THE MACROFAUNA OF MAERL SUBSTRATES ON THE WEST COAST OF IRELAND

by

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Résumé

La macrofaune des substrats de maërl sur la côte occidentale d'Irlande

Un groupe hétérogène d'animaux est associé de façon constante, quoique variée, au maërl infralittoral dans la partie Est de l'Atlantique Nord. Les résultats de cette étude correspondent au schéma général.

Six types de substrats de maërl ont été arbitrairement définis dans la zone étudiée. Dans chaque cas, le *Lithothamnium corallioides* var. *corallioides* constitue la masse du sédiment. Les animaux macrobenthiques associés ont été étudiés quantitativement à l'aide de techniques de prélèvements in *situ.*

Une attention spéciale a été accordée à la présence anormale de populations très denses de *Paracentrotus lividus* et d'agrégats mélangés d'*Antedon bifida* et d'*Ophiocomina nigra.*

Introduction

The notation "Crl", as used on hydrographie charts of the Irish west coast, generally designates deposits of coralline algae (see Keary, 1970).

In the Galway/Kilkerrin area (Map A), the bioclastic fraction of certain bottom deposits is largely of such algae or, more correctly, of their remains. Indeed, some biogenic substrates are almost exclusively of *maerl* origin.

[As explained by Cabioch (1968) : « On désigne couramment sous le nom de maërl, l'accumulation de thalles de Mélobésiées arbusculaires libres constituant de véritables fonds sédimentaires dont l'observation est fort ancienne dans les mers européennes. » In the following text, the term is used in the same collective sense].

Local interest in the potential usefulness of shallow water maerl deposits prompted the author to investigate their associated macrofauna.

Pérès (1967), in keeping with the recommendations of Jacquotte (1961 and 1962), ascribed the fauna of mediterranean maerl substrates to a facies, the Nullipore facies, of the "Coastal Detritic Biocoenosis".

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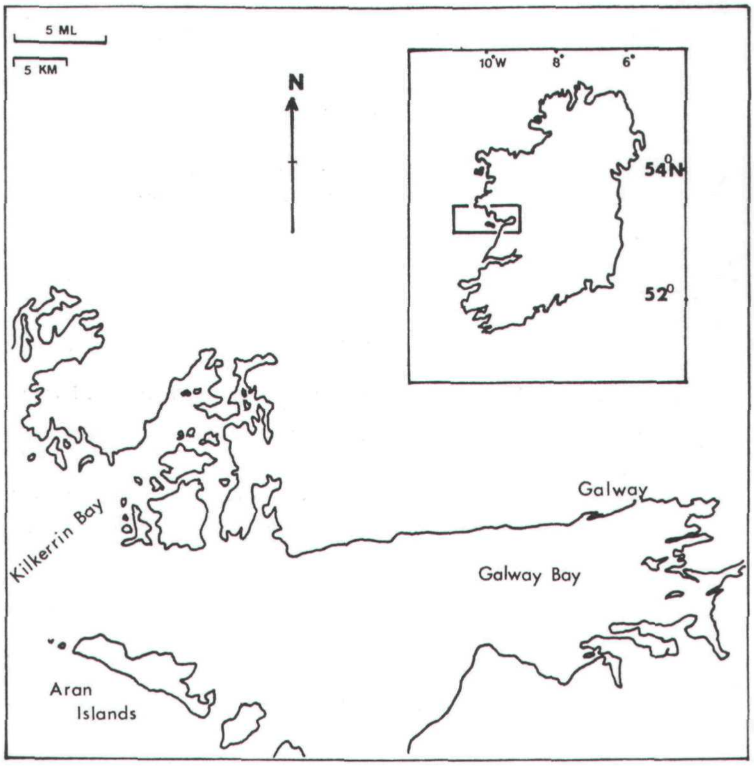
More recently, Cabioch (1968) proposed that the maerl fauna of Northern Brittany be viewed in context of a separate biocoenosis, the "Biocoenose du Maërl".

In reporting on the present work the emphasis is directed away from such general categorisation, the writer preferring to highlight the local character of the maerl deposits and related variations in the macrofauna.



MAP A.
Location Map of Study Areas.

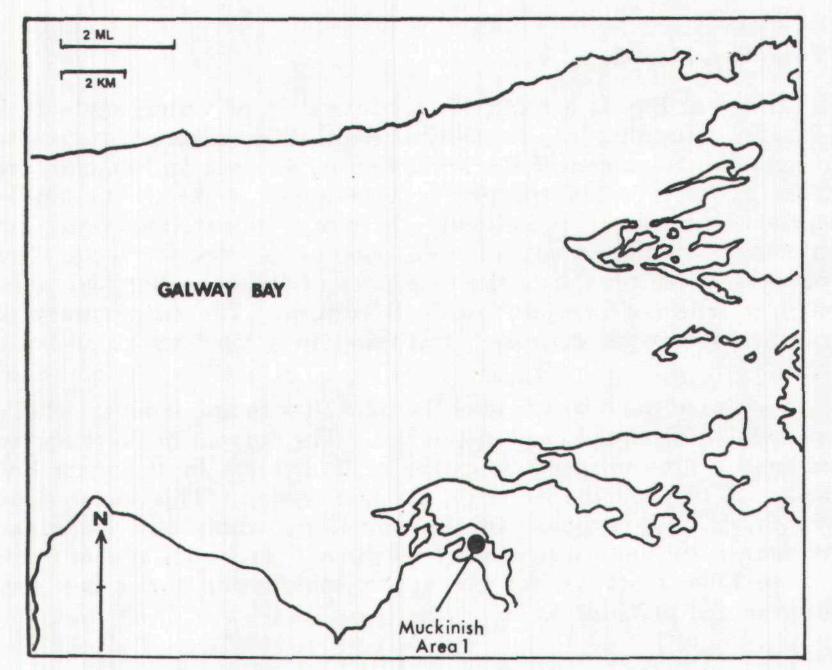
Description of study areas.

