JOINT NATURE CONSERVATION COMMITTEE

Marine Nature Conservation Review

Benthic marine ecosystems of Great Britain and the north-east Atlantic

edited by

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Preface

The first volume of the Marine Nature Conservation Review (MNCR) series (Hiscock 1996) described the rationale to the Review including a historical account of marine conservation in Britain, and the methods used for survey, data storage, data analysis, assessment of marine natural heritage importance and for the dissemination of information. The volume included a glossary of terms.

The first part of the current volume provides a brief review of marine benthic information available for the north-east Atlantic including offshore areas of Great Britain. Chapters of Part 2 describe our knowledge of seabed habitats and communities for inshore (generally within 3 nautical miles, about 5.6 km, of the coast) areas of Great Britain within each of the MNCR coastal sectors.

The review of current knowledge was an early exercise in the MNCR programme and a series of limited circulation reports were published in 1991 and reviewed and updated for this volume. Some of the information reviewed for this volume by the MNCR team has therefore already been incorporated into other undertakings by the Nature Conservancy Council and its successor agencies, including an environmental review undertaken for the Irish Sea Study Group (Holt *et al.* 1990), the Estuaries Review (Davidson *et al.* 1991), the *Directory of the North Sea Coastal Margin* (Doody, Johnston & Smith 1993), and is currently being used for JNCC's *Coastal Directory* series (for instance, Barne *et al.* 1996).

The results of MNCR surveys are referred to briefly in this volume and are being published in a regional report series related to areas within each of the MNCR coastal sectors or to major physiographic habitat types (such as sealochs or lagoons).

The reader wishing to know where surveys have been undertaken which describe the marine biology of particular locations should use the volume of UKDMAP (United Kingdom Digital Marine Atlas Project – electronic information display software) (Barne *et al.* 1994).

Much new work is now being undertaken in Special Areas of Conservation being established under the European Union's Habitats Directive (*Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora*) and this is not reported here.

The species names used in this volume are those from Howson & Picton (1997).

Keith Hiscock
March 1998

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Contents

Part 2 Reviews within MNCR Coastal Sectors 71

Part 1

Introduction and Atlantic-European perspective

Introduction and Atlantic-European perspective*

Keith Hiscock

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Synopsis

This chapter introduces the Marine Nature Conservation Review (MNCR) series describing benthic marine ecosystems in Great Britain. It includes information on seabed habitats and communities for the coastal seas of other countries bordering the north-east Atlantic (North Cape to the Straits of Gibraltar, excluding detailed description of the Baltic) to indicate sources of data to assist with the classification of marine habitats and communities in Great Britain. Our knowledge of seabed habitats and communities for offshore areas of Great Britain is described in this chapter. Aspects of the marine ecosystem not specifically addressed by the MNCR (pelagic habitats, fish, cetaceans, birds, seals and otters) are mentioned to indicate key sources of information.

Studies of the marine natural history of Great Britain can be traced back to the 17th century with the foundations to current knowledge of seabed communities being laid from about the middle of the 19th century. Observations on the shore, the use of dredging, the development of the grab and the much later use of diving have all contributed to our knowledge and understanding of benthic ecology. Studies of marine species and marine ecology to underpin nature conservation have been undertaken since the mid-1970s.

The physical and chemical characteristics of the seas around Great Britain are described. The great range of conditions which exist around these shores create a very wide range of habitats for marine life. This great variety of habitats overlays significant differences in the biogeographical character of the species distributions. Although many biogeographical changes occur gradually over considerable distances rather than abruptly, Great Britain is notable as the centre of the boreal region but including boreal-arctic and boreal-lusitanean characteristics. This leads to the presence of a geographically varied flora and fauna in which a substantial number of species are found only on the south and west coasts while a lesser number are only found on northern and east coasts.

1 Introduction

This chapter describes the characteristic features of the marine environment in which the MNCR is being undertaken, the development of our knowledge of marine ecosystems over the past 150 and more years and our knowledge of the marine ecosystems in other countries in the north-east Atlantic. These reviews are undertaken to place our current work into environmental, historical and geographical contexts and to assist with the assessment of the international importance of the areas surveyed by the MNCR in Great Britain. Later chapters review relevant work done prior to or in addition to that of the MNCR team in Great Britain and note some main results of MNCR surveys. MNCR studies are being published as a series of regional reports for those coastal sectors which have been surveyed.

Many strands of scientific study have to be woven together to provide a reasonably full description and to get as close as possible to understanding marine ecosystems. Major non-biological components of the ecosystem include substratum type (including geology and characteristics of sediments), strength of wave action, strength of tidal currents, current flow, water temperature at the seabed, water chemistry (especially salinity), and geology. On the biological side, plankton, pelagic fish, seabirds, cetaceans and benthic assemblages all interact with the benthos. For the non-biological

* This review was initially undertaken from published sources of information as well as interviews with relevant workers up to 1991 and published in Hiscock (1991). It has been further revised to take account of major additional studies published up to the end of 1996.

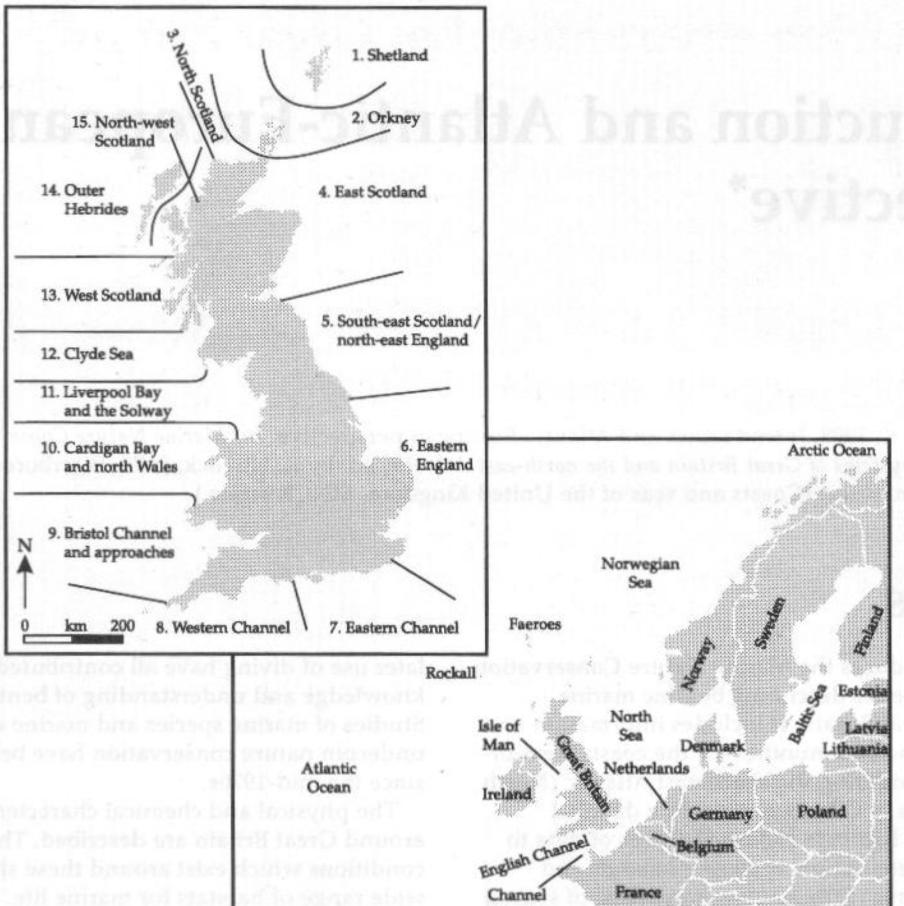


Figure 1. Area included in the north-east Atlantic review and (top left) MNCR coastal sectors.

features, this introductory volume aims to indicate physical and chemical characteristics of the seas around Great Britain, rather than describing their influence on marine ecology. For the biological features, we have concentrated on benthic marine ecosystems in this volume. Whilst drawing attention in this volume especially to the habitats and communities classified in key papers, the concepts of community classification and the development of a classification of habitats and communities (biotopes) for Great Britain are the subject of separate publications (Hiscock & Connor 1991, Connor *et al*. 1996) and the seabed biotopes classification being developed for the British Isles by the MNCR will be published separately.

The Marine Nature Conservation Review of Great Britain is being undertaken in one of the best studied areas of the world and we can therefore use a considerable volume of already documented information on the distribution of marine species and the composition of marine communities. Collating and reviewing that information was a major task during the first two years of the MNCR and information has been continually extended and updated since. In undertaking the review of available literature, we have concentrated on gathering information for Great Britain but have also used publications for the Atlantic, Baltic and Mediterranean coasts of Europe (Figure 1) and, to a much lesser extent, temperate ecosystems in other parts of the world. The literature information we now use is catalogued and abstracted in the MNCR computer database (MacDonald & Mills 1996) and maintained in full as hard copies of reports, papers and books. Information sources for descriptions of benthic marine communities have been published electronically as a volume of the UKDMAP (Barne *et al*. 1994).

Access to all of the material held by the MNCR must be through interrogation of the database and only the major, key or most recent in a series of references to studies of marine biology are described here and given in the bibliographies. Works describing methods and those essentially about the definition of communities are reviewed in other reports. The MNCR database included, at the end of 1996, over 13,000 separate references to published papers and reports.

2 The marine environment of Great Britain

2.1 Introduction
The physical and chemical features of the marine environment are illustrated in the *Atlas of the seas around the British Isles* published by the Ministry of Agriculture Fisheries and Food (Lee & Ramster 1981). Some of the most important features are further illustrated here and are available in electronic form in the UK Digital Marine Atlas Project (UKDMAP), which includes a much wider range of information (British Oceanographic Data Centre 1992).

2.2 Currents
The nature of oceanic currents is determined by the combined effects of prevailing wind, the Earth's rotation and density differences between areas of water of different temperatures or salinity. In the north-east Atlantic, residual current flow is dominated by the north-east Atlantic drift (the Gulf Stream) which starts its journey in the warm waters of the Gulf of Mexico. The direction of currents (Figure 2) has a major effect in distributing water masses of different physical (for instance, temperature) and chemical (for instance, salinity, nutrients) character. Also, the enclosed nature of the Irish Sea and North Sea means that water bodies are retained and are therefore subject to greater physical and chemical fluctuations than those on the open coast.

2.3 Wind and waves
Wind creates waves and the strength and type of wave action is of major importance in determining the inshore benthic communities which occur at a particular location. Although the diagram (Figure 3) illustrating direction, strength and frequency of wind around the coast during January (the month when strongest winds generally occur) gives some indication of the likely exposure of coasts to wave action, other factors are very important, particularly the distance of sea over which the wind blows (the fetch) and the depth of water near to the coast. Swell waves propagated by distant storms are important in maintaining exposed conditions even when local wind is slight. The strength of wave action is attenuated with depth and therefore the deeper the water, the less the seabed is exposed to wave-induced oscillatory water movement. Swell waves have a long distance between crests and are therefore effective to much greater depths than wind-driven waves of similar height. Ballantine (1961) described the effects of wave exposure on rocky shore communities in Pembrokeshire and his work stands today as the most widely used basis for development of biologically defined exposure scales. The physical features of wave action and effects on sublittoral communities around Great Britain are described in Hiscock (1983, 1985) (for example, Figure 4).

2.4 Tides
Tidal rise and fall is of particular importance in determining the vertical distribution of littoral species and the extent of the littoral zone. Around the coast of Britain, 'amphidromic points', where tidal rise and fall is minimal, occur adjacent to the coast near Portland and between Islay and the Mull of Kintyre. Another is centred in the southern North Sea between East Anglia and the Netherlands. Away from these points, tidal range is generally between about 2 m and 5 m at spring tides depending on location. However, distant from the amphidromic points and especially where the tide is funnelled along an inlet, this range will be greater. In the Severn Estuary, tidal range exceeds 11 m, and in estuaries of the east basin of the Irish Sea, 8 m. Air pressure and wind direction also affect the heights on the shore to which tides rise and fall so that predicted heights may be substantially increased or decreased. In areas of very low tidal range, for instance near the amphidromic point in south-west Scotland, air pressure and wind direction and strength may be more important than predicted tidal rise and fall in determining height of sea level on some days.

2.5 Tidal streams
The strength of tidal currents is very important to marine life both directly and indirectly and leads to the development of different communities depending on their strength. Some of those effects are indicated in Figure 4 and are described in Hiscock (1983, 1985). Tidal stream strength, together with the strength of wave action at the seabed and the supply of sediment determines the composition of sediments and therefore indirectly the infaunal communities. The broad geographic trends in maximum strength of tidal streams are illustrated in Lee & Ramster (1981) although it is often the effect of local topographical features which is most important near to the coast. Around Great Britain, tidal stream regimes vary greatly from some of the strongest in the world to areas which are almost still. The strongest tidal streams occur in the narrows between two land masses or off prominent headlands (for example: the Pentland Firth; Portland Bill; Jack Sound and Ramsey Sound in west Wales; Bardsey Sound and the Menai Strait in north Wales; the Mull of Galloway and the Gulf of Corryvreckan in western Scotland). Here tides reach a surface velocity in excess of 5 knots (2.5 m s^{-1}) and, at their strongest in the Pentland Firth and Gulf of Corryvreckan, exceed 10 knots (over 5 m s^{-1}). Tidal streams are also extremely strong where funnelling occurs, for instance in the Severn Estuary and in the Solway Firth. By contrast, embayed areas and the deep parts of sealochs and voes often have negligible flows.

2.6 Temperature
The British Isles lie between latitudes 50°N and 61°N. Seawater temperature range in this area is illustrated in Figures 5 and 6. The western seaboard is greatly affected by the warm water of the North-East Atlantic Drift. However, the enclosed nature of both the Irish Sea and North Sea means that winter temperatures are much colder than on the open oceanic coast although local warming can occur in summer. Temperatures at the seabed are more relevant to the study of benthic communities than are those at the surface although most

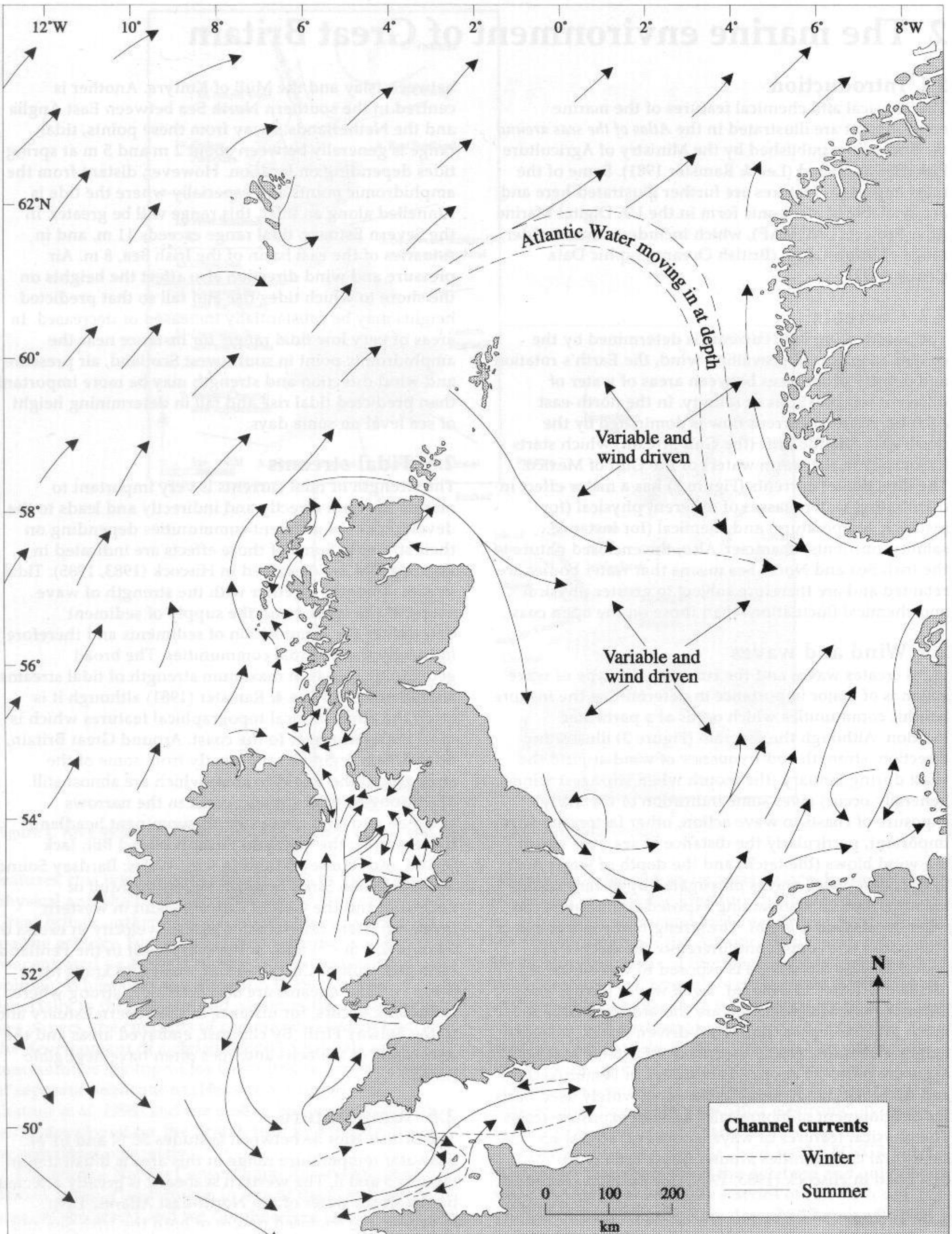


Figure 2. The direction of near-surface residual currents around the British Isles. (Re-drawn from Lee & Ramster 1981. *Atlas of the seas around the British Isles*. Ministry of Agriculture, Fisheries & Food, Lowestoft. © Crown Copyright.)

