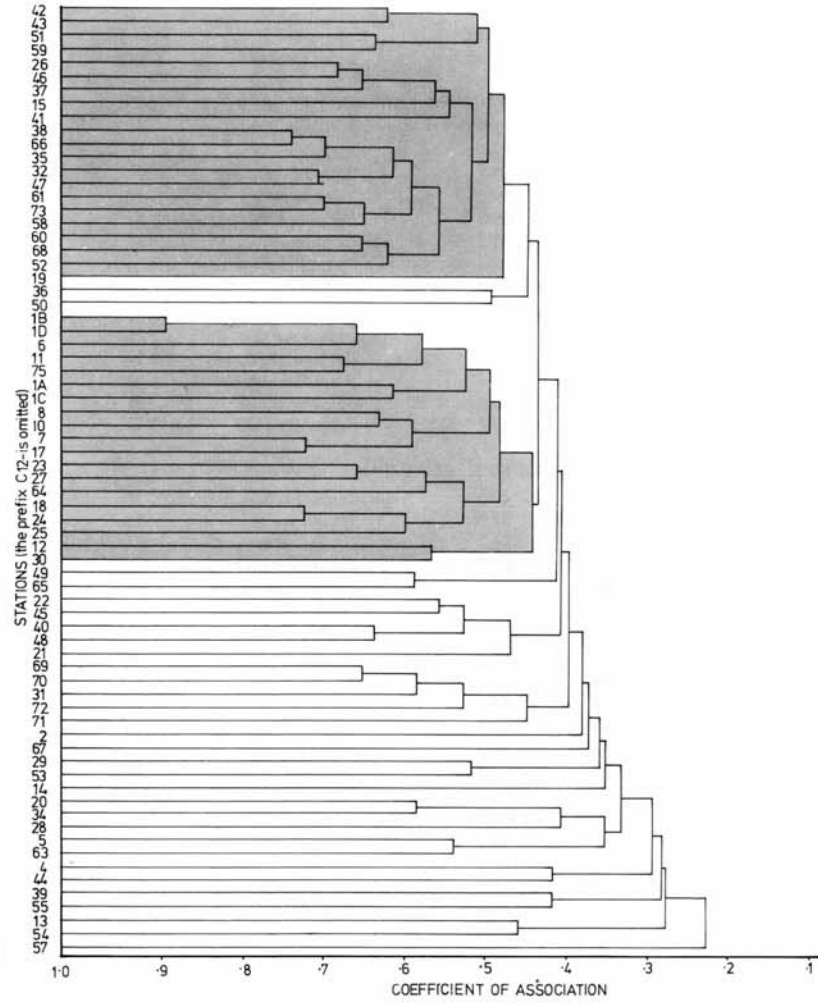
TEXT-FIG. 4. Dendrogram illustrating clustering of stations by cluster analysis of dead fauna.

are dominated by herbivorous and detritus-feeding gastropods, whereas the actual nuclei have abundant carnivores/scavengers, suspension feeders, and deposit feeders in addition to the herbivores. The epifaunal gastropods which are frequently exotic, are being preferentially preserved to dominate the reconstructed trophic nuclei and thus forming an anomalous 'trophic zone' (Sokolova 1964; Neyman 1967).

Stanton (1976) has recently criticized the applicability of Turpaeva's (1949, 1957) work on trophic nuclei to palaeontology by showing that the preservable organisms in a community do not always reflect the original feeding groups in benthic communities with many soft-bodied organisms. In this study from Mannin Bay the trophic nuclei are, in each case, dominated by taxa with hard parts but, due to various taphonomic factors, the dead material cannot be used to reconstruct the living trophic nuclei.

Quantitative analysis of death assemblages

For this study the dead fauna was analysed using the same programmes as were used for the live fauna (see Methods, above) to see if similar groupings could be recognized. The non-parametric cluster analysis produces the clusters shown in the dendrogram in text-fig. 4. Four main clusters are seen at the 0·4 level, the rest of the stations showing no grouping. The clusters produced from this analysis show complete mixing of the stations from the previously defined sedimentary facies and communities. None of the previous clusters can be recognized and no interpretable pattern is produced if the clustered stations are plotted on maps. This result is to be expected from the presence–absence analysis of the fauna because of the high proportion of exotic species in each facies (Table 7). This mixing of the fauna from each facies is also reflected in the level of association which is very much higher than for the live fauna.