Muckinish Inlet - Galway Bay. Map B.

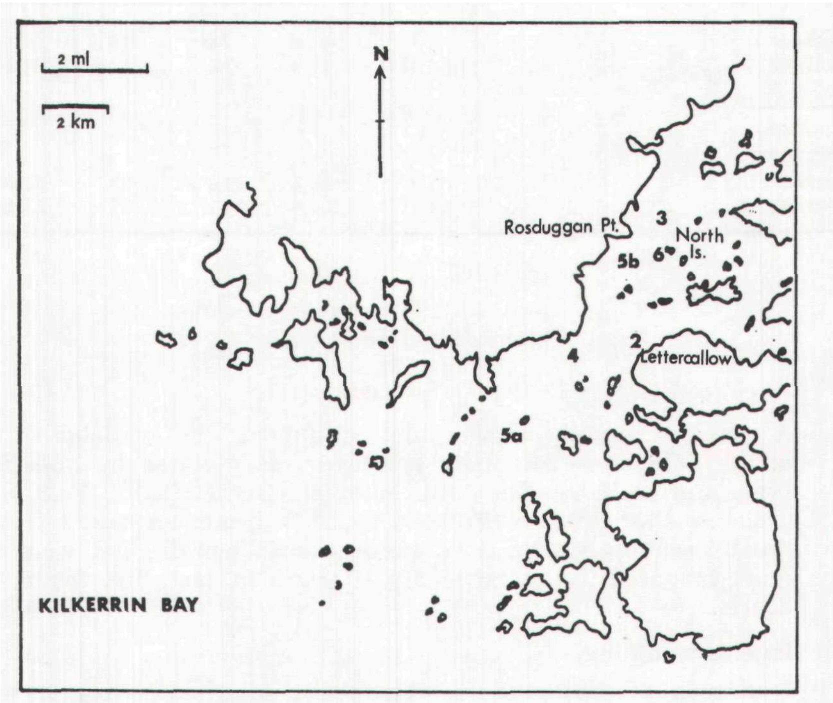
Muckinish inlet, with an overall length of 4 km and an average width of 0.75 km, opens from the southern shore of Galway Bay. A shallow area (maximum depth, 5 m), it communicates with the main bay through two narrow channels and is swept by strong (> 2 m/sec) tidal currents.

The bedrock is of Carboniferous limestone and the deposit substrates include maerl, sand and mud.

Occasional monitoring of hydrographie conditions gave the following range of data: S p. 1 000, 24.2 - 33.1 ; T°C, 4.8 - 22.4.



MAP B.
Galway Bay.



MAP C.
Kilkerrin Bay.

Kilkerrin **Bay.** Map **C.**

Kilkerrin Bay is a relatively narrow strip of water, some 16 km in length. Running in a North-East South-West direction, it is situated near the West end of the main Galway Granite and extends from within a few miles of the northern boundary right to its southern margin. The more prominent shoreline indentations are joint controlled as is the shape and orientation of the offshore reefs. Some geographical features, e.g., the long axes of the subsidiary bays, may similarly reflect either joint or fault control. The sedimentary patterns are somewhat confused, testifying to a very irregular bottom terrain.

A series of narrows channel the tidal flow to and from the shallow basin which forms the head of the bay. The current in these narrows can have a ground-speed in excess of 2 m/sec. In the open lower reaches of the bay the currents are less strong. This latter region, however, is fully exposed to the prevailing winds and experiences pronounced turbulence in stormy weather. Maximum and minimum T°/S p. 1 000 readings, for the upper, middle and lower bay areas, are presented in Table 1.

TABLE 1.
S p. 1000 and T°C values - Kilkerrin Bay, 1971.

T°	Upper		Middle		Lower Bay	
	Max.	**Min.**	Max.	Min.	Max.	Min.
Surface	20.8	6.8	17.8	7.0	18.2	8.2
Bottom	18.1	6.8	17.2	7.3	14.6	8.2
S p. 1000						
Surface	34.3	32.0	34.5	32.6	34.7	33.65
Bottom	34.4	32.3	34.6	32.7	34.8	33.65

Methods and Techniques.

(1) Remote sampling.

A range of qualitative sampling equipment was available to the study. This was variously employed, as dictated by substrate type, and included the Baird sampler (Baird, 1958), Van Veen grabs, anchor dredges (Forster, 1953), a beam trawl and "traditional" scallop dredges. Of these, the anchor dredges were the most favoured, being especially effective in sampling the maerl debris.

(2) In situ sampling.

Hundreds of diving-hours were spent in qualitatively investigating the study areas. Much of this exploration was "controlled", e.g., carried out with reference to a grid system or line-of-transect.

Survey techniques were based on those described by Neushul (1965), Fager *et al* (1966), Knight-Jones *et al* (1967) and by Larsson (1968).

Quantitative sampling was effected by "suction-sampling" techniques (Keegan and Könnecker, 1973) and the results so obtained have the author's confidence as representing the totality of macrobenthic animals living upon and below specified unit areas of sea-bottom.

RESULTS OF THE INVESTIGATION

Six maerl (1) or dominantly maerl substrates have been arbitrarily distinguished. The degree of "faunal confluency" existing between them can be inferred from Appendix 1.

SUBSTRATE I.

Living maerl (Littoral).

Location.

Area 1 ; Map B.