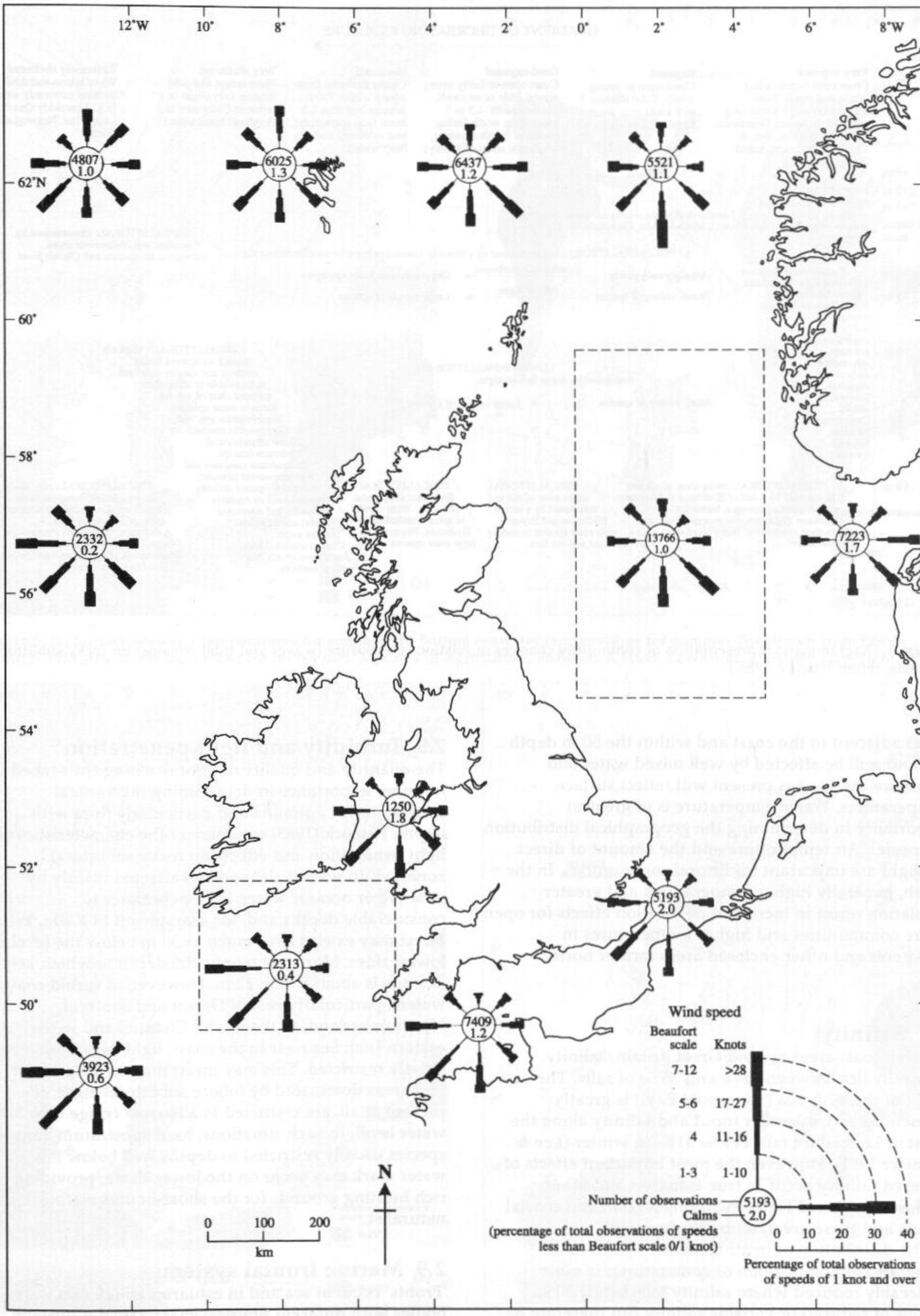


Figure 3. The direction, strength and frequency of wind at locations around Great Britain for the month of January. (Re-drawn from Lee & Ramster 1981 *Atlas of the seas around the British Isles*. Ministry of Agriculture, Fisheries & Food, Lowestoft. © Crown Copyright.)

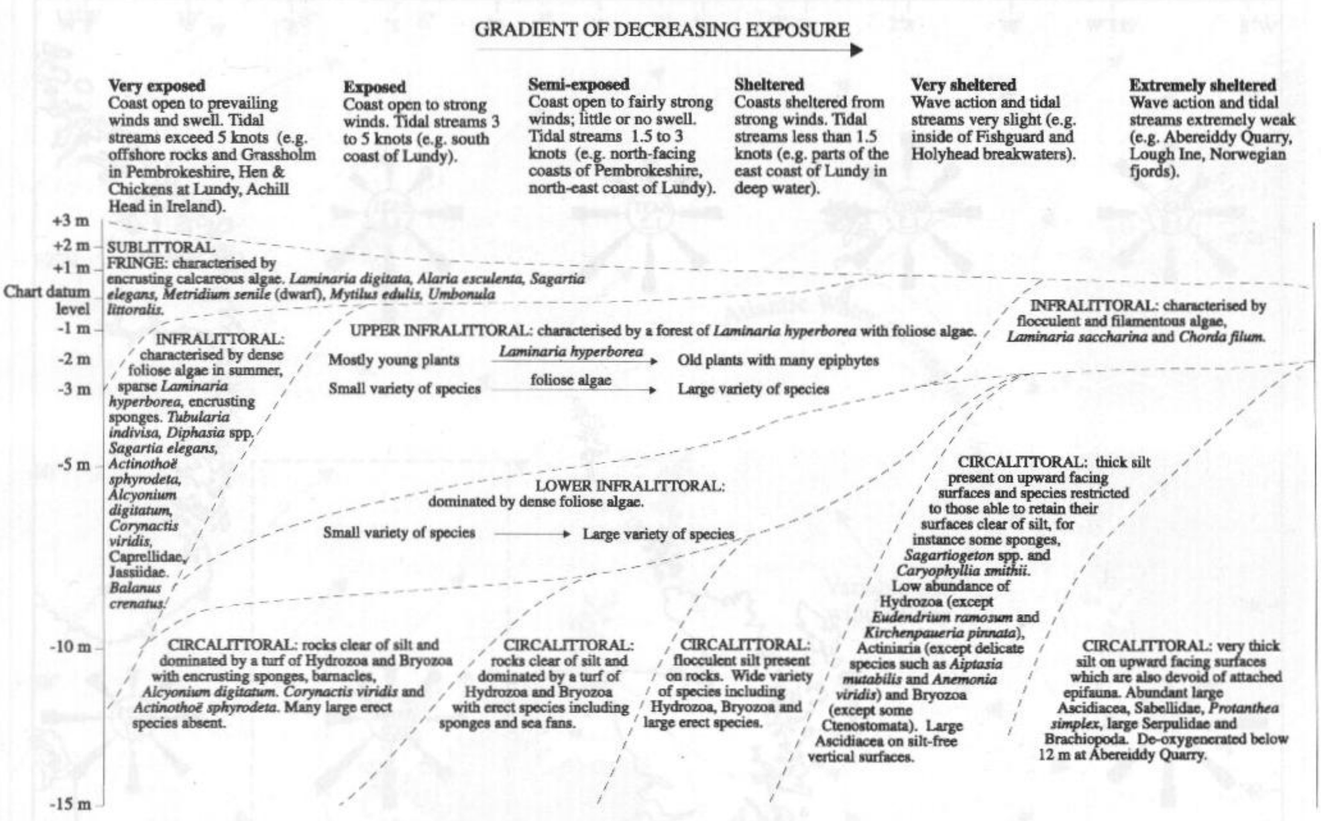


Figure 4. Diagrammatic representation of community changes in relation to exposure (waves and tidal streams) on rocky sublittoral habitats. (From Hiscock 1983.)

areas adjacent to the coast and within the 50 m depth contour will be affected by well mixed water and therefore the species present will reflect surface temperatures. Water temperature is of greatest importance in determining the geographical distribution of species. Air temperature and the amount of direct sunlight are important for littoral communities. In the south, generally higher temperatures and greater insolation result in increased desiccation effects for open shore communities and higher temperatures in rockpools and other enclosed areas farther north.

2.7 Salinity

In open coast areas around Great Britain, salinity generally lies between 33‰ and 35‰ of salts. The east basin of the Irish Sea ('Liverpool Bay') is greatly influenced by freshwater input and salinity along the coast of Lancashire falls below 31‰ in winter (Lee & Ramster 1981). However, the most important effects of lowered salinity occur in true estuaries and other enclosed bodies of water including lagoon and coastal ponds and these are described separately.

The distribution of benthic marine species and therefore the composition of communities is most noticeably reduced where salinity falls below 30‰. Effects of reduced or variable salinity can therefore be detected mainly in enclosed water bodies rather than in general around the coast of Britain.

2.8 Turbidity and light penetration

The quantity and quality of light reaching the seabed is of prime importance in determining the vertical distribution of epifauna and particularly flora with depth. Hiscock (1985) summarises the characteristics of light penetration and effects on rocky sublittoral zonation. In well lit clear waters affected mainly by offshore or oceanic water, light penetrates to considerable depths and, for example off St Kilda, kelp forest may extend to as much as 30 m below the level of lowest tides. More commonly, the depth to which kelp extends is about 8 m to 12 m. However, in turbid coastal waters, particularly east of Dorset and south of Northumberland, in the Bristol Channel and in the eastern Irish Sea near to the coast, light penetration is greatly restricted. This may mean that the kelp forest and areas dominated by foliose sublittoral algae, if present at all, are restricted to a narrow fringe near low water level. In such situations, hard substratum animal species usually restricted to depths well below low water mark may occur on the lower shore, providing rich hunting grounds for the shore-bound marine naturalist.

2.9 Marine frontal systems

'Fronts' occur at sea and in estuaries where two water bodies with different physical characteristics (usually temperature and salinity) converge, meet and sink. There is thus a very sharp change in water properties

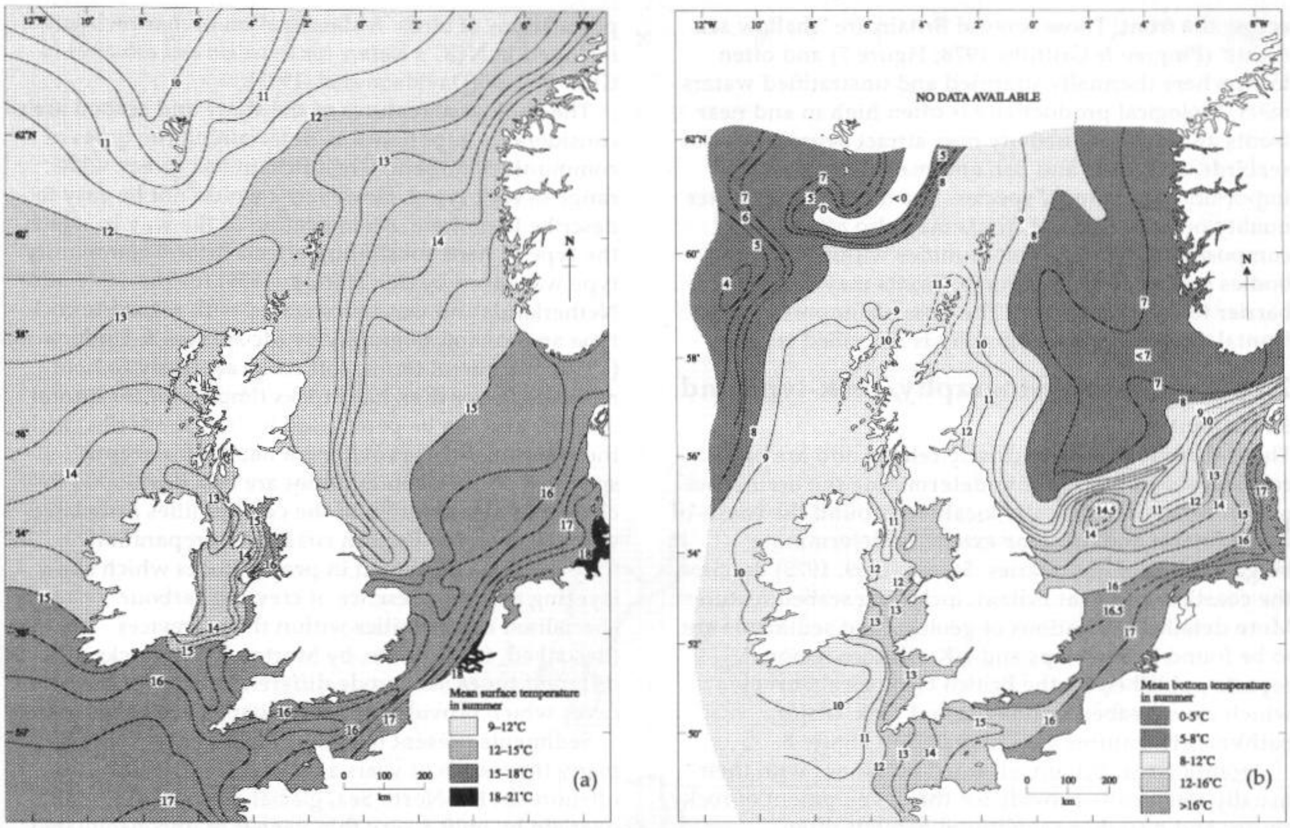


Figure 5. (a) Surface seawater temperatures for summer. (b) Bottom seawater temperatures for summer. (Re-drawn from Lee & Ramster 1981 *Atlas of the seas around the British Isles*. Ministry of Agriculture, Fisheries & Food, Lowestoft. © Crown Copyright.)

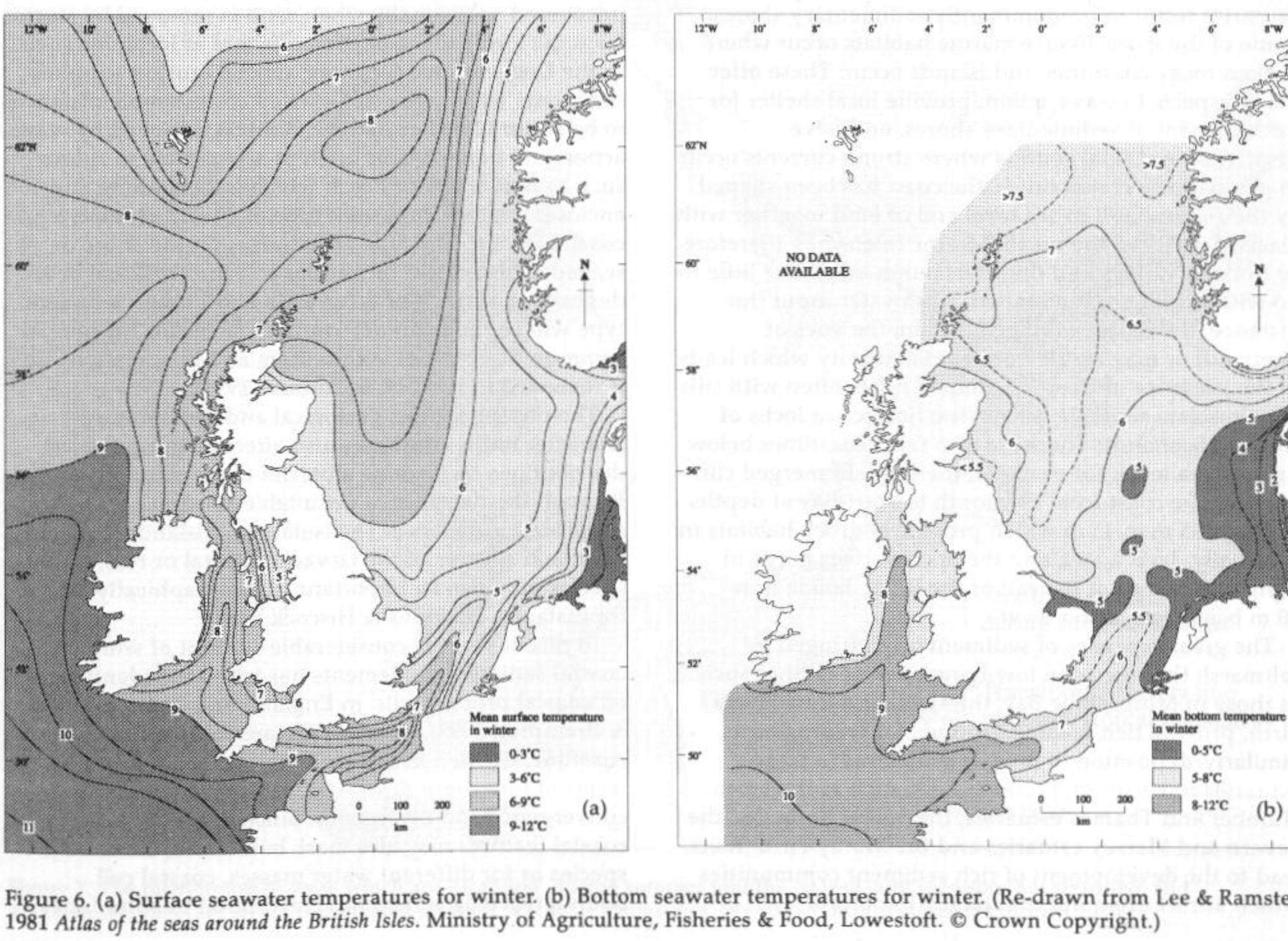


Figure 6. (a) Surface seawater temperatures for winter. (b) Bottom seawater temperatures for winter. (Re-drawn from Lee & Ramster 1981 *Atlas of the seas around the British Isles*. Ministry of Agriculture, Fisheries & Food, Lowestoft. © Crown Copyright.)

across the front. Those around Britain are 'shallow sea fronts' (Pingree & Griffiths 1978; Figure 7) and often form where thermally stratified and unstratified waters meet. Biological productivity is often high in and near fronts and this productivity may attract aggregations of seabirds, cetaceans and fish and may also have some importance for benthic species. The difference in water quality on either side of fronts may also affect composition of marine communities within the water bodies separated by the fronts. Fronts may also act as a barrier to larval dispersal. The possible importance of frontal systems to biogeography is described later.

2.10 Coastal physiography, rock-type and sediments

These three features are closely related and are of considerable importance in determining the occurrence of marine life at particular locations around the coasts of Great Britain and, to some extent, in determining biogeographical boundaries. Steers (1969, 1973) describes the coastline of Great Britain, including seabed features . More detailed indications of geology and sediments are to be found in the maps and UK offshore regional reports published by the British Geological Survey, which cover seabed sediments and rock. Major bathymetric features are illustrated in Figure 8.

Around Great Britain, elevated coastlines with their usually steep cliffs provide for the development of rocky shores and nearshore sublittoral habitats often extending into deep water, while the low-lying coasts of much of eastern England and around many of our estuaries result in predominantly sedimentary shores. Some of the most diverse marine habitats occur where broken rocky coastlines and islands occur. These offer many aspects to wave action, provide local shelter for development of sedimentary shores, and have headlands and tidal sounds where strong currents occur. In geologically recent times, the coast has been shaped by the rise and fall in sea level and of land together with glacial activity in the north. Marine inlets may therefore be flooded valleys and their formation may have little to do with present, often limited, freshwater input (for instance, the rias of southern Britain, the voes of Shetland) or may result from glacial activity which leads to the presence of deep 'U'-shaped inlets often with sills which isolate separate basins (the fjordic sea lochs of western Scotland). There are also relict coastlines below present sea level; for example, the now submerged cliff lines off the coast from Plymouth to Start Bay at depths of about 35 m to 45 m which provide bedrock habitats in unusually deep water, and the ancient river gorge in Plymouth Sound at the exit of the River Tamar, now 20 m below low water level.

The great expanses of sediment often fringed by saltmarsh that occur on low-lying open coastlines such as those of Morecambe Bay, the Wash and the Solway Firth, provide rich feeding grounds for wading birds. Similarly, deposition of muddy sediments in large estuaries or enclosed marine basins, such as the Forth, Humber and Thames estuaries, the Solent harbours, the Severn and Mersey estuaries and the Moray Firth inlets, lead to the development of rich sediment communities which attract often internationally important populations of birds. A classification of marine inlets is included in NCC's *Nature conservation and estuaries in Great Britain* (Davidson *et al.* 1991).

The geological features of the shore and seabed are of considerable importance in determining the types of communities present. Great Britain has a very wide range of rock types. However, it would not be easy to describe them here. An indication of the way in which the type of hard substratum affects littoral community type was given by den Hartog (1959) for the Netherlands and was investigated with regard to rock type and microtopography by McGuiness & Underwood (1986). In general terms, soft rocks are likely to hold moisture better than hard rocks (important for littoral species) and can be penetrated by boring species, with the resulting holes providing a habitat for cryptic species. Soft rock communities are best developed in chalk and a description of the communities associated with chalk on the English coast is in preparation (George, Tittley & Wood in prep.). Rocks which show layering and the presence of crevices harbour specialised communities within those crevices (described, for instance, by Morton 1954). Rocks of different types may erode differentially to form marine caves which provide special habitats for marine species.