The results of the principal-components analysis (based on fifty-nine mollusc species) are shown in Table 8 and text-fig. 5. The first five eigenvalues are used as they account for just over 50% of the total variation of the data. The plots of the stations with respect to the first three eigenvectors (text-fig. 5) show that the samples from the previously defined communities do not plot as separated clusters. However, samples from similar communities plot as very poorly defined clusters reflecting the Clean Algal Gravel, Bank, and offshore Fine Sand communities. The Muddy Algal Gravel and inshore Fine Sand faunas do not plot as recognizable clusters, as was previously predicted, because of the onlap of the Fine Sand Facies (Bosence 1976b). The Clean Algal Gravel Community stations are separated by eigenvectors one, two, and three and the Fine Sand Community stations by eigenvector three. The species causing the highest loading on eigenvector three are the sand living *Thyasira flexuosa*, *Gastrana fragilis*, *Turritella communis*, and *Natica* sp., together with the fauna from the rocky substrates, *Calliostoma zizyphinum* and *Alvania punctura*. The Bank Community stations are defined by variation in eigenvectors one and two.

The principal-components analysis of the dead fauna shows that faunas from stations are more similar, and the clusters are very much more indistinct than those of the live fauna (cf. text-figs. 3 and 5). In conclusion the presence–absence analysis of the dead material cannot recognize the previously defined communities. From the principal-components analysis, which is based on species abundances, some of the stations from the more distinct communities can be recognized but the clustering
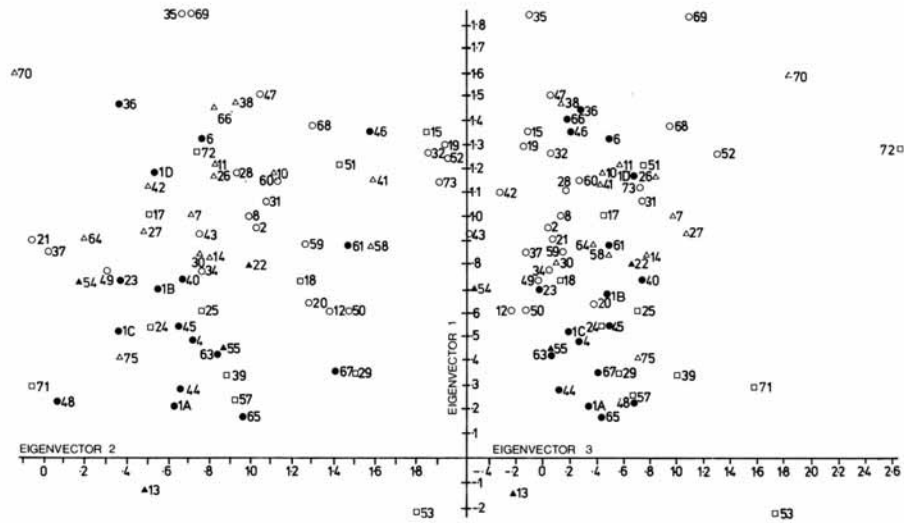
TEXT-FIG. 5. Dead fauna from stations 1–73 plotted with respect to eigenvectors one, two, and three. *Key*: ● Bank Facies, △ Muddy Algal Gravel Facies, ○ Clean Algal Gravel Facies, □ Fine Sand Facies, ▲ Mud Facies.

based on the live fauna cannot be seen. Therefore it is unlikely that the previously defined communities in Mannin Bay could be recognized from an analysis of the dead material.

Comparison with previous work

Perhaps the most detailed study on the relationships between subtidal live and dead faunas is Cadee's (1968) study, over a period of three years, of the molluscs from Ria de Arosa, Spain. His long-term sampling reduced the differences between the live and dead faunas caused by small-scale time fluctuations and patchy distributions. In addition, with surface currents having a mean maximum of 20–30 cm/sec and muddy sediments over most of the bay little physical transport of the shells would be expected. Cadee finds good correlations of species presences between live and dead faunas, but their abundances vary considerably. The differences between the live and dead faunas are thought to be caused by the long-term effects of population fluctuations, patchy distributions, post-mortem transport of shells (particularly epifauna transported on weed from rocky areas), and selective removal by predators.

Johnson (1965) working on molluscs from Tomales Bay, and Warme's (1969) study of molluscs from Mugu Lagoon, California, show that the greatest numbers of dead species occurrences are in the dead only (exotic) group and that the occurrences of the dead only individuals is similar to the occurrences of the live and dead individuals. The large proportion of exotic species in Tomales Bay and Mugu Lagoon may be

explained by the fact that the exotic material was taken with respect to each sample and not from the sedimentary facies as is done in this study. This confirms the difficulties of sampling the species of low abundances. Nevertheless, Warme and Johnson consider that their results show a good correspondence of live and dead molluscan faunas. The two environments are characterized by areas of both high and low hydraulic energy.