Biotope description.

In the Muckinish inlet, banks of maerl are exposed at low tide. Some 24-60 cm in thickness (where sampled), these banks have a streaked and marbled appearance. This results from the colour-contrasting disposition of the living and dead corallines (Plate 1, A).

The causative agencies behind this distribution pattern are, as yet unknown. One possible explanation involves the formidable tidal currents which sweep the inlet and which have been observed to change the topography of the maerl banks in the period between successive spring tides. A considerable shifting of material takes place and this could effectively bury patches of the living algae. The resulting "local" mortality would account for the odd distribution pattern. To the writer's knowledge, the intertidal occurrence of living maerl is unique for Irish coastal waters.

Macrofauna.

The maerl debris is relatively compacted and is strikingly barren of animal life. By comparison, the arbuscular living material is loosely accumulated. This has an epifauna which is not especially diagnostic being restricted to a small number of ubiquitous intertidal and shallow water species. In contrast, this substrate supports a

(1) In each case, *Lithothamnium corallioides* var. *corallioides* constitutes the bulk of the deposit.

spectacular "sub-surface epifauna". Within the highly branched living maerl are located dense aggregations of the echinoid *Paracentrotus lividus*. Layering of these animals results in concentrations of more than 1,600 individuals/m^2 surface area. (Plate 1,B). Associated with these high-density populations, one finds large numbers of the ophiuroids *Ophiothrix fragilis, Ophiocomina nigra,* and, to a lesser extent, *Amphipholis squamata.* The most prominent members of the true endofauna are the bivalves *Venerupis rhomboïdes* and *Dosinia exoleta.*

SUBSTRATE 2.

Living maerl (Sub-littoral).

Location.

Area 2; Map C.

Biotope description.

Large tracts of Kilkerrin and, to a lesser degree, of Galway Bay, are blanketed with living maerl. Typical of such areas are the shallow-water slopes of Lettercallow Spit (Kilkerrin Bay). On these slope the arbuscular maerl presents a distinctive aspect which the author chooses to describe as a "current-winnowed lattice". The open nature of this lattice permits the vertical ranging, within it, of many epifaunal organisms.

Macrofauna.

The Lettercallow maerl has a very varied epifauna (see Appendix I). As arbitrarily defined, it does not have a "true" infauna. The animals of the deposit substrates which variously underlie the maerl blanket are not considered here.

SUBSTRATE 3.

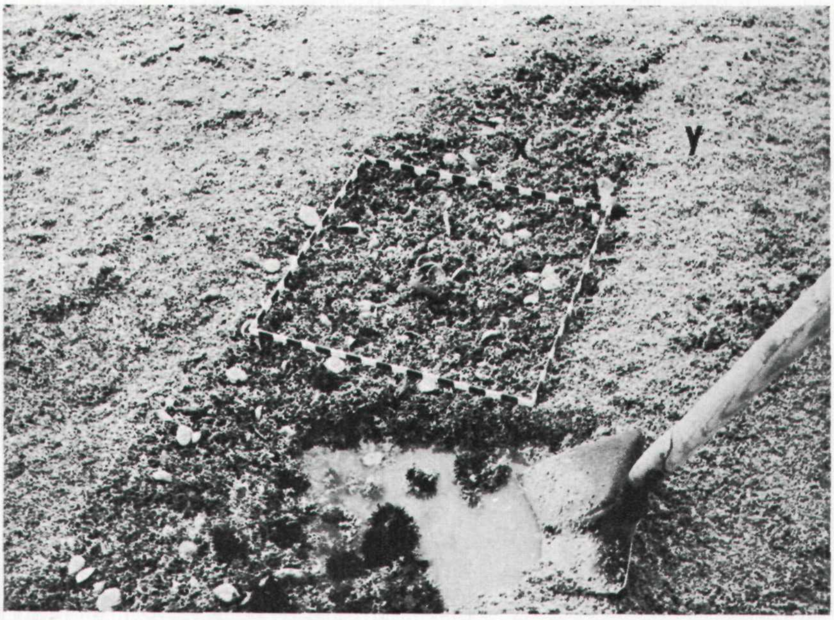
Maerl/soft ground.

Location.

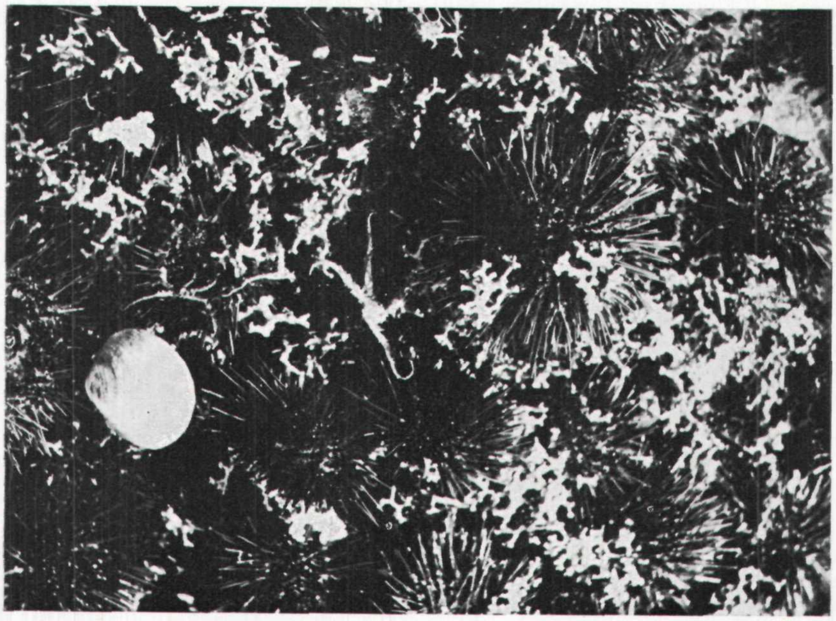
Area 3; Map C.