Sediments present today may have been deposited many thousands of years ago, particularly those offshore. In the North Sea, glacial deposits are often overlain by only a very thin veneer of unconsolidated sediment laid down in the past 10,000 years. The remains of ancient forests and peat deposits are uncovered occasionally when sand is removed by storms from the lower shore or even offshore at locations such as the Dogger Bank. Onshore, coastal erosion supplies sediments which are often carried considerable distances to be accumulated elsewhere. Shingle is moved by wave action and tidal streams often to accumulate in ridges such as that at Chesil Beach which is 29 km long and encloses another important type of coastal feature, a coastal lagoon. The type of sediment on the shore or seabed is dependent on supply and the erosional or depositional effects of wave action and tides. Sediment type will be the main determining factor for the animal communities present within them and this relationship is reviewed in Hiscock & Connor (1991).

The physiographic, geological and sedimentary character of the coast may also affect biogeographical distributions by creating a barrier to distribution through the presence of unsuitable substrata for a considerable distance. The isolation of islands from mainland sources of the larvae of littoral or rocky coast species may also be important biogeographically (see, for instance, Hawkins & Hiscock 1983).

In recent years, a considerable amount of work on coastal sediment movements has led to the identification of 'coastal process cells' in England and Wales (Motyka & Brampton 1993). Coastal cells are compartments of coastline, divided from neighbouring sections of coast in terms of longshore drift, current flow, and wave convergence and divergence. Since headlands and other coastal features may also mark boundaries for marine species or for different water masses, coastal cell boundaries may sometimes correspond to boundaries

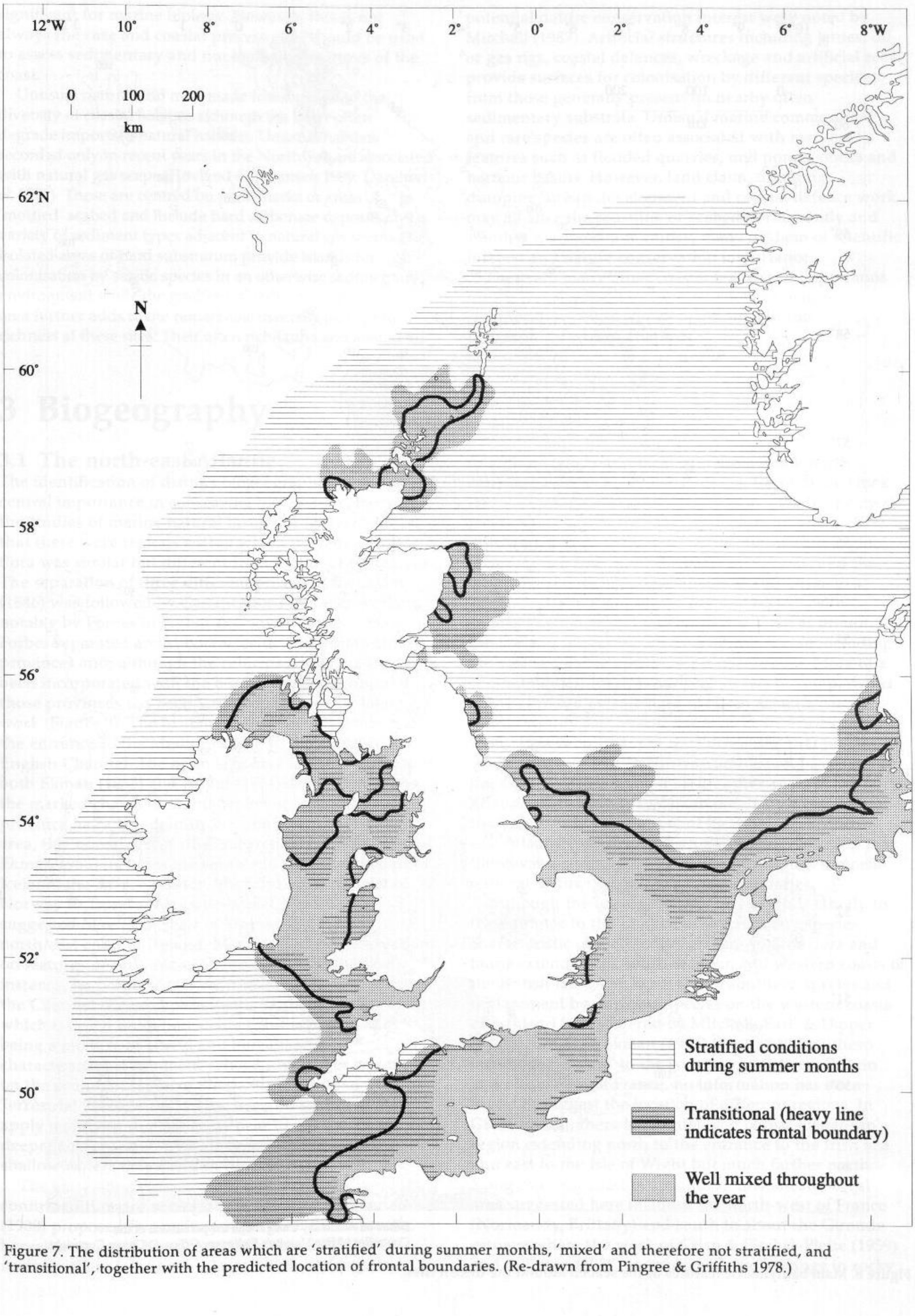


Figure 7. The distribution of areas which are 'stratified' during summer months, 'mixed' and therefore not stratified, and 'transitional', together with the predicted location of frontal boundaries. (Re-drawn from Pingree & Griffiths 1978.)

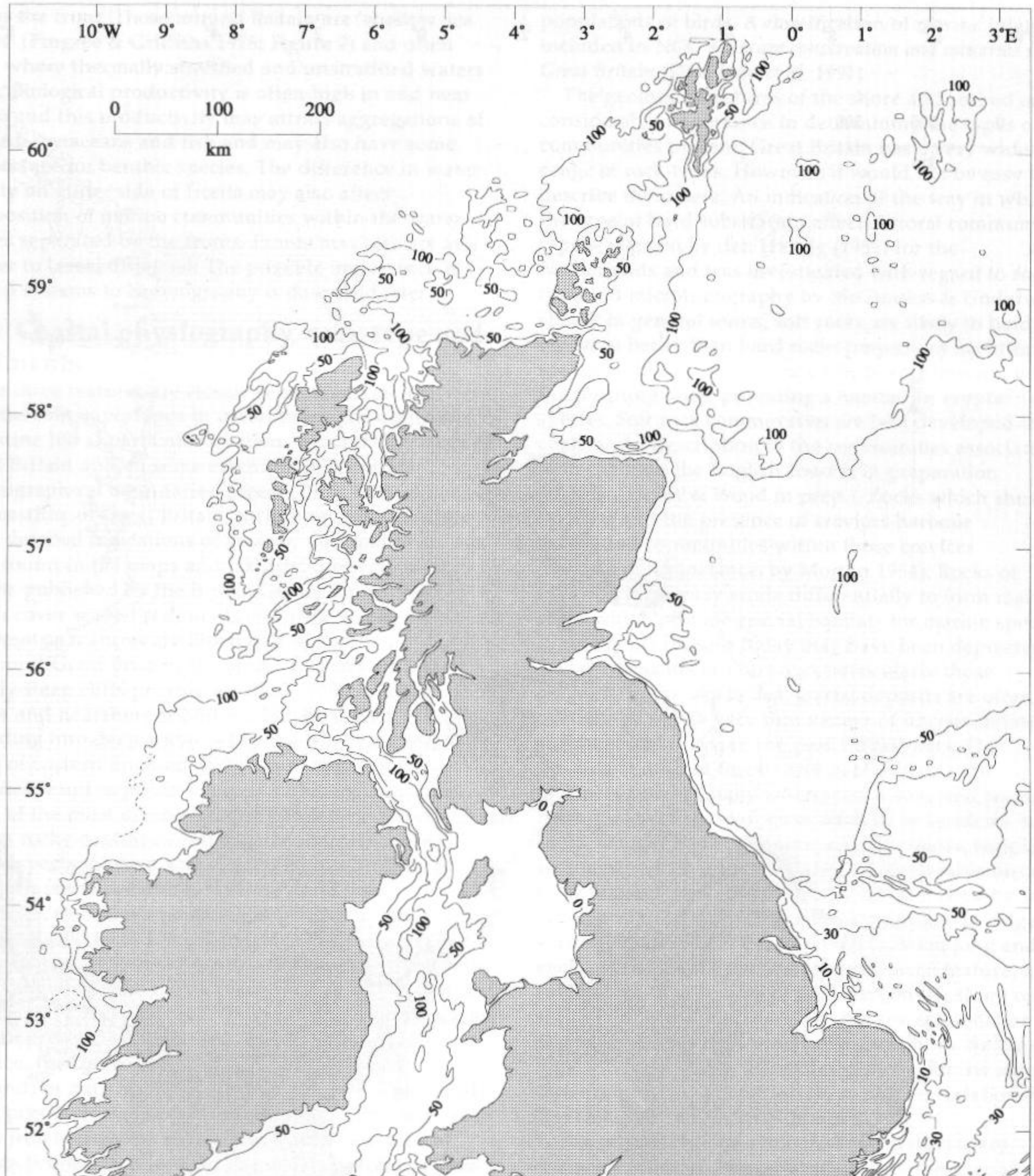


Figure 8. Main bathymetric features of the seabed around the British Isles.

significant for marine biology. However, this is not always the case and coastal process cells should be used to assess sedimentary and not biological features of the coast.

Unusual natural and man-made features add to the diversity of coastal habitats although the latter often degrade important natural habitats. Unusual habitats recorded only in recent years in the North Sea are associated with natural gas seeps (Hovland & Thomsen 1989; Dando *et al.* 1991). These are centred on pock-marks or areas of 'mottled' seabed and include hard carbonate deposits and a variety of sediment types adjacent to natural gas seeps. The isolated areas of hard substratum provide islands for colonisation by sessile species in an otherwise sedimentary environment while the gradient of sediment types in the area further adds to the remarkable diversity and species richness at these sites. Their often rich fauna and associated potential nature conservation interest were noted by Mitchell (1987). Artificial structures including jetties, oil or gas rigs, coastal defences, wreckage and artificial reefs provide surfaces for colonisation by different species from those generally present on nearby often sedimentary substrata. Unusual marine communities and rare species are often associated with man-made features such as flooded quarries, mill ponds, docks and harbour basins. However, land claim, dredging, dumping, urban development and coastal defence work may all alter the coastline or seabed permanently and smother marine communities, many of them of scientific interest and nature conservation importance.

There are many other coastal features of importance for the development of a wide variety of marine communities which will be mentioned in the geographical review chapters.

3 Biogeography

3.1 The north-east Atlantic

The identification of distinct biogeographical areas is of central importance in conserving biodiversity. Early in the studies of marine natural history, it was recognised that there were regions within which the fauna and/or flora was similar but different from that of other regions. The separation of three different provinces by Lovén (1846) was followed by classifications by other workers, notably by Forbes in Forbes & Godwin-Austen (1859). Forbes separated arctic, boreal, celtic and lusitanean provinces and, although the celtic province has since been incorporated with the boreal, the distribution of those provinces has been largely supported by later work (Figure 9). The lusitanean province stretches from the entrance to the Mediterranean to the entrance to the English Channel. The boundary here is a strong one and both Ekman (1953) and Briggs (1974) draw attention to the marked change in fauna which occurs. The arctic province has a less definite boundary and a transition area, the 'boreal-arctic' (the 'subarctic transition zone' of Ekman 1953) includes the south and north-west coast of Iceland, the Faeroe Islands, Shetland and the coast of Norway to Tromsø. An arctic-boreal province is suggested here to the east of Tromsø and on the north-east coast of Iceland. Many of Forbes' observations on features of certain areas are also significant. For instance, he points to the very lusitanean character of the Channel Isles compared with Vigo Bay in Portugal, which is much more boreal. Shetland is indicated as being a mixture of boreal and boreal-arctic characteristics, a comment echoed much later in a report on the sediment fauna of Shetland (Institute of Terrestrial Ecology 1975). However, these comments apply mainly to shallow areas near to the coast and, in deeper colder water, animals typical of boreal-arctic shallow waters may occur in the south.

The early observations of botanists essentially confirmed those of zoologists. Börgesen & Jonsson (1908) proposed five main groupings: arctic, subarctic, boreal-arctic, cold-boreal and warm-boreal. More recently, there have been a large number of papers describing biogeographical provinces in the north Atlantic based on algal distributions; for instance Hoek (1975), Lüning (1985) and Alvarez *et al.* (1988). The most recent summary of such work (Hoek & Breeman 1989) illustrates a 'cold-temperate north-east Atlantic region' including Iceland, all of the coast of Norway, and the North Sea coasts including Shetland and Orkney; a 'warm-temperate north-east Atlantic region' with a sub-region including western coasts of Great Britain, Ireland and western France and a sub-region including the western Iberian peninsula and Morocco. More of a community approach is adopted in recent comparisons of the seaweed assemblages of north Atlantic islands (most recently for the eastern Atlantic by Tittley *et al.* 1985). However, Tittley *et al.* (1989a) note that further studies are required in Norway and Iceland to compare the algal assemblages there with other areas of the north Atlantic. Tittley *et al.* (1989b) analysed seaweed floras from a much larger number of locations in the north-east Atlantic than previous workers and concluded that there was a continuum of change from south to north without distinct biogeographical boundaries.

Although the lusitanean province extends strictly to the entrance to the English Channel, many species characteristic of the Mediterranean-Atlantic flora and fauna extend to the south-western and western coasts of the British Isles. The extension of southern species and replacement by northern species on the western coasts of Scotland is considered by Mitchell, Earll & Dipper (1983). Although Ekman (1957) mentions a 'southern intermediate zone' to the south-west of Great Britain and north-west of France, no information has been found to suggest the location of different regions. In Great Britain, there is essentially a 'boreal-lusitanean' region extending north to the entrance to the Irish Sea and east to the Isle of Wight but much farther north along the west coast of Ireland. A 'lusitanean-boreal' area suggested here includes the north-west of France (Normandy, Brittany) and south to about the Gironde estuary where the work of Crisp & Fischer-Piette (1959) and of Evans (1957) suggests a marked change in rocky shore flora and fauna. The extensive sediment shores south of the Gironde estuary provide a further break in the distribution of rocky shore biota. However, without local knowledge, it is difficult to suggest a boundary area. A further marked biogeographical gradient occurs along the coast of northern Spain to the Basque coast in the region of the Gulf of Gascony (for instance, Fischer-Piette 1938, 1955; Hoek & Donze 1966; Ibanez *et al.* 1989). Here, the eastern part of the north coast has the greatest proportion of southern species, and Hoek (1975) clearly indicated the area as phytogeographically intermediate between Morocco and north-west Spain.

Wolff (1973) provides a review of estuarine and other brackish water communities in the north-east Atlantic from Denmark to Arachon in southern France including Britain. He concludes that the faunas of brackish water areas as well as those of the freshwater tidal areas are very similar to one another throughout this geographical spread.

Despite some disparity between workers and the difficulty of drawing boundaries in what is essentially a transition from one province to another, Figure 9b has been prepared to illustrate major biogeographic provinces of the north-east Atlantic.

Taking account of the conclusions above, comparison of data from Great Britain to assess international importance is considered valid for locations from northern Norway to the entrance to the Mediterranean including the Faeroe Islands, the Azores and southern Iceland but particularly from Brittany north to about Trondheim in Norway. However, similar communities, though not species, occur on a much wider scale and here, British seas are comparable with the Mediterranean and Arctic Seas and with temperate ecosystems in other parts of the world.

3.2 Great Britain

Conclusions regarding areas of biogeographical change around Great Britain have to be determined from a variety of sources. For the North Sea, Adams (1987) identifies Shetland within an 'Offshore northern' region, Orkney to off Flamborough as 'British coastal', and the coast to Thanet as 'South British coastal' based on the plankton communities present. A critical division of the North Sea occurs at about the 40 m isobath which, in the southern North Sea approximates to the boundary between stratified and well mixed waters (Dietrich 1950). This isobath also approximately separates the Infralittoral and Coastal étages (Glémarec 1973) (described more fully later in the text).

In the English Channel, the work of Cabioch *et al.* (1977) indicates five points along the English Channel coast which mark the eastern limits of groups of species. Their discontinuity off Start Point in South Devon is also indicated by Henderson, Seaby & Marsh (1990) as a location across which different populations of *Crangon crangon* occur. The work of Crisp & Southward (1958) and Holme (1966) points to the rapid reduction in numbers of western species which occurs east of Poole Bay.

In the western approaches, there are clear changes in distribution of species brought about by the distribution of oceanic and coastal water masses as well as the local conditions in the Bristol Channel. These changes in

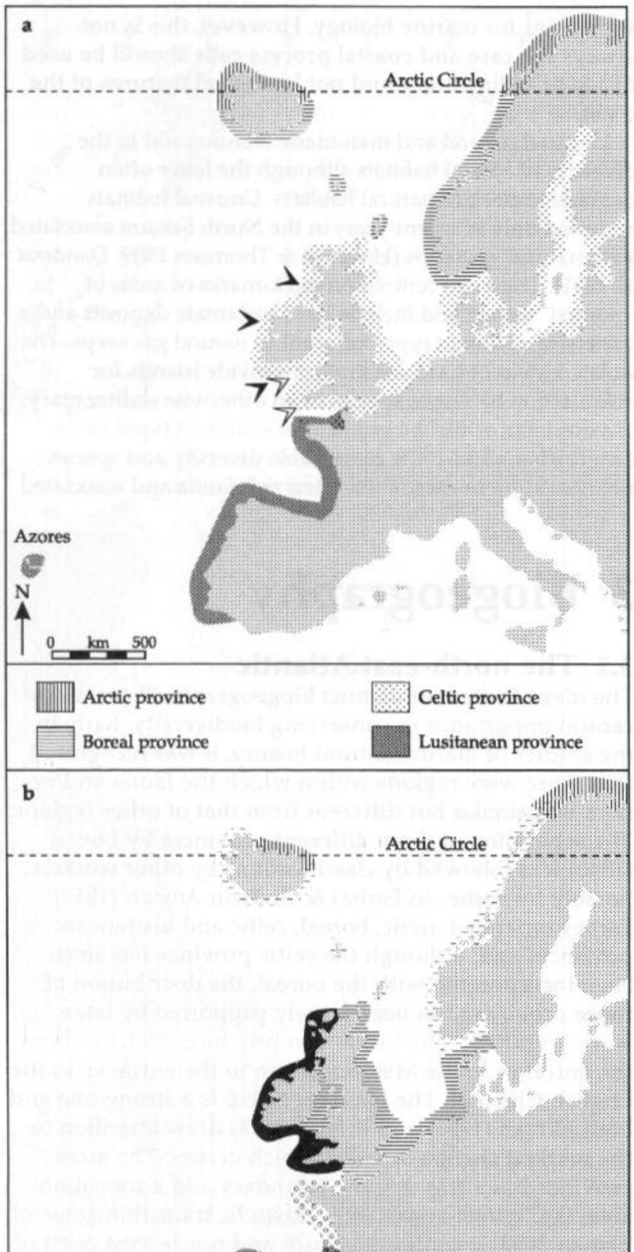


Figure 9. Biogeographical regions of the north-east Atlantic. (a) shows the biogeographical provinces suggested by Forbes in Forbes & Godwin-Austen (1859). (b) is based on Ekman 1953 and Briggs 1974 but with further original interpretation by the author and advice from Dr Torleiv Brattegard and Professor Michel Glémarec. Re-drawn from Hiscock 1996.

species characteristics of the coast were brought together as a conclusion to the NCC-commissioned survey of sublittoral benthic ecosystems in south-west Britain (Hiscock 1981). That work, together with previous studies, suggested separation of Outer Bristol Channel (Bideford Bay/Carmarthen Bay to Porlock Bay/Swansea Bay), Inner Bristol Channel (Porlock Bay/Swansea Bay to Watchet/Lavernock Point near Cardiff) and Severn Estuary provinces. The boundary suggested at the entrance to the Bristol Channel between Bideford Bay and Carmarthen Bay is supported by the work on *Crangon* mentioned above. Farther north, in the Irish Sea, Crisp & Knight-Jones (1955) suggested a boundary at Carmel Head on Anglesey. Local but widespread characteristics occur as a result of the presence of particular physiographic or substratum features. For instance, the sandy Cardigan Bay and the coast of Cumbria appear to be closely similar with the tubeworm *Sabellaria alveolata* characteristically present on the shore and similar ephemeral communities of algae and animals on the Sarns (in Cardigan Bay) and the scar grounds off Cumbria (Cunningham *et al.* 1984a).