Petersen's (1976) study of the mollusc fauna from the very high-energy (250 cm/sec) sandy-channel habitat in Mugu Lagoon and Tijuana Slough in California produced results similar to those of Johnson (1965) and Warme (1969) for the presence and absence of live and dead molluscs and the relative abundances of the live and dead species. Of particular value in Petersen's study is his repeated sampling of the two environments for three times a year over three years. This repeated sampling showed that the temporal variability of the communities was the major cause of the discrepancies between his live and dead populations.

In a larger-scale study Warme et al. (1976) studied molluscs from both high- and low-energy environments on the Yucatan shelf. They found that there was a good correspondence between the live and dead faunas on the basis of species abundances analysed by cluster analysis. They emphasized the time-average effect of shell accumulation which results in the shell assemblages closely reflecting community structure. In addition they suggest that the assemblages provide more information on the community than one sampling of the live fauna. Post-mortem transport is not considered important.

The results from Mannin Bay show some similarities with this previous work in that the dead fauna contains many exotic species. However, this exotic material consists of large numbers of species with small numbers of individuals so that the bulk of the dead individuals come from species that live within the facies. It is perhaps surprising that the results from the sheltered coastal lagoons are similar to those from the more exposed environment of Mannin Bay. This similarity suggests that the ecological factors which effect dead-shell distribution are as important as the more commonly cited physical factors. In this study some of the exotic species can be identified as coming from the near-by rocky areas. Where one facies is overlapping another there is considerable mixing of both the live and the dead faunas. If the dead faunas are examined in more detail to see if the communities and trophic nuclei can still be recognized, then my results differ from those of previous workers. Whereas Warme et al. (1976) find good correlation between communities recognized from the live and the dead material, no such relation is found in Mannin Bay. Statistical analysis of the dead material shows that the fauna has been extensively mixed and that the live communities and the trophic nuclei can no longer be recognized. There are a number of reasons which could explain these differences. Firstly, my community analysis is based on the entire macrofauna whereas previous workers have just studied molluscs. Clearly the molluscs have a more equal preservation potential than the total fauna with both hard- and soft-bodied organisms represented. In fossil examples from similar habitats it may be possible to predict the molluscan communities from the molluscan death assemblages but these may not be a good representation of the total macrofaunal communities or biocoenoses (Stanton 1976). Secondly, this study is on a more detailed scale than those of Cadee (1968), Johnson

(1965), Warme (1969), and Warme *et al.* (1976). The Mannin Bay communities and sedimentary facies have dimensions measured in terms of hundreds of metres whereas those of previous workers are on a kilometre scale. If there are areas of mixing of dead faunas at community boundaries then these will be more important in small-scale studies than in large-scale studies. In addition, the initial differences between the communities may not be as great. Thirdly, the hydraulic energy of the environment will affect the transport and distribution of the dead fauna. Although detailed studies are lacking, it would appear that Mannin Bay is more exposed than some of the other areas described and therefore more post-mortem transport would be expected.

CONCLUSIONS

Descriptions of the benthic fauna from Mannin Bay, backed up with multivariate statistical analysis of species abundances, show the existence of five communities. The communities are specific to previously defined sedimentary facies. The fauna from the coralline algal sediments is similar to Ford's (1923) *Venus fasciata* community, but in addition has a diverse epifauna of gastropods and crustacea together with a boring infauna. Although no detailed studies are available from the tropical coralline algal banks the information to date suggests a similarly diverse fauna. The lack of any palaeosynecological studies from Tertiary coralline algal limestones precludes comparisons or assessment of community evolution.

A study of the death assemblages produces results which differ from those of previous workers. In particular, Warme *et al.* (1976) suggest that molluscan death assemblages 'contain more information on the total community living in a particular habitat than do the live assemblages'. In Mannin Bay the dead material cannot be used to reconstruct the trophic nuclei or the communities. The good correlation between the distribution of the live and dead material found by previous workers could well be the result of the good preservation potential of molluscs. If the whole fauna is taken into account for community evaluation then the correlation may not be so good. In addition in this study exotic molluscs are found which are probably derived from near-by rocky areas. The relationships between live and dead faunas would be expected to be different in different environments. These differences will depend particularly on temporal changes in community structure, patchy faunal distributions, and varying amounts of post-mortem transport. Further work on this problem is clearly required, particularly on the geologically important open-shelf areas.

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