Biotope description.

The shallow upper reaches of Kilkerrin Bay are populated by extensive beds of sea grass *(Zostera).* Fringing these beds towards the open bay and bounded by deeper water at its western extremity, is found a most interesting substrate. A "basement" deposit of terrigenous material, mixed through with some biogenic remains, is overlaid with a light covering of living and dead maerl.



A



B

B.F. KEEGAN.

A: intertidal maerl banks (Muckinish Inlet, Galvvay Bay).
X = living maerl; Y = maerl debris;
B: aggregated *Paracentrotus Hindus* (within living maerl).

This coralline cover is not evenly distributed but tends to be thrown into low wide ridges by the tidal current which sweeps the area. In creating these ridges, the current causes the intervening troughs to be denuded of cover. With the exception of the extreme uppermost layer, the basement deposit is markedly cohesive. The average depth of water in the area is 16 m (L.W.S.).

Macrofauna.

The dual nature of the substrate is naturally reflected in its animal population. As might be expected, the mobile cover has a rather limited epifauna. Its instability no doubt similarly restricts, in kind if not in number, the fauna of the underlying sediment.

Table 2 lists the quantitative returns from some eighteen stations, In every instance the sediment was excavated to a depth which, as visually confirmed, ensured the capture of all the macrofauna below a unit area of 0.25 m². Layered sampling revealed that the great bulk of the infauna occurred in the upper 25 cm of sediment.

A lower limit of burrowing (for this substrate) was established for the following species:

Species	Max. depth of burrowing (± 2 cm)
Golfingia elongata	40
Golfingia vulgaris	36
Upogebia spp.	46
Mya arenaria	58

SUBSTRATE 4.

Maerl/hard ground.

Location.

Area 4; Map C.

Biotope description.

Many of the narrows and tidal channels in Kilkerrin Bay are scoured clean, exposing either bed-rock or rock-gravel. These surfaces are usually littered with a transient debris which may include greater or lesser amounts of maerl. Flanking one such area, the author discovered a relatively stable substrate, removed from the main tidal stream and comprising maerl debris and rock gravel. The bottom terrain is variously banked and irregular with numerous outcropping reefs and boulders. The average depth of water in the area is 17 m (L.W.S.).

Macrofauna.

This substrate has a restricted, if highly spectacular, epifauna which is dominated by *Antedon bifida* and to a lesser degree, by *Ophio-*

TABLE 2.

SUBSTRATE 3

List of species occurrences at 18 stations
(Quantitative suction-sampling; sample size 0.25 m²/≃40 cm penetration)

Species	Station n°																	
	1	2	3	9	5	5	7	8	9	10	11	12	13	14	15	16	17	18
Anemonia sulcata	2	7	1	—	1	1	—	—	5	—	—	—	6	—	—	—	1	—
Peachia hastata	—	1	—	—	—	1	—	—	—	—	2	—	—	—	—	—	1	—
Cerianthus lloydi	3	—	—	1	1	1	2	1	—	—	—	1	—	—	—	—	—	—
Golfingia elongata	23	20	13	16	3	22	8	17	13	11	10	13	13	3	—	5	2	12
Golfingia vulgaris	—	1	1	—	2	1	—	—	—	—	2	—	—	2	1	—	—	—
Aphrodite aculeata	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gattyana cirrosa	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—
Harmothoe sp.	—	2	—	4	—	—	—	—	—	1	—	1	—	—	—	—	—	3
Polynoe scolopendrina	—	—	1	—	—	—	1	—	—	—	—	—	1	—	—	—	—	1
Halosydna gelatinosa	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sthenelais boa	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—
Nereis irrorata	1	1	1	1	3	2	1	4	3	1	—	1	1	1	—	—	1	7
Nephthys hombergii	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	—	1	1
Nephthys cirrosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Glycera convoluta	1	3	4	1	—	—	1	3	—	—	—	1	1	—	—	—	2	1
Goniada maculata	—	1	1	—	—	—	—	—	—	—	—	1	—	—	—	—	2	—
Marphysa sanguinea	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Nematonereis unicornis	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Lumbriconereis latreilli	2	3	3	6	1	4	1	5	3	4	3	4	4	1	2	3	2	3
Arabella iricolor	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Aricia cuvieri	—	—	—	—	1	—	7	—	1	—	—	—	—	—	—	—	—	—
Laonice cirrata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—
Chaetopterus variopedatus	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	1
Scalibregma inflatum	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Notomastus latericeus	—	—	—	—	—	—	2	—	—	—	—	1	1	—	—	—	—	—
Amphitrite edwardsi	—	2	2	—	—	—	—	4	—	—	3	—	2	—	—	—	—	2
Lanice conchilega	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—
Pista cristata	5	3	4	—	—	—	1	—	—	1	1	2	2	—	1	2	11	5
Terebellides stroemi	—	—	—	2	—	—	2	—	—	—	—	—	—	—	—	—	2	—
Sabella pavonina	—	1	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—
Branchiomma vesiculosum	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Amphipoda (unidentified)	3	3	—	—	1	—	1	4	2	—	—	3	3	—	—	—	1	—
Conilera cylindracea	—	—	—	—	—	—	—	—	1	—	—	—	—	1	1	—	1	—
Pandalina brevirostris	—	1	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—
Hippolyte varians	—	—	—	2	—	—	—	—	—	1	—	—	1	—	1	—	—	1
Galathea intermedia	—	—	—	—	1	—	—	1	—	—	—	—	—	—	1	—	—	—
Galathea squamifera	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Galathea strigosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Porcellana longicornis	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Upogebia deltaura	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Upogebia stellata	—	—	—	—	1	—	2	1	2	—	1	1	—	1	—	—	1	—
Paguridae (unidentified)	—	2	—	2	—	—	3	—	—	1	2	1	—	—	—	—	—	—
Cancer pagurus	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Macropipus corrugatus	—	—	—	—	—	—	1	1	—	2	—	1	—	1	—	—	—	—
Portunus puber	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Portunus depurator	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
Portunus arcuatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Xantho pilipes	—	1	—	—	—	1	—	2	—	1	—	1	2	1	—	—	—	1
Pilumnus hirtellus	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	2	—
Maia squinado	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Macropodia rostrata	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Gastropoda (unidentified)	—	4	3	4	12	—	—	6	3	3	2	3	1	7	4	8	8	—
Gibbula magus	2	1	1	2	—	4	2	4	—	4	1	—	4	2	1	—	7	1
Gibbula cineraria	—	—	1	—	—	1	—	—	1	—	1	—	2	—	—	—	1	—
Gibbula umbilicalis	1	1	1	—	1	1	—	1	—	—	1	3	1	—	—	2	—	1
Bittium reticulatum	2	9	2	6	4	11	4	1	3	2	2	4	—	6	—	—	8	4
Aplysia punctata	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—