Whilst temperature regimes associated with water depth are clearly of key importance in determining distribution of benthic species, an increasing amount of evidence points to the biogeographical importance of frontal systems. This possible importance was drawn to attention by Mitchell (1987). Crisp (1989) summarises information on the location of tidal fronts in the British Isles and discontinuities in the distribution of intertidal fauna and flora to demonstrate a clear correlation in the two. He also points to the contribution of other factors, notably estuarine warming in summer, the dispersive influence of headlands and the effect of barren stretches of sandy coasts in determining the quantitative biogeographical distribution of intertidal species. Henderson, Seaby & Marsh (1990) demonstrated the separation of different populations of the common shrimp *Crangon crangon* brought about, they suggest, by reduced dispersal of planktonic larvae across fronts.

4 Historical perspective to studies of marine natural history

4.1 Introduction

The marine natural history of Great Britain is documented in a rich heritage of publications. These studies can be traced back to the 17th century, although it is only much later, in the mid-19th century, that a prolific volume of both popular accounts and authoritative monographs on species groups began to appear.

4.2 Early collectors

The descriptions of marine life around the coast of Great Britain started with the predominant desire to discover and describe species new to science using the binomial system of taxonomy developed by Linneaus and applied consistently for the first time in his *Species Plantarum* published in 1753. The first general account of shore animals on the coast of Britain was published by Thomas Pennant in 1777 in volume 4 of *British Zoology.* Enthusiastic naturalists of the late 18th and early 19th centuries included the London merchant John Ellis who collected seaweeds and other 'corallines' (Hydrozoa, Bryozoa) in south-east England, George Johnson of Berwick, George Montagu who did much of his collecting in the Kingsbridge area of South Devon, William Morris of Anglesey, and Jonathan Couch of Polperro. Collectors were largely restricted to their local areas until the arrival of steam trains provided the opportunity to travel more widely. Between about 1820 and 1880 activity was intense. Many collectors supplied specimens to taxonomists such as Harvey (algae), Bowerbank (sponges), Hinks (hydroids and bryozoans), M'Intosh (polychaetes) and Darwin (barnacles). Seaweeds and shells were the most popular collected items mainly because of their beauty and the ease with which they could be displayed. The early collectors helped in the production of the first monographs describing particular groups of organisms; many of which continued to be the only comprehensive reference for species identification until very recently.

The use of a dredge (Figure 10) was essential to much of this collecting and was mentioned by George Montagu in a paper delivered to the Linnaean Society in 1804. The Irish naturalist Robert Ball was credited as the "inventor and improver of the naturalists' dredge" in his election as Fellow of the Royal Society in 1857 (Ross & Nash 1985). Edward Forbes, in his short career, did much to describe communities sampled by the dredge and to develop and encourage this means of sampling the seabed. It was as a schoolboy of 15 that Forbes started dredging off the Isle of Man, and later, in 1835, he published his findings in the *Magazine of Natural History.* In 1840 the British Association formed a Committee for "the investigation of the marine zoology of Great Britain by means of the dredge". In that year a grant of £50 was awarded for that purpose (of which only £15 was spent,

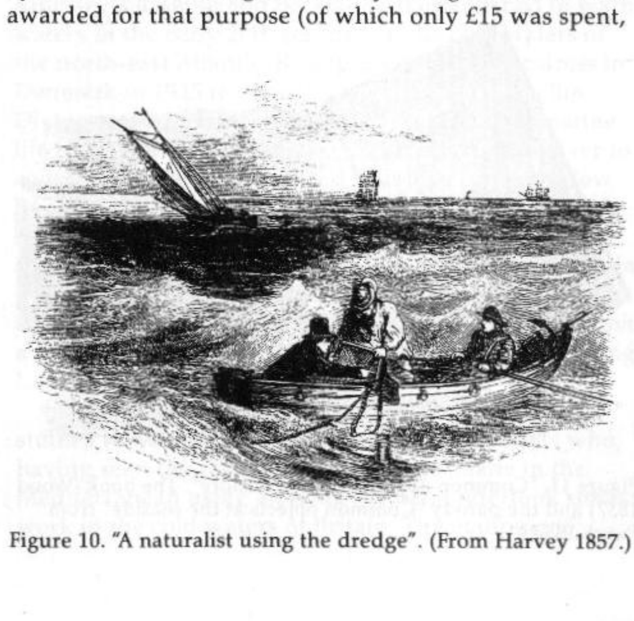


Figure 10. "A naturalist using the dredge". (From Harvey 1857.)

in part because of the "state of the weather, which prevented dredging in the open sea during a great part of the summer"). Further grants followed, and in 1851 Forbes reported on the records of over 140 dredging excursions. Perhaps the most successful programme of dredging was off Shetland, reported by Jeffries (1869), which produced both species lists and a comparison of the fauna of the Shetland Islands with that of other parts of the British Isles. However, only a few of the collecting expeditions resulted in the description of assemblages of species from particular locations and might therefore have contributed to an understanding of what we now describe as 'communities' or 'biotopes'. Much of the information gleaned by dredging was brought together by Forbes in *The natural history of European seas*, completed posthumously (Forbes & Godwin-Austen 1859). *The natural history of European seas* provides a description of many aspects of marine ecology, mainly related to the distribution of species according to geographical location and the nature of the seabed together with accounts of zonation on the shore and underwater.

4.3 Popularisation

The middle of the 19th century also saw the popularisation of natural history and the writing of many natural history books (Figure 11). Pre-eminent amongst marine naturalists in this field was Philip Henry Gosse. His forays to the shore led to the writing of enthusiastic descriptions from places such as Torbay, Ilfracombe and Tenby. Some of these descriptions provide a basis for comparison today. Interest in marine zoology greatly increased during the 1850s. The destructive approach to collecting marine life on the shore is reflected in the writings of Lewes (1858). The equipment he advises for a day's hunting includes: "a geologist's hammer (let it be a reasonable size), and a cold chisel; to these add an oyster-knife, a paper knife, a landing net, and, if your intentions are serious, a small crowbar". At about this time, the marine aquarium became a source of amusement. Gosse is credited with the popularity of the aquarium, for which the collection of specimens had severe consequences for intertidal marine life in some areas (Gosse 1906).

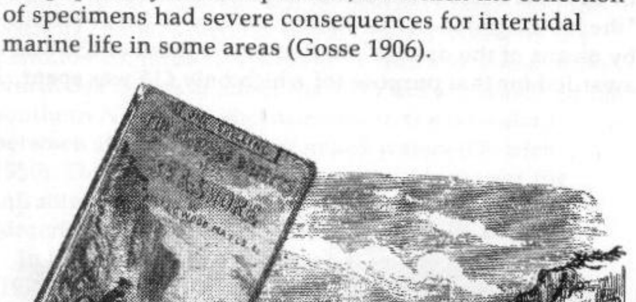


Figure 11. "Common objects of the sea-shore". The book (Wood 1857) and the parody "Common objects at the seaside" from *Punch* 1857.

4.4 Consolidation and the description of communities

The advantage of a centre for marine biological research was put forward in 1870 by Anton Dohrn and taken up by the British Association in appointing a committee for the foundation of zoological stations in different parts of the world. After about 1870, marine biology became a more professionally established science and the opportunity to build a station dedicated to the study of marine biology arose after the International Fisheries Exhibition in London in 1883. The following year, a meeting held at the Royal Society resulted in the founding of the Marine Biological Association of the United Kingdom and the establishment of its laboratory at Plymouth in 1888 (Southwood & Roberts 1984). However, this institute was pre-dated in 1884 by the establishment of a marine station at St Andrews (Laverack & Blackler 1974) and a floating laboratory situated in a flooded quarry near Edinburgh. A year later, the latter was towed through the Forth and Clyde canal to Millport where it became a precursor of the Scottish Marine Biological Association laboratory (Marshall 1987). In 1887, after several years of successful operations, the Liverpool Marine Biology Committee established a marine station on Puffin Island off Anglesey. This continued operations only until 1891 when the centre of interest for marine research in the area changed to Port Erin, Isle of Man, where the marine laboratory established by Herdman in 1892 became a part of Liverpool University after World War I (Herdman 1920).

Some of the earliest studies at the Plymouth laboratory (Heape 1888) led to the description of the benthic algae and animals in the region. Allen (1899) described the seabed and animal assemblages off Plymouth whilst Allen & Todd (1900) undertook a systematic survey of the Salcombe estuary followed by the Exe estuary in 1901. The work undertaken at Plymouth led to the compilation of the *Plymouth marine invertebrate fauna* (Marine Biological Association 1904); the precursor of many such detailed accounts of local marine faunas. Later studies of mudflat communities in the Tamar (Spooner & Moore 1940) provided important descriptive information and a basis for separating different assemblages of species.

In the early part of the 20th century, work was being undertaken outside of Great Britain which would greatly influence studies in this country. In Ireland, the Royal Irish Academy's Clare Island Survey provided important ecological information. In the Clare Island studies, Cotton (1912) provided "the first detailed account of the algal associations of any areas of the British Isles" and Southern (1915) described the fauna including the description of 30 main types of habitat and association. In 1913, Petersen (1914) described the animal communities of the sea bed off Denmark. The work was undertaken using a grab to provide quantitative samples of sediments rather than the "superficial dredge" (the use of which he subjected to some scorn) and it was this quantitative approach which revealed the different communities. Communities were characterised by the conspicuous organisms, particularly molluscs and

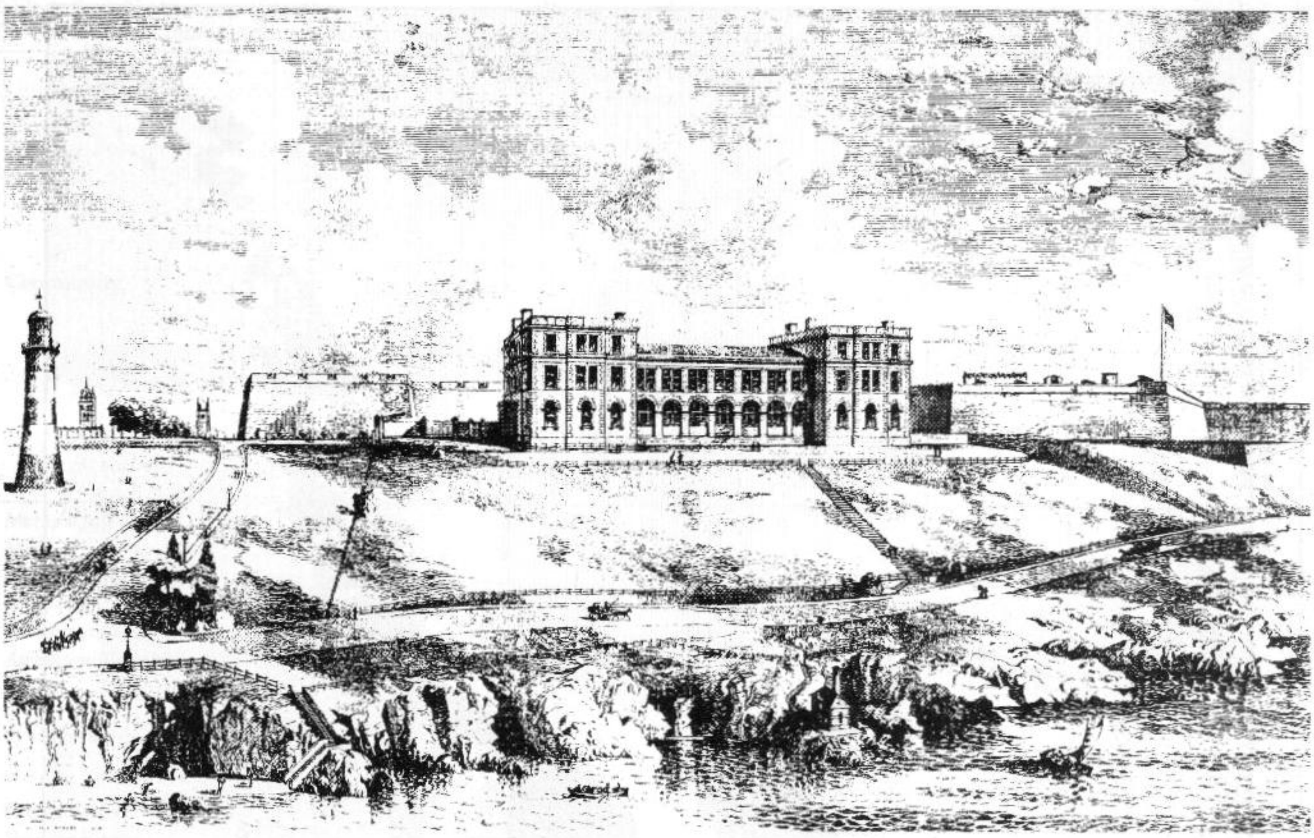


Figure 12. The Marine Biological Association of the United Kingdom Laboratory at Plymouth. (Courtesy of the Marine Biological Association of the United Kingdom.)

echinoderms, present in samples. Later, Petersen (1915) produced a map showing the likely distribution of sediment communities in the north-east Atlantic (Figure 13). The work of Ford (1923) offshore of Plymouth Sound and of Stephen (1923, 1933, 1934) in the North Sea, followed the pioneering methods developed by Petersen for describing sediment communities. Davis (1925) had also undertaken quantitative studies in the southern North Sea and suggested in relation to the distribution of communities that: "the simple number of the soil groups will show what species may be expected therein", thus stating the primary importance of sediment type in determining the communities likely to be present. The results of these early studies and of some later ones such as those of Jones (1950) from the south end of the Isle of Man were brought together by Thorson (1957) to describe the level-bottom animal communities and their distribution from throughout the world; those noted for the north-east Atlantic are listed in Table 1.

4.5 The advent of diving

For over a hundred years, sampling seabed marine life around Great Britain relied on remotely operated equipment. Although the French naturalist Milne-Edwards had, in 1845, used a diving helmet and leaden shoes in the Mediterranean, many boat or shore-bound naturalists must have echoed the words of Charles Kingsley in his book *Glaucus* published in 1855:

> And the sea-bottom, also, has its zones, at different depths, and its peculiar forms in peculiar spots, affected by the currents and the nature of the ground, the riches of which have to be seen, alas! rather by the imagination than the eye; for such spoonfuls of the treasure as the dredge brings up to us, come too often rolled and battered, torn from their sites and contracted by fear, mere hints to us of what the populous reality below is like. Often, standing on the shore at low tide, has one longed to walk on and in under the waves...and see it all but for a moment.

The use of diving techniques was the answer to Kingsley's longing and became well established in warm waters in the early 20th century. In the cold waters of the north-east Atlantic, Kramp used full diving dress in Denmark in 1925 to observe and sample marine life. Diving was first briefly employed for sampling marine life in British waters by Lyle (1929), who used a diver to collect algae from the scuttled warships in Scapa Flow. At about the same time, the Swedish biologist T. Gislén employed a diver in standard gear in a wide-ranging survey to collect samples mainly from sublittoral rock in the Gullmar Fjord. The results (Gislén 1930) revealed 45 associations. In the same volume, Gislén also undertook a thorough review of the European literature describing hard-substratum communities.

One of the most remarkable of the early diving studies was by a small group of marine biologists who, having seen the results of observations made in the Mediterranean using a diving helmet, undertook similar work in the cold waters of Britain. The equipment

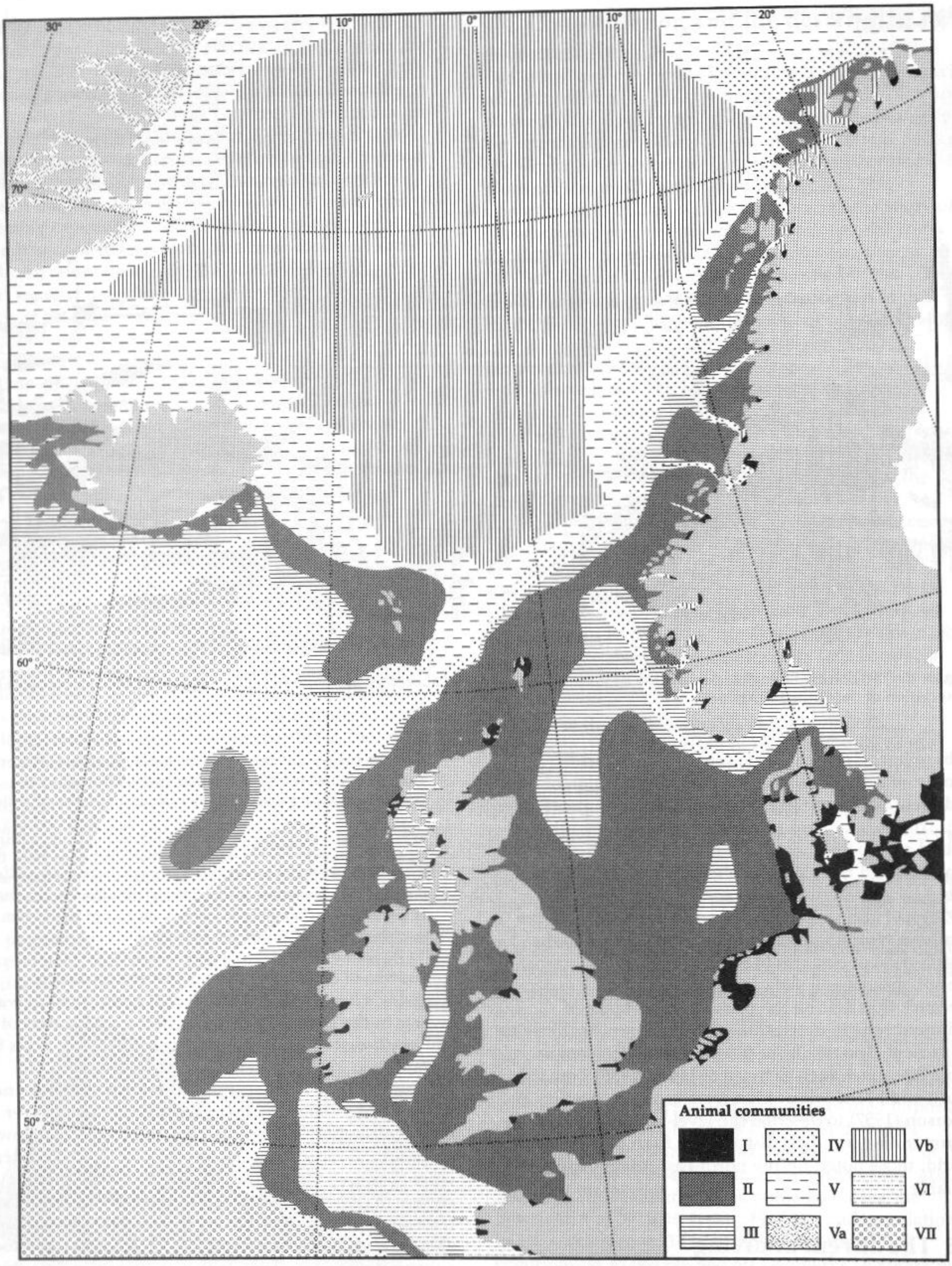


Figure 13. The likely distribution of sediment communities in the north-east Atlantic (re-drawn from Petersen 1915). I = *Macoma balthica* community with *Macoma balthica, Mya arenaria, Cardium edule, Arenicola marina*, etc.; II = *Venus* communities with Spatangidae found mainly on sandy bottoms; III = *Brissopsis* community on soft clay bottom with *Brissopsis lyrifera, Amphiura chiajei, Calocaris m'andreae, Nucula sulcata* and *Eumenia crassa* etc.; IV = communities from deeper water than the *Brissopsis*, not yet subject to valuation but presumably on soft clay bottom with *Pecten vitreus, Abra longicallis* and various other species as characteristic types; V = northern communities (may include *Macoma calcarea* and *Astarte borealis* communities) (Va includes *Yoldia arctica* and is present in the coastal regions of the extreme Arctic; Vb is a habitat for *Pecten frigidus* in the deepest part of the Norwegian Sea); VI = communities of the Lusitanean region; VII = bottom fauna of the Atlantic.

Table 1. Level bottom communities recorded in the north-east Atlantic from northern Norway to Southern Spain and listed by Thorson (1957). Communities are listed in the order of first mention in the paper and nomenclature is that used in the paper.

Community					Scandinavia, NW Germany and Holland		Deeper North Sea, Great Britain and Ireland				
	Arctic part of the Atlantic – Arctic Norway	North Atlantic Islands – Faroes	The Baltic & Sea of Bothnia	Inner Danish Waters	Swedish West Coast, Norwegian South Coast Skagerack	Danish, German and Dutch North Sea coasts	North Sea basin	Scottish Coast	English coast & coast of Wales	West coast of Ireland	Lusitanian part of the Atlantic coast of Portugal)
Macoma balthica	+	–	+	+	+	+	–	+	+	–	–
Macoma calcarea	+	+	+	+	+	–	–	–	–	–	–
Arca-Astarte crenata (reduced)	+	–	–	–	–	–	–	–	–	–	–
Venus (reduced)	–	+	–	–	–	–	–	–	–	–	–
Amphiura filiformis	–	+	–	+	+	+	+	–	+ (= *Turritella*)	+ (indications)	–
Synodysma alba	–	–	+ (W. Baltic only)	+	–	+	–	+	+	–	–
Pontoporeia	–	–	+	–	–	–	–	–	–	–	–
Venus gallina	–	–	–	+	–	+	+	+	–	–	+
deep *Venus*	–	–	–	+	+	+	+	–	+	–	+
Haploops	–	–	–	+ (local only)	–	–	–	–	–	–	–
Maldane sarsi-Ophiura sarsi	–	–	–	–	+	–	–	–	–	–	–
Amphilepis norvegica-Pecten vitreus	–	–	–	–	+	–	–	–	–	–	–
Tellina fabula	–	–	–	–	–	+	–	–	–	–	–
Foramanifera	–	–	–	–	–	–	+	–	–	–	–
Ophiura affinis-Echinocyamus	–	–	–	–	–	–	+	–	–	–	–
Tellina tenuis – Tellina fabula	–	–	–	–	–	–	–	+	–	–	–
Tellina tenuis (with *Tellina incarnata*)	–	–	–	–	–	–	–	–	–	–	+
Cardium edule – Scrobicularia (= reduced *Macoma*)	–	–	–	–	–	–	–	–	–	–	+

included the helmet, constructed by a local blacksmith, a car tyre pump and piping to supply air, and a telephone. The systematic programme of description and sampling undertaken at depth of a few metres at Wembury in South Devon by Kitching, Macan & Gilson (1934) is outstanding. That work was followed by forays into the Sound of Jura on the west coast of Scotland studying light and kelp growth (Kitching 1941). Such studies were interrupted by World War II and not revived in Great Britain until ten years after the end of hostilities.

4.6 Post-war ecology

After World War II, a largely new band of marine naturalists (although the word 'naturalist' was becoming unfashionable) became active. Professor C.M. Yonge, who had started his career on the staff of the marine biological laboratory at Plymouth, published his volume on *The sea shore* in the Collins New Naturalist series (Yonge 1949, 1966) and this remains today as a fascinating, readable and authoritative guide. In the late 1940s, J.R. Lewis began his studies of zonation on rocky shores which led to the publication in 1964 of *The ecology of rocky shores*. N.S. Jones used material mainly from the northern Irish Sea, particularly molluscs and echinoderms, to propose a now widely used classification of sediment benthos (Jones 1950). D.J. Crisp and E.W. Knight-Jones undertook their study of species distribution on the north Wales coast published in 1955, and D.J. Crisp and A.J. Southward a similar study along the coast of the English Channel, published in 1958. N.A. Holme undertook his wide-ranging investigation of sediment benthos in the English Channel (Holme 1961, 1966) largely following the Jones school of naming communities. Other studies were being undertaken by fisheries scientists in nearshore areas such as the Scottish lochs and voes and offshore particularly in the North Sea. Remote cameras offered a further means of exploring underwater areas. Vevers (1952) describes the results of photographic survey of ground off Plymouth whilst Barnes (1952) published initial studies of the use of underwater television.

The teaching of marine natural history was an important element of many university courses and students were trained in identification and principles of marine ecology. Universities with the good fortune to be by the sea could develop marine laboratories such as the Marine Science Laboratory at Menai Bridge of the University College of North Wales. Several universities expanded existing laboratories or established new marine field stations such as those of the University of Leeds at Robin Hood's Bay, the University of London's laboratory at Whitstable, the Port Erin laboratory of the University of Liverpool and the Dove Marine Laboratory at Cullercoats which served Durham and Newcastle Universities. Staff and students from the University of Bristol went abroad to Lough Ine (Hyne) in Ireland to contribute very valuable studies to our knowledge of marine ecology.

Newly established field centres for teaching, such as those at Dale and Orielton in Pembrokeshire, provided a focus for research and the description of the relationship between environmental factors such as wave exposure and the marine communities of the seashore (for instance the biologically defined wave exposure scale of Ballantine (1961)). Methodology was also being further developed. Quantitative grab samples were being used in preference to the qualitative dredges, and systematic studies of rocky shores required a more quantitative approach (for instance Southward & Orton 1953; Southward 1953) or semi-quantitative approach using abundance scales (Crisp & Southward 1958).

However, the 1960s showed a decline in interest, indeed respectability, of marine ecological studies with the rise in opportunities to investigate the biochemistry, behaviour and fine structure of marine organisms in the laboratory. Paradoxically, a new technique – Self Contained Underwater Breathing Apparatus (SCUBA) – was becoming widely available but recognised by only a few for its value in direct observation of sublittoral habitats and communities. The earliest studies using this new equipment were those of R. Forster near Plymouth and E.W. Knight-Jones and his co-workers in north Wales during the early 1950s (Forster 1954; Knight-Jones & Jones 1955; Knight-Jones, Jones & Lucas 1957). Joanna Jones (Kain) used diving to study the distribution of algae in the Isle of Man (Kain 1960) and especially the biology of kelp (reviewed in Kain 1979). In the mid-1960s, expeditions from Britain to Malta to undertake a variety of studies using diving, led to the formation of the Underwater Association, an organisation which was to encourage a great deal of the work in British waters using diving.

During the mid-1960s, the potential impact of human activities on the marine environment and its life was becoming of some concern. The wreck of the *Torrey Canyon* in 1967 and subsequent oiling of beaches in the south-west drew attention to the need for a better understanding of the effects of oil pollution and clean-up techniques on natural communities. From then on, the oil industry was to fund much research directed at studying effects of oil pollution but which also enhanced our general knowledge of marine communities and ecology.

In the 1970s, the Institute of Terrestrial Ecology (ITE), through its Biological Records Centre, co-ordinated a series of marine recording projects for a range of taxonomic groups, and provided an impetus for biological recording generally. Harding (1992) includes a history and overview of this work and its applications. Several atlases showing the distribution of marine species have been published. These include Clark (1986) (crabs), Dodge (1981) (dinoflagellates), Norton (1985) (algae), and Seaward (1982, 1990, 1993) (molluscs).

Studies of benthic ecology and of communities increased greatly in the 1970s and it is these studies which are reviewed in sections 5 and 6.

4.7 Studies of marine ecology for nature conservation

Studies of marine species and marine ecology for nature conservation were largely incidental or accidental to studies of coastal habitats and birds up to the early 1970s. Marine biology was included in the survey of Shetland undertaken by the Institute of Terrestrial Ecology (ITE) for the then Nature Conservancy Council (NCC) in 1974 (ITE 1975). The NCC then began properly to address the collection of marine biological data to provide a basis for site assessment, responding to proposals for development or to other aspects of human impact on the marine environment. The first major marine biological project to be commissioned by NCC was the (incomplete) Intertidal Survey of Great Britain undertaken by the Scottish Marine Biological Association and the Marine Biological Association of the United Kingdom between 1975 and 1980. The South-West Britain Sublittoral Survey was carried out by the Field Studies Council between 1977 and 1980 and included nearshore areas surveyed by diving from west Cornwall to Pembrokeshire (the final report is Hiscock 1981). The survey of Harbours, Rias and Estuaries in Southern Britain, carried out by the Field Studies Council between 1984 and 1988, included both littoral and sublittoral habitats. There were many smaller surveys especially in the Hebrides (summarised in Mitchell, Earll & Dipper 1983) and at proposed marine nature reserves, as well as studies of particular habitat types such as saline lagoons (Barnes 1989, Sheader & Sheader 1989). Work on the ecology, restoration and management of disused dock basins received initial funding from NCC (Cunningham *et al.* 1984b, Hendry *et al.* 1988). These early NCC studies provided the initial basis for the Marine Nature Conservation Review of Great Britain which commenced in 1987 (Hiscock 1996).

5 General descriptions of benthic marine ecosystems in the north-east Atlantic

5.1 Introduction and general texts

A general background to marine ecosystems in the north-east Atlantic can be found in several text books, which describe principles rather than site-related descriptions.

The volume entitled *The sea shore* (Yonge 1966) gives an excellent and highly readable introduction to seashore ecology in Great Britain. Other informative texts on the seashore are Southward (1965) and Barrett (1974). McLusky (1989) describes the ecology of estuaries. Other more recent volumes such as Fincham (1984), Meadows & Campbell (1988), Hawkins & Jones (1992) and Little & Kitching (1996) are intended as student text books for the study of marine ecology whereas a wider audience is served by volumes such as *Sea life of Britain and Ireland* (Wood 1988).

5.2 Benthic ecology

5.2.1 *Introduction*

The benthos is the flora and fauna living on and in the seabed, including rock and sediment, littoral and sublittoral. Because the seabed is mainly sediment, studies and descriptions of 'the benthos' have been greatly oriented towards animals living in the sediment (infaunal species) and on the sediment (epifaunal species). The nomenclature according to size is also animal-oriented. The 'megafauna' is greater than about 20 cm in size, the 'macrofauna' about 20 cm to 0.5 mm, 'meiofauna' 0.5 mm to 50 µm, and 'microfauna' 50 µm to 5 µm. These categories are convenient to apply to all benthos although they might not be easily applied to plants as well as animals or to hard substrata. Descriptive terms applied to the benthos are incorporated into the framework of MNCR biotope classifications currently being prepared. In this section, attention is drawn to the texts which describe general features or ones which are not site-related.

5.2.2 *Littoral rock*

Rocky intertidal habitats in Great Britain must be the most thoroughly studied and sampled of all the major marine habitats. Nevertheless, published descriptive information relates mainly to aspects of zonation and the effect of wave exposure and not to particular habitats on the shore. The classic text by Lewis (1964) comes closest to an overall view of rocky shore ecology in the British Isles dealing especially thoroughly with zonation but also with effects of wave exposure, communities in crevices and geographical distribution. Several more detailed topics were addressed in a series of essays presented to Dr Lewis on his retirement (Moore & Seed 1985). A more brief description of rocky shore ecology is given in Brehaut (1982), Little & Kitching (1996) and Rafaelli & Hawkins (1996). However, little work has been carried out to describe communities in many of the major rocky shore habitats especially rockpools, caves or under boulders. The importance of wave action in determining species present and their abundance on rocky shores has been recognised since studies of marine ecology first started but it was not until 1961 that a study of shores in Pembrokeshire was used to provide a structured description of the communities occurring in different conditions of wave exposure (Ballantine 1961). Although locally based, that scale has been widely used in the British Isles and found, with some modification, to be generally applicable. Rocky shores have been separated into four 'selection units' for the identification of Sites of Special Scientific Interest on the basis mainly of exposure to wave action and that classification provides a useful separation of major types illustrated in Figure 14 (JNCC 1996).

5.2.3 *Sublittoral rock and other hard substrata*

Up to the mid-1970s, remarkably little was known of the communities present in sublittoral rocky areas around Great Britain or their distribution in relation to environmental factors. However, as diving equipment has become widely available, so descriptive studies have been undertaken. The general principles of rocky sublittoral ecology in the British Isles are included in papers by Hiscock & Mitchell (1980), Hiscock (1983) and Hiscock (1985) and are included in Wood (1987). Two main environmental factors determine the distribution and abundance of rocky sublittoral species: light and water movement. Zonation on sublittoral rock is determined mainly by light penetration (Figure 15). There is an 'infralittoral' region dominated by foliose algae (except where grazing pressure is high) to a maximum depth where about 0.1% of surface illumination is present. This is followed by the 'circalittoral' which is dominated by animals. Both wave action and the strength of tidal streams are important in determining the type of community present although only in extremely exposed and extremely sheltered situations is it possible to predict with reasonable certainty what assemblages of species will be present.

Rocky sublittoral habitats are mainly restricted to nearshore areas. However, where tidal streams are strong and there is little sediment present, hard substrata occur offshore. These hard substrata can include gravel, pebbles and cobbles sometimes consolidated by the tubeworm *Sabellaria spinulosa*. Extensive areas of these consolidated coarse sediments occur in the English Channel east of Lyme Bay, Dorset and in the Bristol Channel.

Studies of the very rich communities associated with natural gas seeps and pockmarks, which include carbonate-cemented sediment, in the North Sea off the coast of Britain have been undertaken (Dando *et al.* 1991). A general description for various locations in the North Sea is given in Hovland & Thomsen (1989).

Offshore in depths below about 100 m, hard substratum is very restricted in occurrence and reefs of the coral *Lophelia pertusa* provide a significant habitat.

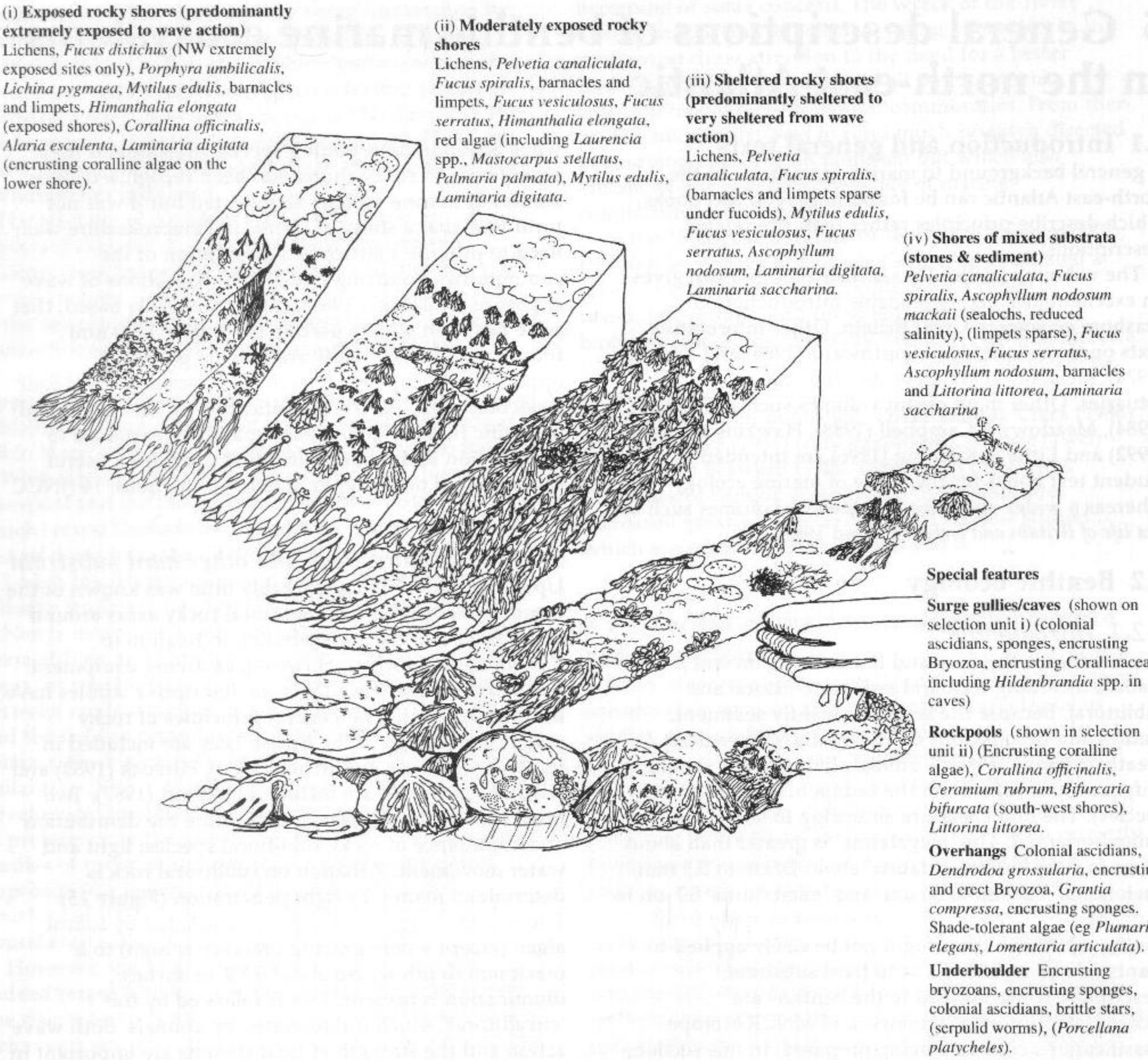


Figure 14. Diagrammatic representation of rocky shore communities including those in minor habitats from wave-exposed to sheltered conditions. (From *Guidelines for selection of biological SSSIs: intertidal marine habitats and saline lagoons*, JNCC (1996).) (Drawing by R. Foster-Smith.)