TABLE 2 Contd.

Species	Station n°																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Nucula sulcata	9	5	9	11	2	11	56	7	9	17	14	12	34	3	5	31	22	27
Arca tetragona	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Modiolus modiolus	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—
Anomiidae								very common										
Chlamys varia	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Chlamys opercularis	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Chlamys distorta	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Thyasira flexuosa	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—
Lucinoma borealis	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Myrtea spinifera	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Parvicardium ovale	—	—	—	—	—	—	—	1	—	1	—	—	1	—	—	1	—	—
Parvicardium exiguum	3	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Dosinia exoleta	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Dosinia lupinus	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Venus verrucosa	—	1	1	—	—	—	—	2	—	—	1	1	1	1	1	—	—	1
Venerupis rhomboides	—	1	—	2	1	1	—	1	—	—	—	—	1	—	2	1	—	—
Venerupis aurea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Irus irus	—	2	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—
Lutraria lutraria	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Lepton squamosum	—	—	—	—	3	1	3	1	1	2	—	—	—	3	—	—	1	—
Corbula gibba	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Sphenia binghami	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Lyonsia norvegica	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—
Antedon bifida	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—
Leptosynapta inhaerens	1	—	—	3	—	—	—	—	3	—	1	—	—	—	1	—	—	—
Asterias rubens	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1
Marthasterias glacialis	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
Astropecten irregularis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Henricia sanguinolenta	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—
Ophiothrix fragilis	—	—	—	2	—	—	—	—	—	1	—	—	—	—	—	—	—	1
Ophiocomina nigra	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—

comina nigra. The crinoids are very densely aggregated, concentrations of more than $1{,}200/m^2$ being quite usual over much of the ground. By comparison, *Ophiocomina* exhibits a "clumped" distribution pattern and is at its most numerous ($90/m^2$) where the incidence of *Antedon* is also relatively high.

Other prominent members of the macrofauna are listed in Appendix 1.

SUBSTRATE 5.

Maerl debris - unstable.

Location.

Areas 5a and 5b; Map C.

Biotope (5a) description.

The label "maerl debris - unstable" qualifies a type of substrate which is common to the study area. Two examples were chosen for investigation. The first of these, designated 5a, lies below the main tidal channels and is possibly the most extensive of its kind in

Kilkerrin Bay. Whilst the great bulk of the sediment is of maerl origin, there is a variable admixture of other bioclastic elements.

The upper deposit, largely devoid of fine material, is thrown into regular ripples by the ground swell. Reflecting the south-westerly exposure of the bay, the configuration of the ripples varies from one gale to the next. A pronounced swell causes the ripples to have sharp crests (average crest height, 20 cm). The moderate tidal currents tend to round and flatten these crests and, by so doing, to fill and raise the level of the troughs. This cyclic process, and the instability it confers, must constitute a major selective control where the animal population is concerned. The average depth of water in the area is 17 m (L.W.S.).

Macrofauna (5a).

With the exception of, perhaps, *Molgula oculata,* the epifauna is not especially diagnostic and is, in the main, very poor. However, any relatively stable projection above the sediment surface, e.g. *Chaetopterus* tubes, etc., tends to be heavily settled by both plants and animals.

The infauna is that of the boreal *Venus fasciata* community (see Appendix 1). Table 3 lists some typical quantitative returns.

Layered sampling revealed that where the upper deposit is relatively uncompacted the bulk of the infauna can be found at depths of more than 20 cm. Indeed, the depth-ranging of many filter-feeders, e.g. *Astarte triangularis,* suggests that their requirements of food and oxygen are wholly supplied by the ground water!

Biotope (5b) description.

This substrate is far less typical than at 5a and is taken to reflect a particular topographical milieu. Constituting the floor of an ill-defined channel, a transitory accumulation of maerl debris is rendered mobile by strong (2 m/sec; spring tide) tidal currents. The channel, open to the west, has a cul-de-sac eastern extremity. At this closed upper end, in the "topographical funnel" between Rosduggan Point and North Island, are found great irregular dunes (5 m in height) of living and dead maerl.

It is postulated that these are formed by an overspill of material from the upper, more shallow basin. In turn, current erosion of the dunary deposits replenishes the substrate within the channel proper.