These corals appear to occur especially where the continental shelf breaks into very deep water. Little is known of the community associated with *Lophelia* in British waters although available information is summarised by Wilson (1979). Studies undertaken off the coast of the Faeroe Islands (Jensen & Frederiksen 1992) reveal a highly diverse and rich associated fauna whilst work undertaken off the Norwegian coast (Mortensen *et al.* 1995) reveal a more limited community of species of which some are specifically associated with the coral. Recent studies undertaken in relation to offshore oil explorations on the continental margin to the north-west of Britain have revealed several epifaunal species, possibly attached to small pieces of hard substratum which sparsely colonise the seabed.

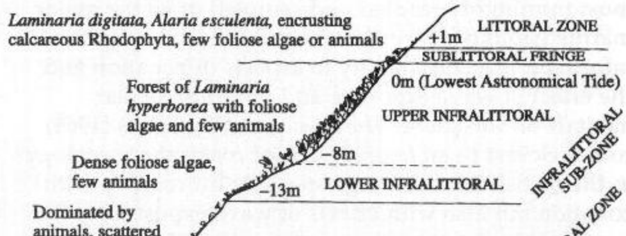


Figure 15. Zonation on sublittoral rocks around Lundy. (From Hiscock 1985.)

5.2.4 Littoral sediment

The biota of unconsolidated sediments is determined mainly by the type of sediment present. This in turn is determined by the strength and type of water movement and the supply of sediment. Wave exposed coarse sediments on the open coast generally have an impoverished fauna able to withstand frequent disturbance. Similarly, some fine sediments frequently suspended by wave action or strong tidal streams usually in enclosed areas will also have an impoverished fauna. The stable sediments of sheltered areas often have rich communities living on and in them showing gradients of change in composition not only in relation to sediment grade but also to salinity changes which occur along sheltered estuarine areas. The flora and fauna of sediments is described in the general texts on marine ecology mentioned above. General texts specifically on sediments, for instance those by Eltringham (1971), Brafield (1978) and Gray (1981), provide a description of the ecology of littoral sediments but little information which describes communities.

Macrofaunal species live on and, as burrowing species, in the sediment. Meiofaunal species live between the grains of sediment. Surface dwelling species are few when the tide is out but many mobile species including crustacea and fish in particular are present when covered by the tide. Seagrass (species of *Zostera*) and some algae occur on many sheltered beaches often with surface dwelling snails such as *Littorina littorea* and *Hydrobia ulvae*. Signs of other species may be present: for instance, the mounds created by the lugworm *Arenicola marina*, the tubes of worms such as *Lanice conchilega*, the feeding marks of *Scrobicularia plana*, or the burrows of crustacea such as *Corophium volutator.* Microalgae colonise sediments, appearing as a brown or green film. There is a zonation on sediment shores which is less easy to observe than for rocky shores but includes, in the terminology of Dahl (1953), a 'subterrestrial fringe' harbouring mainly talitrid amphipods, a 'midlittoral zone' with the cirolanid isopod *Eurydice pulchra* and haustoriid amphipods such as *Bathyporeia pilosa* and *Haustorius arenarius*, and a sublittoral fringe which includes a great variety of species from many taxonomic groups. An alternative scheme (Salvat 1964) includes four zones based on physical factors: a drying or dry zone above normal high tide mark; a zone of retention where sands remain damp but not wet as the tide recedes; a zone of resurgence characterised by interstitial water flow in and out of the sediment with the tide; a zone of saturation. These schemes have been widely used and modified including in studies around Great Britain (McLachlan & Jaramillo 1995). Following their review, McLachlan & Jaramillo (1995) concluded a scheme very similar to that of Dahl (1953).

The types of communities occurring in littoral sediments have recently been assessed to establish 'selection units' for the identification of intertidal Sites of Special Scientific Interest (JNCC 1996) and major groupings are illustrated in Figure 16.

5.2.5 Sublittoral sediment

The great majority of sublittoral seabed is of sediment and considerable research effort has been applied to sampling communities there and defining the distribution of communities. Gray (1981) and Rafaelli & Hawkins (1996) provide general accounts of the ecology of marine sediments. In the sublittoral, sediment type is of predominant importance in determining the infaunal species present and their abundance. However, temperature and thermal stability is also an important structuring factor and Glémarec (1973) identified three 'étages' based on temperature and thermal stability of the water column:

1. the infralittoral étage – depth less than 40 m in the North Sea, temperature variation more than 10 °C;
2. the coastal étage – depth between about 40 m to 100 m in the North Sea, temperature below 12 °C and variation less than 5 °C;
3. the open sea étage – deeper than 100 m in the North Sea with temperature below 10 °C and little variation.

Since the early work to describe marine sediment communities in the north-east Atlantic (included in Section 5) there have been many offshore studies and reviews which add significantly to our knowledge. They are most conveniently separated into descriptions for the North Sea, English Channel and Irish Sea and are included in Section 6. There is very little information on the communities present in offshore areas of the Western approaches or north-west Scotland.

5.3 Brackish habitats (estuaries, lagoons and coastal saline ponds)

5.3.1 Introduction

Brackish habitats are defined by Remane (1971) as including brackish inland seas, estuaries, fjords, coastal lagoons, shore pools, saltmarshes and coastal interstitial ground water. To these, Barnes (1991) adds brackish pools and ditches created by man. The brackish lochs of Scotland must also be considered as an additional category. These habitats and their associated communities in Great Britain are referred to in the texts describing coastal sectors in this volume. Much work which establishes principles of distribution of species and communities in relation to salinity has been carried out in Europe and these are referred to in Section 6.

5.3.2 Estuaries

The definition of an estuary adopted by the MNCR is that it is "a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage" (Pritchard 1967). Estuaries are usually considered to be the downstream parts of a river and are often characterised by extensive mudflats and sandflats. The term 'measurably' used by Pritchard (1967) with regard to dilution by fresh water is difficult

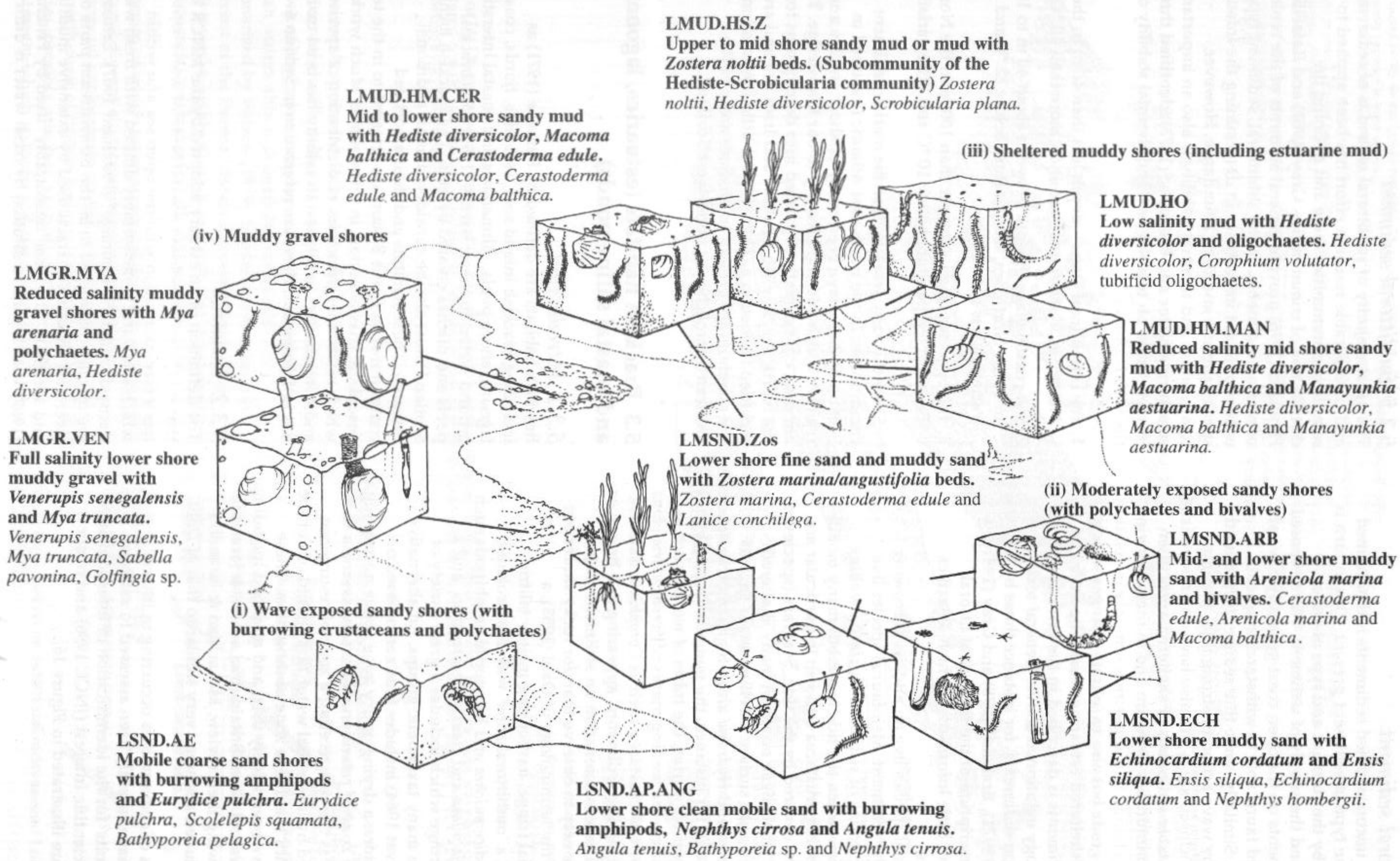


Figure 16. Diagrammatic representation of littoral sediment communities from wave-exposed coarse sediments to those of mud and low or variable salinity. (From *Guidelines for selection of biological SSSIs: intertidal marine habitats and saline lagoons,* JNCC (1996)). (Drawing by R. Foster-Smith.)

to apply but significant reduction in the numbers of species with decreasing salinity occurs below 30‰, and 'estuarine' habitats can be considered to occur where that amount of dilution or more occurs. However, the term 'estuaries' has often been used to include open bays where salinity is near to that of the open sea but where certain characteristics, such as extensive mudflats or sandflats, are similar to true estuaries. A review of the conservation of estuarine habitats, communities and species for Great Britain was undertaken by the NCC (*Nature conservation and estuaries in Great Britain*, Davidson *et al.* 1991). As a part of that review, the marine habitats and associated communities were described according to MNCR methods for community classifications at the time; 37 different major marine communities were identified. Estuaries were classified into nine different types of which ria, bar-built, coastal plain and complex types correspond to the definition of estuaries applied by the MNCR.

5.3.3 *Lagoons and coastal saline ponds*

Coastal lagoons are shallow bodies of coastal salt water (from brackish to hypersaline) partially separated from an adjacent sea by a barrier of sand or other sediment, or less frequently, by rocks (definition based on Ardizzone *et al.* 1988). Coastal saline ponds are deliberately constructed or formed as a consequence of coastal engineering work (Barnes 1991). The species and communities found in these different types are broadly similar. Brackish lagoons in Great Britain are classified into five types by JNCC (1996):

(i) Isolated saline lagoon
These are pools which are completely isolated from the sea by a barrier of rock or sediment. No seawater enters the pool by percolation (see: ii Percolation saline lagoon), the only input of salt water occurring by limited groundwater seepage (such as in some dune pools), by overtopping of the barrier (sill) on extreme high water spring tides, or by salt water inundation during storms. Because of the limited water exchange, salinity may vary considerably with time.

(ii) Percolation saline lagoon
These pools are separated from the sea by a permeable barrier of shingle or pebbles and small boulders. Sea water exchange occurring through the barrier to varying degrees dependent on the permeability of the barrier. In highly permeable conditions tidal fluctuation matches that of the open coast and salinity is only marginally reduced from that of the open sea. At the other extreme, there is little fluctuation with rise in level occurring during spring tides and fall in level during neap tides. In these sites salinity may be substantially reduced.

(iii) Sluiced saline lagoons
These are lagoons where the ingress and egress of water from the lagoon to the open sea is modified by human mechanical interference. This may take the form of a simple pipeline to culvert the water under a road, to a system of valves which restrict water flow as necessary to prevent tidal flooding. These lagoons may be rocky and may have many of the features of silled ponds such as being relatively deep (up to 10 m) and may cover a large area (over 40 ha in some cases).

(iv) Silled saline lagoons
These are in many respects similar to some examples of sluiced lagoons. They are generally rocky basins which have a sill between mean high water of spring tides and mean low water of spring tides. This sill restricts water exchange with the open sea and maintains standing water within the lagoon at all states of the tide. Where sites have a sill close to mean high water of spring tides, salinity is often low (around 15‰). The basin of the lagoon is usually sediment filled, though generally fringed with rock.

(v) Saline lagoon inlets
These are saline lagoons where there is a permanent connection with the sea. Any sill which is present is subtidal. Water exchange with the open sea is limited by the restricted nature of the connecting channel, both in terms of width and any subtidal sill. Because of the reduced water exchange, conditions may become brackish due to freshwater input, and a halocline may develop.

These habitats contain species largely of marine origin and have salinities varying from less than 1‰ to full strength sea water or even hypersaline water at times. For the lagoons of East Anglia, Barnes (1991) quotes 58% of the dominant macrofauna as also inhabiting the sea, 13% essentially fresh water in nature and 28% as more typically associated with lagoons. More detailed descriptions of the types of lagoon and coastal saline ponds in Britain and the species found in them can be found in Barnes (1989) and Sheader & Sheader (1989) respectively. Barnes (1989) and Bamber *et al.* (1992) list lagoonal species. Lagoons may support salt-tolerant freshwater species, stenohaline marine lagoonal specialists, euryhaline marine species, and estuarine species which may be pre-adapted to lagoonal conditions.

Obs are ponds connected to the sea by a narrow inlet and flooding over a shallow sill. They are often rocky and of variable salinity. Many are brackish.

Docks resemble lagoons in many ways, but have hard substratum margins. Disused docks in particular can be restored or managed to support surprisingly diverse marine communities (Cunningham *et al.* 1984b; Hendry *et al.* 1988; Hawkins *et al.* 1992).

5.4 Plankton, birds, fish and mammals

5.4.1 *Introduction*

Although marine life which lives in the water column or at the sea surface are not directly within the remit of the MNCR, pelagic species and fish, especially benthic fish, may be important to the algae and invertebrate communities of the seabed especially through food-web links. Some of those links are briefly mentioned below.

5.4.2 *Plankton*

The distribution of major planktonic populations is illustrated in Lee & Ramster (1981). The larvae and spores of most benthic species spend time in the water column as a part of their dispersal. Phytoplankton and zooplankton form the basis of food chains which directly feed many benthic organisms but also fish, which are in turn prey to dolphins, seals, seabirds and to humans. The largest of marine organisms, including the basking shark and some of the whales, also rely on plankton for food. Plankton productivity is of importance to the distribution of species and tends to be high where estuaries enter the sea or at frontal systems. Excessive productivity as a result of eutrophication may affect the composition of the benthic fauna. Changes in the dominance structure of the benthic communities in the German Bight since the 1920s were attributed to eutrophication (Rachor 1990). Mortality in benthic species off the Danish coast and in the German Bight may have been the result of eutrophication, causing plankton blooms and subsequent depletion of oxygen by decomposition of falling plankton during 1982-83 (Dyer *et al.* 1983b; Niermann *et al.* 1990). Mass mortality of the benthos following the collapse and local concentration of consequent organic matter from blooms of the dinoflagellate *Phaeocystis* has been recorded several times in the eastern Irish Sea (E.I.S. Rees pers. comm.).

5.4.3 Birds

The distribution, migrations, breeding and feeding of birds has been intensively studied and a great deal is known of their habitat and food requirements. Wading birds, which rely on the fauna of intertidal flats together with wildfowl, for instance geese, which often feed on intertidal beds of green algae and seagrass, may have a major impact on the ecology and the abundance of benthic species there. They are mainly found in estuaries and bays with extensive sediment flats and their distribution and biology summarised in the NCC's *Nature Conservation and Estuaries in Great Britain* (Davidson *et al.* 1991). The principal prey species of the main wading birds in the Wash (from Goss-Custard, Jones & Newbery 1977) are given below.

BIRD		PREY
Oystercatcher	*Haematopus ostralegus*	*Cerastoderma edule* *Mytilus edulis*
Knot	*Calidris canutus*	*Macoma balthica* *Cerastoderma edule*
Dunlin	*Calidris alpina*	*Hydrobia ulvae* *Hediste diversicolor*
Redshank	*Tringa totanus*	*Carcinus maenas* *Crangon* spp. *Hydrobia ulvae* Nereidae
Bar-tailed godwit	*Limosa lapponica*	*Lanice conchilega* Nereidae *Macoma balthica*
Turnstone	*Arenaria interpres*	*Cerastoderma edule* Amongst mussel beds
Grey plover	*Pluvialis squatarola*	*Lanice conchilega* various
Curlew	*Numenius arquata*	*Carcinus maenas* *Lanice conchilega* *Arenicola marina*

A great deal of research on the flora and fauna of intertidal flats has been undertaken to investigate sources of food and energy budgets for the birds that rely on them and, where these studies describe benthic communities, they are included in the reviews of current knowledge for each coastal sector.

Many wading bird species are dependent on the intertidal flats for food, but they are much less reliant on the sea than are 'seabirds' which include a range of species using the open sea for food and often living there for all but their nesting period. They feed mainly on fish near to the surface of the sea by diving and by underwater swimming. A few species of seabird, for instance eider *Somateria mollissima* in northern Britain and common scoter *Melanitta nigra* in the south and west, inhabit inshore waters and feed on benthic invertebrates, especially molluscs and crustaceans, in shallow waters. The distribution of seabirds around Great Britain is the subject of a major study undertaken by JNCC's Seabirds at Sea Team (Tasker *et al.* 1987; Webb *et al.* 1990; Stone *et al.* 1995). For the North Sea, studies of seabird distributions have involved work by several countries and the distribution and abundance of important bird species is brought together and mapped in Skov *et al.* (1995).

5.4.4 Fish

The great majority of information on fish populations relates to commercial species and no attempt is made here to summarise the extensive literature generated from the fisheries departments. Potts & Swaby (1991) list the species characteristic of different habitats relevant to the MNCR (summarised in Table 2).

5.4.5 Seals and otters

These mammals rely on the land for production of young but feed in the sea. The British population of Atlantic grey seals *Halichoerus grypus* is estimated to be 108,500 and of harbour (common) seals *Phoca vitulina* 28,720 following counts up to and including 1994 (Hiby *et al.* 1996). The count for common seals was taken after the death of a high proportion of the population on the east coast of England following the outbreak of infection with a phocine distemper virus in 1988 (Hall, Pomeroy & Harwood 1992) and reflects continued recovery of the population. Seals live in full salinity seawater and rarely enter true estuaries although they are commonly found in sealochs and in the voes of Shetland. The Atlantic grey seal is a creature mainly of open rocky coasts, whereas the common seal is often found in sheltered areas and on sandy beaches or sand banks. The food of grey seals is predominantly of sandeels (Ammodytidae) and gadoids (Hammond & Prime 1990) and seals may affect the size of inshore fish populations (Rae 1962) but other ecological effects appear to be minimal. However, Howson (1988) attributed certain unusual communities on the walls of caves in Shetland to the presence of deposited organic material from seal faeces. Otters *Lutra lutra* feed on inshore fish populations, particularly those of smaller species living in the shallow kelp forest, and this has been researched in Shetland and was described by Kruuk *et al.* (1989).