The average depth of water over this ground is 19 m (L.W.S.).

Macrofauna (5b).

Having witnessed the extreme mobility of this substrate, the tendency was to dismiss it as being unsuited to the majority of animals. Detailed examination however found the "hostile" conditions to be highly selective for a limited infauna. This can be seen from the sampling results listed in Table 4.

TABLE 3.

SUBSTRATE 5a

List of species occurrences at 10 stations
(Quantitative suction-sampling; typical set of results; sample size: 0.1 m²/$\simeq$50 cm penetration).

Species	Station n°									
	1	2	ε	4	5	6	7	8	9	10
Lanice conchilega	—	—	—	—	—	—	—	—	—	1
Harmothoe sp.	—	—	1	—	—	—	—	—	1	—
Nephthys sp.	1	—	2	—	—	—	—	—	1	—
Glycera alba	2	—	4	—	—	1	1	—	1	—
Notomastus latericeus	—	3	1	1	—	1	—	—	—	1
Pista cristata	—	—	—	4	—	—	—	—	—	—
Chaetopterus variopedatus	—	—	1	—	—	—	—	—	1	—
Polygordius lacteus	3	—	—	—	2	4	—	—	2	—
Sipunculus nudus	—	2	2	2	—	—	—	—	1	—
Amphipoda sp.	5	—	—	1	—	—	3	—	3	—
Conilera cylindracea	—	—	4	1	—	1	8	—	—	—
Macropipus marmoreus	—	—	—	—	—	—	—	—	—	1
Cancer pagurus	—	—	—	—	—	1	—	—	—	—
Trivia arctica	—	1	—	—	3	—	—	—	—	—
Balcis alba	—	4	—	3	3	1	1	5	—	—
Dentalium entalis	1	2	—	—	—	3	2	—	3	—
Nucula nucleus	—	—	4	1	—	1	1	—	—	1
Glycymeris glycymeris	1	3	1	—	—	—	2	—	1	—
Pecten maximus	—	—	—	—	—	—	—	—	—	1
Lima loscombi	—	—	—	—	—	—	—	—	—	1
Astarte triangularis	17	12	4	1	5	2	2	—	9	4
Diplodonta rotundata	—	—	—	—	—	—	—	1	—	—
Lucina borealis	—	—	—	1	—	—	—	—	—	—
Montacuta substriata	12	1	—	4	8	—	—	5	5	—
Laevicardium crassum	—	—	1	—	—	—	1	—	—	—
Parvicardium scabrum	—	2	—	—	—	—	1	1	—	—
Parvicardium minimum	—	1	—	2	—	—	—	1	—	—
Gafarium minimum	—	2	—	1	—	—	1	—	—	1
Dosinia exoleta	3	1	4	1	3	1	—	—	2	1
Dosinia lupinus	—	—	—	2	—	—	—	1	—	—
Venus casina	—	—	—	—	1	—	—	—	—	—
Venus ovata	—	2	—	—	—	—	4	—	1	1
Venus fasciata	6	1	—	5	7	8	7	1	5	9
Venerupis rhomboides	2	—	—	1	—	—	1	—	—	—
Venerupis pullastra	—	—	—	—	—	—	1	—	—	—
Venerupis aurea	—	—	—	—	1	—	—	—	—	—
Spisula elliptica	—	—	—	1	—	—	—	—	1	—
Lutraria lutraria	—	—	—	—	—	—	—	—	—	1
Lutraria angustior	—	—	—	—	—	1	—	—	—	—
Gari depressa	—	—	1	—	—	—	—	1	—	—
Gari fervensis	—	—	—	—	—	—	—	—	—	1
Gari tellinella	—	—	—	—	—	1	—	—	—	—
Tellina crassa	1	—	—	—	1	—	—	—	—	—
Tellina donacina	—	—	—	—	—	—	—	—	1	—
Ensis arcuatus	—	—	—	—	—	—	—	—	—	1
Antedon bifida	—	—	—	—	3	—	—	—	—	—
Ophiothrix fragilis	—	—	1	—	—	—	—	—	2	—
Ophiura albida	—	2	—	1	—	—	—	1	—	—
Ophiura texturata	1	—	—	1	—	—	1	2	—	—
Ophiopsila annulosa	—	—	1	—	—	—	—	—	—	—
Echinocyamus pusillus	4	—	—	3	3	4	—	—	—	1
Spatangus purpureus	1	—	—	1	2	—	—	1	1	—
Spatangus raschi	—	2	—	—	—	—	3	1	—	—
Molgula oculata	—	—	1	—	—	—	—	—	—	9
Branchiostoma lanceolatum	1	2	1	—	—	6	—	2	—	—

TABLE 4.

SUBSTRATE 5b

List of species occurrences at 10 stations

(Quantitative suction-sampling; sample size: 0.25 m²/~45 cm penetration).

Species	Station n°									
	1	2	3	4	5	6	7	8	9	10
Pseudocucumis mixta	18	20	9	16	5	10	14	10	16	5
Balcis alba	28	24	11	9	8	11	15	8	22	11
Branchiostoma lanceolatum	—	2	—	—	1	—	—	—	—	—
Glycera alba	—	—	—	2	—	2	—	—	—	—
Nereis sp.	2	1	—	1	—	—	—	1	—	—
Echinocyamus pusillus	—	2	—	—	—	1	—	—	1	—
Luidia ciliaris	—	—	1	—	—	—	—	—	—	1

The occurrence of high density populations of the boreal sea-cucumber *Pseudocucumis (= Neopentadactyla) mixta* commanded the author's special attention. This included a continuous monitoring, by closed-circuit T.V., of the holothurian's diurnal activity. The results of this study are described by Konnecker and Keegan, 1973.

SUBSTRATE 6.

Composite of maerl and muddy sand.

Location.

Area 6; Map 6.

Biotope description.

Where investigated, this ground was seen to comprise a patchwork of deposit substrates and large-scale rocky outcrops. Causing major interruptions in current flow, the outcrops give rise to a range of sheltered sub-systems which variously facilitate the deposition of silt, etc.

Macrofauna.

Appendix 1 lists those animals which have positive association with the coarse fraction of the sediment. The following polychaetes are taken to manifest the sand/mud fraction.

Nereis irrorata
Perinereis cultrifera
Nephthys hombergii
Lumbriconereis latreilli
Pectinaria auricoma
Melinna palmata
Polynoe scolopendrina
Amphitrite edwardsi
Myxicola infundibulum
Terrebellides stroemi

DISCUSSION AND CONCLUSIONS.

A heterogeneous group of animals is consistently if variously associated with the infralittoral maerl of the eastern North-Atlantic. As qualified by Cabioch (1968): « Bien que les groupements faunistiques ou floristiques composants peuplent, chacun de son côté, d'autres milieux, l'association qu'ils constituent sur les bancs de maërl est, dans le détail, particulière à ces fonds et présente une certaine permanence ».

Whilst the findings of this investigation conform to the general pattern, some features of the macrofauna are without recorded precedent. Two of these are discussed in context of the associated substrate types:

Substrate I.

The phenomenon of aggregation among echinoids, and indeed among echinoderms generally, is well documented. Reese (1966), in reviewing echinoderm behaviour patterns, lists population densities for a number of species. The degree to which *Paraeentrotus lividus* is aggregated in the Muckinish inlet far exceeds that reported for other areas:

Density	Sampling area	Investigators
$120/m^2$	Malta	Gamble (1967)
$80/m^2$	Bay of Marseilles	Kempf (1962)
$40/m^2$	Lough Ine	Hitching & Ebling (1961)

The urchin's seeming predilection for living maerl and its extreme gregariousness within this substrate at Muckinish are attributed to a number of factors:

(a) As indicated by their distribution patterns, free-living corallines appear to thrive in areas of continuous water flow. This type of milieu must also favour the maintenance of high-density populations of P. *lividus.* Apart from the matter of oxygen renewal, current-flow about the aggregated animals would curtail their self-fouling capacity whilst, at the same time, ensuring a continuous supply of food. It is postulated that when crowding severely restricts their mobility and browsing activity, the echinoids may be primarily sustained by absorbing free amino-acids from the surrounding sea-water (see Ferguson, 1967).

(b) *Paracentrotus,* when occurring in the intertidal or in shallow water, tends either to live in the shade or else to cover its upper surface with shells, pieces of algae, gravel, and other debris. A "sub-surface" settlement by the larvae or active burrowing within the arbuscular maerl would serve the same end.

(c) The topography of the Muckinish inlet is such that a substantial renewal of the water-body may take place only during equinoxial spring-tides. *Paracentrotus* larvae, even with a long planktonic phase, could be confined to the area right up to their critical settlement time. (Pearson, 1970, discusses the containment of larvae within a fjordic system and its effect on recruitment to the adult benthic populations).

Substrate 2.

Fell (1966), writing on crinoid ecology, states that: "... in marked contrast to the case with ophiuroids, crinoids seldom feature as dominant or sub-dominant members of benthic communities ...". As an exception, he cites the example of the "curious and systematically isolated comatulid genus *Ptilometra",* which "at certain localities forms almost pure associations of numerous individuals". Far from being anomalous, high-density populations of *Antedon bifida* are very common throughout the area of the investigation. This is the only instance, however, where the crinoids were seen to have colonised a deposit substrate.

Dense aggregations of *Ophiocomina nigra* are equally common to West coast waters.

Mixed populations of *Antedon* and *Ophiocomina* had been noted many times but were not accorded special significance until direct surveying revealed the "clumped" distribution pattern. A subsequent study of their feeding behaviour suggested that the localised association of these species may reflect a form of commensalism ! 0. *nigra,* with its flexibility of feeding habits (see Fontaine, 1965), was seen to exploit the rain of nekton which is precipitated by the "baffle-effect" of the crinoids' arms.

Thanks are due to Prof. P. O'Ceidigh who supervised this work and to my colleague and diving companion Gerd Könnecker. The writer profited from discussions with R. Keary and Dr. L. Cabioch. Dr. J. Cabioch and P. Cooke identified the coralline algae.

Besondere Aufmerksamkeit wurde dem anormalen Auftreten von ausserst dichten Populationen des Seeigels *Paracentrotus lividus* und gemischten Aggregationen von *Antedon bifida* und *Ophiocomina nigra* geschenkt.

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APPENDIX 1.

A catalogue of macrobenthic animals associated with maerl or dominantly maerl substrates in Galway and Kilkerrin Bays.