Table 2. Fish assemblages of benthic habitats. Derived from Potts & Swaby (1991) but not including species listed as uncommon. No fish assemblages are listed for littoral and inshore gravel where very few species are associated with the gravel

ESTUARINE HABITATS

Mud	Sand	Rock	*Zostera marina*
Benthic Fishes	**Benthic Fishes**	**Benthic Fishes**	**Benthic Fishes**
Anguilla anguilla	*Anguilla anguilla*	*Neropis lumbriciformis*	*Lepadogaster lepadogaster*
Nerophis lumbriciformis	*Agonus cataphractus*	*Syngnathus acus*	*Syngnathus acus*
Pholis gunnellus	*Pomatoschistus microps*	*Syngnathus typhle*	*Syngnathus typhle*
Agonus cataphractus	*Pomatoschistus pictus*	*Cyclopterus lumpus*	*Liparis montagui*
Pomotoschistus microps	*Pomatoschistus minutus*	*Gobius niger*	
Platichthys flesus	*Platichthys flesus*	*Gobius paganellus*	**Epibenthic Fishes**
Pleuronectes platessa	*Pleuronectes platessa*		*Gasterosteus aculeatus*
		Epibenthic Fishes	*Spinachia spinachia*
Epibenthic Fishes	**Epibenthic Fishes**	*Lepadogaster lepadogaster*	*Taurulus bubalis*
Salmo trutta	*Salmo trutta*	*Pollachius pollachius (juv.)*	*Centrolabrus exoletus (juv.)*
Salmo salar	*Salmo salar*	*Spinachia spinachia*	*Crenilabrus melops (juv.)*
Pollachius pllachius	*Osmerus eperlanus*	*Taurulus bubalis*	*Ctenolabrus rupestris (juv.)*
Trisopterus minutus	*Pollachius pollachius*	*Liparis liparis*	*Labrus bergylta (juv.)*
Gasterosteus aculeatus	*Trisopterus minutus*	*Liparis montagui*	*Gobiusculus flavescens*
Mullus surmuletus	*Gasterosteus aculeatus*	*Dicentrarchus labrax*	
	Dicentrachus labrax	*Centrolabrus exoletus (juv.)*	
	Mullus surmuletus	*Crenilabrus melops (juv.)*	
	Pholis gunnellus	*Ctenolabrus rupestris (juv.)*	
		Labrus bergylta (juv.)	
		Gobiusculus flavescens	

LITTORAL HABITATS

Mud	Sand	Bedrock & boulders	Rockpool & crevices
Benthic Fishes	**Benthic Fishes**	**Benthic Fishes**	**Benthic Fishes**
Anguilla anguilla	Rajidae (juv.)	*Apletodon microcephalus*	*Apledon microcephalus*
Nerophis lumbriciformis	*Agonus cataphractus*	*Lepadogaster lepadogaster*	*Lepadogaster lepadogaster*
Agonus cataphractus	*Trachinus vipera*	*Nerophis lumbriciformis*	*Ciliata mustela*
Pomatoschistus microps	*Pomatoschistus minutus*	*Nerophis sp.*	*Nerophis lumbriciformis*
Platichthys flesus	Ammodytidae	*Syngnathus acus*	*Nerophis sp.*
Pleuronectes platessa	Callionymidae	*Syngnathus typhle*	*Myoxocephalus scorpius*
	Psetta maxima	*Myococephalus scorpius*	*Taurulus bubalis*
Epibenthic Fishes	*Scophthalmus rhombus*	*Taurulus bubalis*	*Cyclopterus lumpus*
Salmo trutta	*Limanda limanda*	*Cyclopterus lumpus*	*Coryphoblennius galerita*
Salmo salar	*Platichthys flesus*	*Liparis liparis*	*Lipophrys pholis*
Pollachius pollachius	*Pleuronectes platessa*	*Liparis montagui*	*Parablennius gattorugine*
Trisopterus minutus	*Solea solea*	*Coryphoblennius galerita*	*Gobius cobitis*
Gasterosteus aculeatus		*Lipophris pholis*	*Gobius niger*
Dicentrachus labrax	**Epibenthic Fishes**	*Parablennius gattorugine*	*Gobius paganellus*
Mugilidae	*Osmerus eperlanua*	*Gobius niger*	*Zeugopterus punctatus*
Pholis gunnellus	*Mullus surmuletus*	*Gobius pagenellus*	
	Mugilidae	*Zeugopterus punctatus*	**Epibenthic Fishes**
	Ammodytidae*		*Centrolabrus exoletus*
		Epibenthic Fishes	*Crenilabrus melops*
		Spinachia spinachia	*Ctenolabrus rupestris*
		Centrolabrus exoletus	*Labrus bergylta*
		Crenilabrus melops	*Gobiusculus flavescens*
		Ctenolabrus rupestris	
		Labrus bergylta	
		Gobiusculus flavescens	
		Thorogobius ephippiatus	

* Also present in the seabed

(cont'd overleaf)

6 Benthic marine ecosystems in the north-east Atlantic

6.1 Introduction

Descriptive marine ecological studies undertaken in offshore areas and in inshore areas of countries other than Great Britain in the north-east Atlantic (Figure 1) provide important information to:

- assist with the classification of marine habitats and communities of inshore areas in Great Britain, and
- compare against MNCR findings for Great Britain so as to provide a geographical context to the occurrence

Table 2 *(continued)*

SUBLITTORAL HABITATS

Inshore mud & sand	Inshore bedrock, boulders, artificial substrate and wrecks	Inshore crevices	Offshore seabed
Benthic Fishes	**Benthic Fishes**	**Benthic/Epibenthic Fishes**	**Benthic Fishes**
Squatina squatina	*Conger conger*	*Conger conger*	Rajidae
Rajidae	*Gaidropsarus vulgaris*	*Lepadogaster lepadogaster*	*Raja clavata*
Lophius piscatorius	*Raniceps raninus*	*Gaidropsarus vulgaris*	Scophthalmidae
Cepola rubescens	*Myoxocephalus scorpius*	*Molva molva*	*Psetta maxima*
Trachinus vipera	*Taurulus bubalis*	*Raniceps raninus*	*Scophthalmus rhombus*
Callionymidae	*Liparis liparis*	*Trisopterus luscus*	Bothidae
Gobiidae	*Gobius niger*	*Trisopterus minutus*	Pleuronectidae
Pomatoschistus minutus	*Gobius paganellus*	*Liparis liparis*	*Hippoglossus hippoglossus*
Limanda limanda	*Thorogobius ephippiatus*	*Centrolabrus exoletus*	*Microstomus kitt*
Pleuronectes platessa	*Zeugopterus punctatus*	*Crenilabrus melops*	*Pleuronectes platessa*
		Ctenolabrus rupestris	Soleidae
Epibenthic Fishes	**Epibenthic Fishes**	*Labrus bergylta*	*Solea solea*
Scyliorhinus canicula	*Molva molva*	*Labrus mixtus*	
Scyliorhinus stellaris	*Trisopterus luscus*	*Blennius ocellaris*	**Epibenthic Fishes**
Gadus morhua	*Trisopterus minutus*	*Parablennius gattorugine*	Gadidae
Melanogrammus aeglefinus	*Zeus faber*	*Anarhichas lupus*	*Gadus morhua*
Trisopterus luscus (juv.)	*Centrolabrus exoletus*	*Chirolophis ascanii*	*Melanogrammus aeglefinus*
Trispoterus minutus (juv.)	*Crenilabrus melops*	*Thorogobius ephippiatus*	*Merlangius merlangus*
Triglidae	*Ctenolabrus rupestris*	*Zeugopterus punctatus*	*Molva molva*
Mullus surmuletus	*Labrus bergylta*	*Balistes carolinensis*	*Merluccius merluccius*
Ammodytidae*	*Labrus mixtus*		
	Gobiusculus flavescens		
	Balistes carolinensis		

* Also present in the seabed

of habitats, communities and species and therefore of their importance at an international scale.

'Inshore' areas are taken as those encompassed within about 5 to 6 km offshore of low water on the open coast but may include more extensive areas within shallow (taken as less than 50 m deep) bays or inlets (for instance Cardigan Bay in west Wales, the Bristol Channel in south-west England) or enclosed by islands (for instance, The Minch in north-west Scotland). The historical importance of various studies undertaken outside Great Britain has been referred to in the Section 2. In the current section, special attention is given to the identification of recent sources of data describing marine habitats and communities comparable to those occurring in Great Britain. Review of the literature for areas outside of Great Britain has necessarily been less thorough than for our main study area.

Studies undertaken solely in the Baltic have not been included in detail as its special features make descriptions of the benthos less relevant for comparison with Great Britain.

A final section (6.21) gives a brief description of some Mediterranean literature.

6.2 The North Sea

Studies of the North Sea benthos in British waters can be said to have started with the work of Davis (1923, 1925) and Stephen (1923, 1933, 1934). Recent descriptions based on physical conditions and communities of species associated with those conditions were undertaken by Glémarec (1973), Dyer *et al.* (1983a), Basford & Eleftheriou (1988), Eleftheriou & Basford (1989) and Basford, Eleftheriou & Raffaelli (1989, 1990). Many of the papers describing North Sea benthos are included in the review of biological effects of human activities (Rees & Eleftheriou 1989). Künitzer *et al.* (1992) combined the results of benthos sampling undertaken in 1986 by participants of the Benthos Ecology Working Group of the International Council for the Exploration of the Seas (ICES) with the results of Eleftheriou & Basford (1989) to produce descriptions of the benthic infauna for the whole of the North Sea proper. There is a great deal of localised work undertaken in the region of oil exploration and production areas but usually described in limited-circulation reports (results published in the scientific literature include those of Addy *et al.* (1978), Hartley (1984) and Hartley & Bishop (1986)). The proceedings of an international symposium on the ecology of the North Sea held in May 1988 were published in Volume 25 (parts 1 & 2) of the *Netherlands Journal of Sea Research*. Most recently, the series of Assessment Reports contributing to the North Sea Quality Status Report (QSR) (Anonymous 1993) includes summaries of information on the biology of the North Sea.

The work of Glémarec (1973) is particularly important in describing sediment benthos in the North Sea. The distribution of infralittoral, coastal and open sea étages (Glémarec 1973) together with the major macrofaunal communities indicated by Kingston & Rachor (1982) is illustrated in Figure 17.

The term 'infralittoral' in the terminology of Glémarec (1973) can be confused with the 'infralittoral' of rocky substratum zonation where light penetration and consequent algal coverage determines its extent. Nevertheless, the étages of Glémarec have been widely used in describing level bottom (sediment) communities in the North Sea. The importance of depth and thermal stability is also suggested by later authors. For instance, studying epibenthic species, Dyer *et al.* (1983a) and Frauenheim *et al.* (1989) separate the North Sea benthic

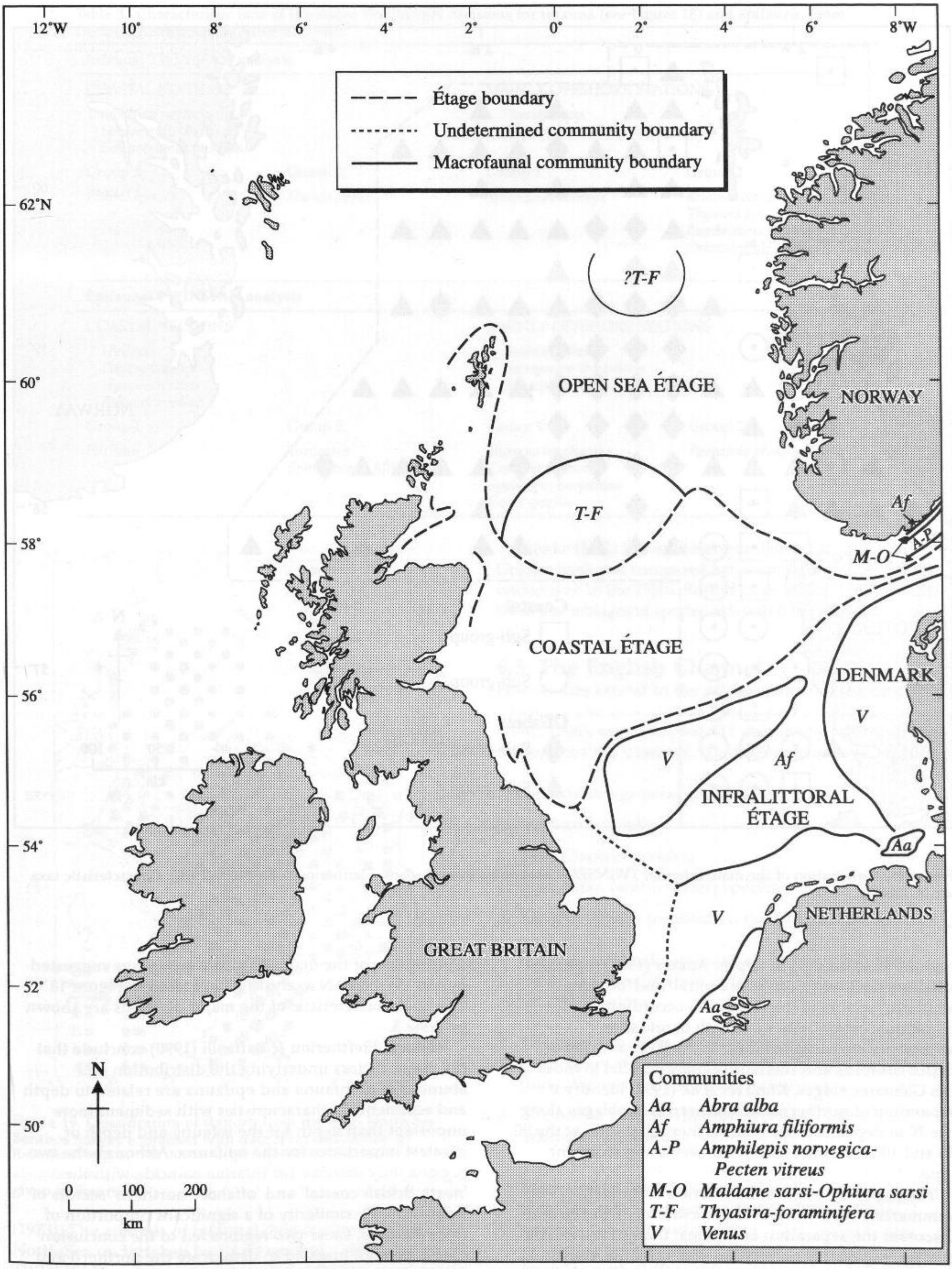


Figure 17. The distribution of infralittoral, coastal and open sea étages and of major macrofaunal communities in the North Sea. (After Glémarec 1973 and Kingston & Rachor 1982. Re-drawn from Mitchell 1987.)

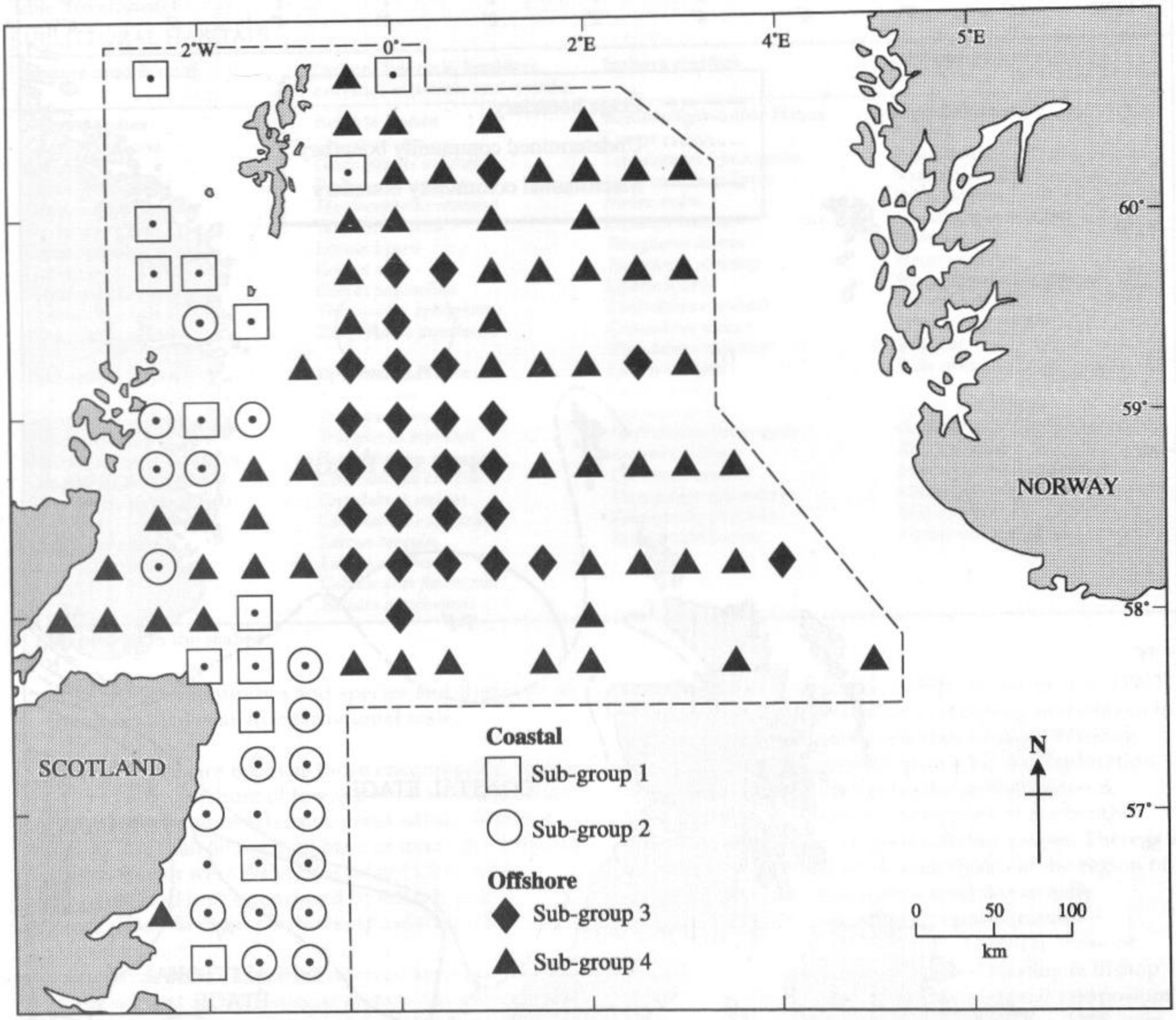


Figure 18. Distribution of the main infaunal TWINSPAN groupings from Basford, Eleftheriou & Raffaelli (1990). Characteristic taxa are in Table 3.

regions at around 50 m depth. Adams (1987) separates 'offshore northern', 'offshore central' and 'offshore southern' sectors of the North Sea according to planktonic communities but with boundaries approximately corresponding to the 50 m and 100 m depth contours and therefore closely parallel to those of the Glémarec étages. Künitzer *et al.* (1992) identify a separation of northern and southern assemblages along the 70 m depth contour with further separation at the 30, 50 and 100 m depth contours as well as by sediment type.

The paper by Basford, Eleftheriou & Raffaelli (1990) summarises their work in the northern North Sea and discusses the separation of regions. Using TWINSPAN analysis separately on infauna and epifauna, they describe the main groupings including separation of coastal and offshore stations for infauna. The distribution of the major faunistic groupings suggested by the TWINSPAN analysis is illustrated in Figure 18. The taxa characteristic of the major divisions are shown in Table 3.