Species	Substrate						
	1	2	3	4	5a	5b	6
Stylostichon plumosum		X		X			X
Haliclona rosea		X		X			X
Mycale rotalis		X		X			X
Amphilectus fucorum				X			
Polymastia mamillaris				X			
Hymedesmia brondstedi				X			
Adocia cinerea				X			
Anemonia sulcata		X	X	X	X		X
Peachia hastata			X	X			X
Cerianthus lloydi				X			X
Epizoanthus sp.				X			X
Metridium senile				X			X
Adamsia palliata		X	X	X	X		X
Sagartia sp.				X			X
Alcyonium digitatum				X			X
Caryophyllia smithi				X			X
Golfingia elongata			X				
Golfingia vulgaris		X	X				
Sipunculus nudus				X			X
Phascolion strombi		X	X	X			
Polygordius lacteus				X	X		X
Aphrodite aculeata			X				
Gattyana cirrosa			X				
Harmothoe sp.			X		X		X
Halosydna gelatinosa			X				
Sthenelais boa			X				X
Nephthys cirrosa	X		X	X	X		X
Glycera alba	X			X	X		X
Glycera maculata			X				
Goniada maculata			X				
Marphysa sanguinea			X				
Nematonereis unicornis			X				
Arabella iricolor			X				X
Aricia cuvieri			X				X
Laonice cirrata			X				
Chaetopterus variopedatus	X		X		X	X	X
Scalibregma inflatum			X				X
Notomastus latericeus	X		X	X	X		X
Lanice conchilega			X		X		X
Pista cristata	X		X		X		X
Myxicola infundibulum							X
Sabella pavonina			X				X
Euchone rubrocincta							X
Serpulidae (unidentified)	X	X	X	X	X	X	X
Branchiomma vesiculosum					X		
Amphipoda spp.	X	X	X	X	X	X	X
Conilera cylindracea		X		X	X	X	X
Pandalina brevirostris			X				
Hippolyte varians			X				X
Galathea intermedia	X	X	X	X			
Galathea squamifera	X	X	X	X			
Galathea strigosa		X	X	X	X		X
Porcellana longicornis	X	X	X				
Upogebia deltaura			X				
Upogebia stellata			X				
Paguridae (unidentified)		X	X	X	X	X	X
Ebalia tuberosa	X	X		X	X		X
Cancer pagurus		X	X	X	X	X	X
Macropipus marmoreus	X	X		X	X	X	X

APPENDIX 1. Contd.

Species	Substrate						
	1	2	3	4	5a	5b	6
Portunus corrugatus		X	X	X	X		X
Portunus arcuatus		X	X	X	X		X
Portunus depurator		X	X	X	X		X
Portunus puber	X	X	X	X	X	X	
Xantho incisus		X		X	X		X
Xantho pilipes		X	X	X	X	X	X
Pilumnus hirtellus		X	X		X		
Maia squinado			X	X	X		X
Inachus sp.		X		X	X		
Macropodia rostrata	X	X	X	X	X	X	X
Prosobranchia (unidentified)		X	X				X
Gibbula magus		X	X				
Gibbula cineraria		X	X				
Gibbula umbilicalis		X	X				
Bittium reticulatum		X	X				
Calliostoma zizyphinum		X	X	X			
Buccinum undatum			X				
Aporrhais pes-pelecani					X	X	X
Balcis alba		X		X	X	X	X
Aplysia punctata		X					
Philine aperta							X
Dentalium entalis							
Nucula nucleus			X				
Nucula sulcata			X				
Nucula turgida			X				
Arca tetragona			X	X	X		
Glycymeris glycymeris		X			X		
Modiolus modiolus			X				
Anomiidae	X	X	X	X	X	X	X
Chlamys varia	X	X	X	X	X		X
Chlamys opercularis	X	X	X	X	X		X
Chlamys distorta			X				
Pecten maximus		X	X	X	X	X	X
Lima hians				X	X	X	
Lima loscombi		X	X	X	X		X
Thyasira flexuosa			X				
Astarte triangularis					X		
Diplodonta rotundata							
Lucinoma borealis			X		X		
Myrtea spinifera			X				
Montacuta substriata					X		
Laevicardium crassum		X	X		X		
Parvicardium ovale			X				X
Parvicardium exiguum			X				X
Gafarium minimum	X			X	X		
Dosinia exoleta	X		X	X	X	X	X
Dosinia lupinus			X		X		X
Venus fasciata	X	X	X	X	X	X	X
Venus verrucosa	X		X				
Venus ovata			X	X	X		
Venus casina			X	X	X		
Venerupis pullastra			X		X		
Venerupis rhomboides	X		X	X	X		X
Venerupis aurea			X	X	X		
Irus irus			X	X			X
Spisula elliptica				X	X		
Lutraria lutraria			X		X		
Lutraria angustior					X		
Gari depressa	X			X			X
Gari fervensis	X	X		X			X
Gari tellinella	X		X	X	X		X
Tellina crassa	X		X	X			
Tellina squalida					X		
Tellina donacina				X	X		
Ensis arcuatus					X		X
Lepton squamosum			X				

APPENDIX 1. Contd.

Species	Substrate						
	1	2	3	4	5a	5b	6
Corbula gibba			X	X			X
Sphenia binghami			X				
Lyonsia norvegica			X				X
Antedon bifida		X	X	X	X		X
Ophiothrix fragilis	X	X	X	X	X		X
Ophiura albida				X	X		X
Ophiura texturata				X	X		X
Ophiopsila annulosa					X		
Ophiocomina nigra	X	X	X	X			
Amphipholis squamata	X						
Echinocyamus pusillus		X		X	X	X	X
Spatangus purpureus					X		
Spatangus raschi					X		
Paracentrotus lividus	X						
Echinus esculentus							
Asterias rubens	X	X	X	X	X	X	X
Marthasterias glacialis			X	X	X	X	X
Luidia sarsi				X	X		
Luidia ciliaris			X		X		
Astropecten irregularis			X	X	X		X
Henricia sanguinolenta			X	X	X		X
Pseudocucumis mixta				X	X		X
Cucumaria normani				X			X
Cucumaria saxicola	X	X					
Leptosynapta inhaerens			X		X	X	X
Molgula oculata					X		
Branchiostoma lanceolatum				X	X	X	X