Basford, Eleftheriou & Raffaelli (1990) conclude that the major factors underlying the distribution and abundance of infauna and epifauna are related to depth and sedimentary characteristics with sediment more important than depth for the infauna and depth of greatest importance for the epifauna. Although the two regions they describe for infauna coincide with the 'north British coastal' and 'offshore northern' sectors of Adams (1987), similarity of a significant proportion of the infauna in those two regions led to the conclusion that it was not justified to demarcate the northern and central parts of the North Sea at the 100 m depth contour in the manner of Adams (1987) or Glémarec

Table 3. Characteristic taxa of the major TWINSPAN divisions for infauna (see Figure 18) and epifauna. From Basford, Eleftheriou & Raffaelli (1990).

Infaunal TWINSPAN analysis			
COASTAL STATIONS		MAINLY OFFSHORE STATIONS	
Ophelina neglecta *Sphaerosyllis bulbosa* *Echinocyamus pusillus*		*Thyasira* spp. *Prionospio mulibranchiata*	
Group 1	Group 2	Group 1	Group 2
Pisione remota	*Nucula tenuis*	*Spiophanes bombyx*	*Eriopisa elongata* *Thyasira* spp. *Lumbrineris gracilis* *Ceratocephale loveni*
Epifaunal TWINSPAN analysis			
COASTAL STATIONS		MAINLY OFFSHORE STATIONS	
Porifera *Flustra foliacea* *Hyas coarctatus* *Bolocera tuediae*		*Asterias rubens* *Astropecten irregularis* *Brissopis lyrifera*	
Group 1	Group 2	Group 1	Group 2
Porifera	Tunicates *Spirontocaris lilljeborgi*	*Pagurus bernhardus* *Crangon allmanni* *Spatangus purpureus* *Colus gracilis*	*Pennatula phosphorea*

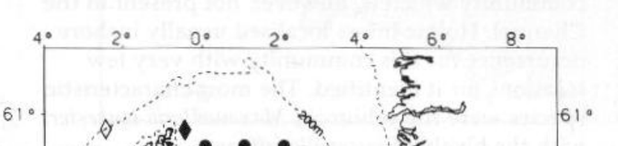


Figure 19. Classification of stations from the ICES North Sea Benthos Survey combined with data from Eleftheriou & Basford (1989) by TWINSPAN, incorporating species abundances. (From Künitzer *et al.* 1992.) Indicator species are given in Figure 20.

(1973). The analysis of infaunal data for the whole of the North Sea undertaken by Künitzer *et al.* (1992) also used TWINSPAN and came to somewhat different conclusions regarding the species assemblages which could be identified (Figures 19 & 20).

Krönke (1992) has undertaken a detailed study of the Dogger Bank and compared her results with those of work undertaken in the 1950s. Results from 1985 to 1987 revealed three assemblages of species illustrated in Figure 21.

6.3 The English Channel

Few studies extend to the offshore areas of the English Channel. The most detailed undertaken is that of Holme (1961, 1966), who sampled 311 stations by anchor dredge throughout the Channel. He differentiated species into:

1. those with a general distribution;
2. western species;
3. west Channel species;
4. Cornubian (warm water) species;
5. Sarnian species (centred on the Channel Isles).

The seven animal communities he identified were based on the classification of Jones (1950), and are summarised below.

1. The boreal shallow-sand association. A shallow water community with *Arenicola marina*, *Nephtys* sp., *Tellina* (now *Angulus*) *tenuis*, *Donax vittatus*, etc.
2. The boreal shallow-mud association. Petersen's '*Macoma*' community.
3. The boreal offshore-sand association. Petersen's '*Venus*' community. Characteristic molluscs and echinoderms include *Cardium echinatum*, *Dosinia lupinus*, *Venus striatula*, (now *Chamelea gallina*), *Gari fervensis*, *Abra prismatica*, *Echinocardium cordatum* and *Acrochnida brachiata*, with *Callista chione*, *Tellina* (now *Fabulina*) *fabula*, *Mactra corallina* (now *Mactra stultorum*) and *Ensis siliqua* mainly confined to shallow parts.

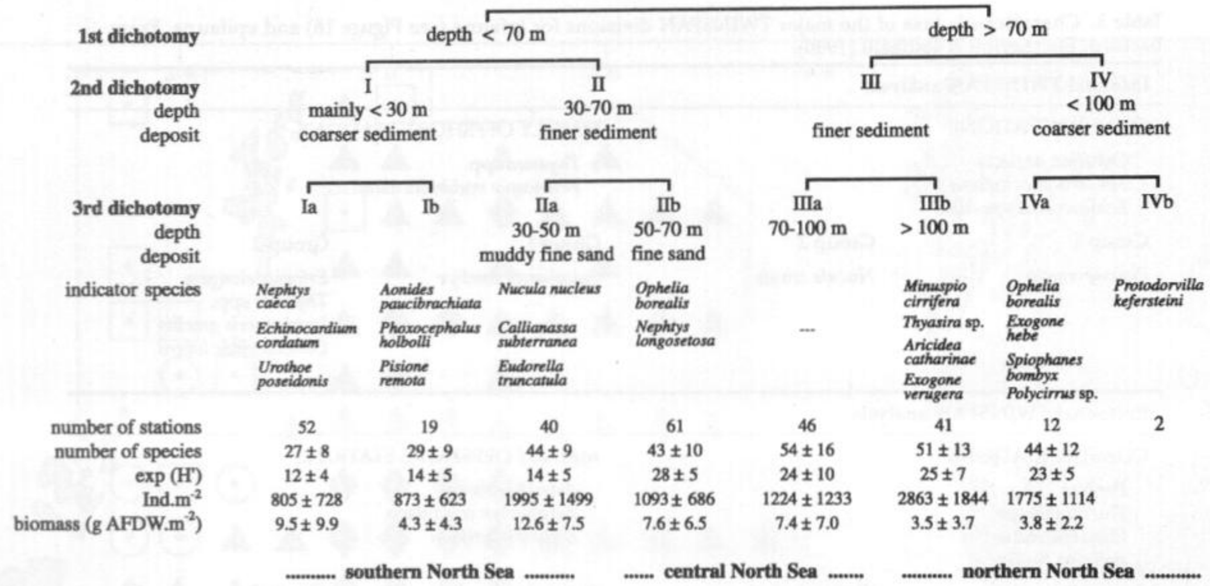


Figure 20. TWINSPAN classification incorporating species abundance data. (Adapted from Künitzer *et al.* 1992.)

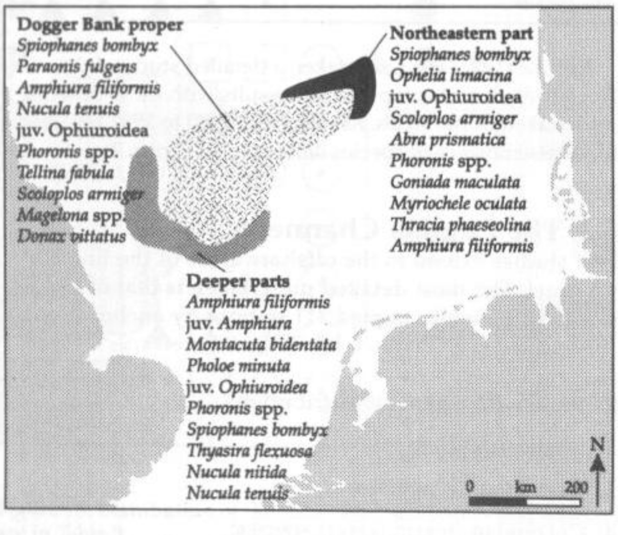


Figure 21. Macrofaunal communities in 1985 to 1987 on the Dogger Bank. The ten numerically dominant species from each of three groupings identified by cluster analyses are listed. Based on Krönke 1992.

4. Boreal offshore muddy-sand association. Petersen's '*Echinocardium cordatum-Amphiura filiformis*' community and '*Abra*' community. Typical species include: *Nucula turgida, Cyprina* (now *Arctica*) *islandica, Cardium echinatum, Dosinia lupinus, Abra alba, Abra prismatica, Phaxas pellucidus, Ensis ensis, Spisula subtruncata, Lutraria lutraria, Corbula gibba, Dentalium* (now *Antalis*) *entalis, Aporrhais pespelecani, Philine quadripartita, Callianassa subterranea, Ophiura texturata* (now *Ophiura ophiura*), *Amphiura filiformis, Echinocardium cordatum, Cucumaria elongata, Leptosynapta inhaerens* and *Labidoplax digitata*.

5. Boreal offshore mud association. Corresponds to Petersen's '*Brissopsis lyrifera-Amphiura chiajei*' community which is, however, not present in the Channel. Holme infers localised usually inshore occurrence for this community with very few locations for it identified. The most characteristic species were the echiuroid *Maxmuelleria lankesteri* with the bivalve *Saxicavella jeffreysi*.

6. Boreal offshore gravel association. Characteristic species include *Nucula hanleyi, Glycymeris glycymeris, Venus* (now *Circomphalus*) *casina, Venus* (now *Timoclea*) *ovata, Venerupis* (now *Tapes*) *rhomboides, Gari tellinella, Ensis arcuatus, Spisula elliptica, Lutraria angustior, Echinocyamus pusillus, Echinocardium flavescens, Spatangus purpureus, Amphioxus* (now *Branchiostoma*) *lanceolatus*. Often associated with beds of the brittlestar *Ophiothrix fragilis* on harder ground.

7. Boreal offshore muddy-gravel association. (Not recognised by Jones 1950.) Commonest species are certain burrowing crustacea, particularly *Upogebia deltaura, Upogebia stellata* and more rarely *Squilla* (now *Meiosquilla*) *desmaresti*. Molluscs include *Nucula nucleus, Venus verrucosa, Turritella communis* and *Gibbula magus*. There are also the sipunculid worms *Golfingia elongata* and *Golfingia vulgaris*, species of the holothurian *Thyone* and the burrowing sea anemone *Mesacmaea mitchelli*.

The distribution of the communities described by Holme (1966) is illustrated in Figure 22. Holme also recognised a number of faunistic boundaries in the Channel including separation of the Channel Isles fauna from that of the English side of the Channel and of abrupt boundaries associated with headlands, particularly Start Point, St Alban's Head and the Cotentin Peninsula with the main faunistic boundary identified with the boundary between the summer-stratified waters of the western Channel with the unstratified waters of the eastern Channel. A further

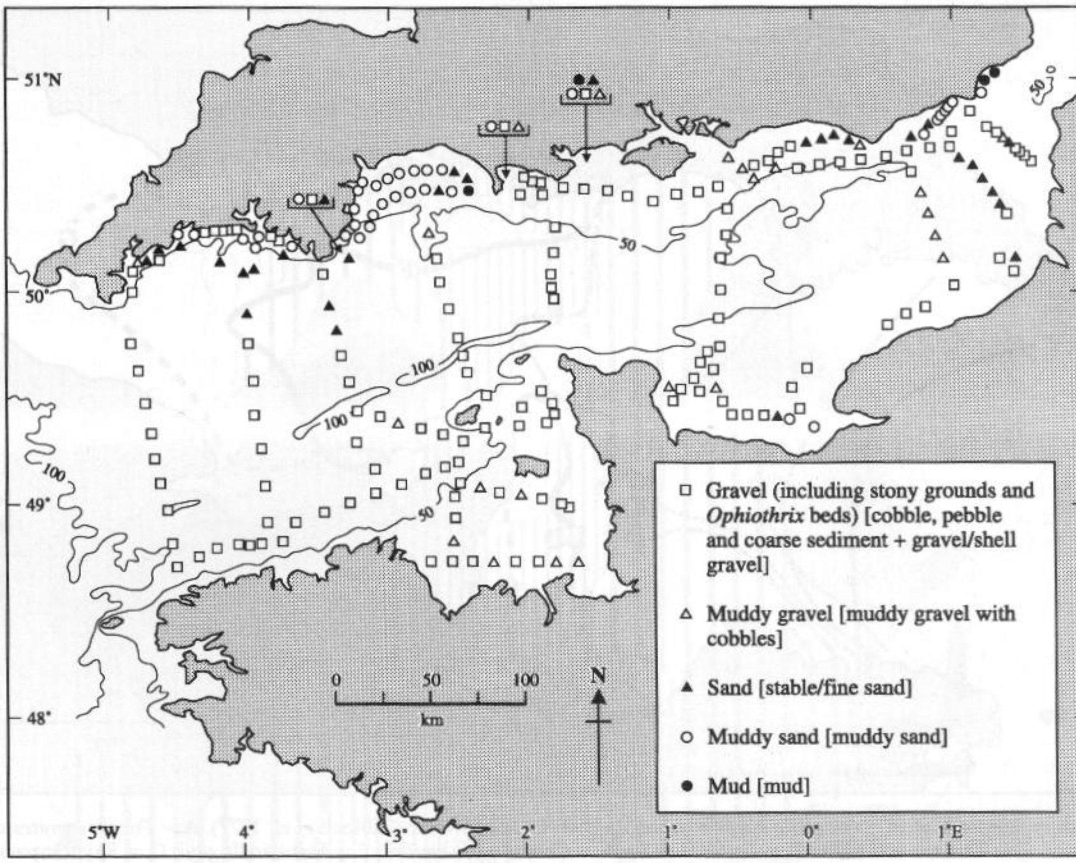


Figure 22. Distribution of benthic communities in the English Channel. (Re-drawn from Holme 1966.)

boundary area is suggested off Looe in Cornwall. The samples collected by Holme (1966) were further studied for their bryozoan populations by Grant & Hayward (1983), who identified three distinct assemblages characterised as 'shallow', 'intermediate' and 'deep'.

Cabioch *et al.* (1977) used the results of dredge sampling to indicate distribution of hard substratum species in the English Channel (Figure 23). Offshore areas of the English Channel were further investigated using towed video and still cameras by Holme & Wilson (1985). The area studied, about 37 km south of the Dorset coast, was predominantly of hard substrata often with transitory sand cover. The epifaunal assemblages encountered were separated into:

Type A		Stable faunal assemblage with diverse sponge cover;
Type B	B1	Well developed faunal assemblage with *Polycarpa violacea*
	B2	Impoverished *Polycarpa violacea – Flustra foliacea* assemblage
	B3	Impoverished *Balanus – Pomatoceros* assemblage;
Type C		Cobble floor covered by sand.

6.4 The Celtic Sea

The Celtic Sea is the area to the south of Ireland and west of Cornwall in south-west England. The most extensive published survey of the benthic fauna of the Celtic Sea is that undertaken in 1974 and 1975 by the Field Studies Council Oil Pollution Research Unit (Hartley & Dicks 1977; Hartley 1979). The fauna at most sites was typical of a 'deep *Venus* community' as described by Mackie (1990) and included in the next section. At the edge of the Celtic Deep, the communities were typical of a 'boreal deep mud association' and included the brittlestars *Amphiura chiajei* and *Amphiura filiformis*, the bivalves *Nucula sulcata, Nucula tenuis, Thyasira flexuosa* and *Abra nitida*, and polychaetes *Myriochele heeri*, *Lagis* (now *Pectinaria*) *koreni* and *Amphicteis gunneri*. Bryozoan species occurring on hard substratum in depths of 159 to 1582 m are recorded by Hayward & Ryland (1978).

6.5 The Irish Sea

Published and unpublished information on the offshore sediment macrofaunal benthic communities of the Irish Sea are brought together and their distribution mapped by Mackie (1990) (Figure 24). Nine separate community types are noted:

1. The *Amphiura* community [the 'Boreal offshore muddy sand association' of Jones 1950] present in offshore sandy muds at shallow to moderate depths (15 m to 100 m) and typically including the brittle-star *Amphiura filiformis*, the urchin *Echinocardium cordatum* and the tower shell *Turritella communis*.

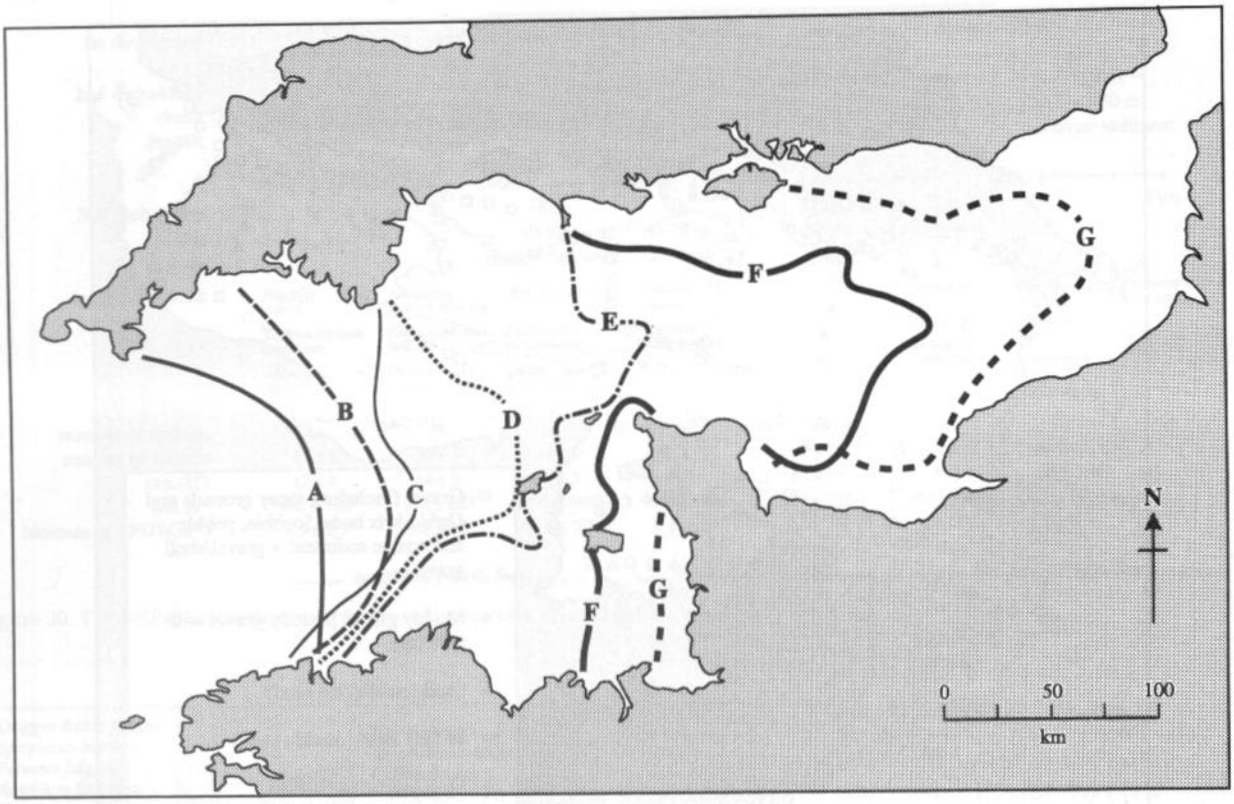


Figure 23. Eastern boundaries of epibenthic species in the English Channel (from Cabioch *et al.* 1977). A = *Porella compressa;* B = *Diphasia pinaster;* C = *Thuiaria articulata;* D = *Lafoea dumosa;* E = *Caryophyllia smithii;* F = *Sertularella gayi:* G = *Rhynchozoon bispinosum.*

2. The *Brissopsis* community [the 'Boreal offshore mud association' of Jones 1950] present in offshore muds at shallow to moderate depths (15 m to 100 m) and typically including the urchin *Brissopsis lyrifera* and the brittle-star *Amphiura chiajei.*
3. The *Abra* community [included in the 'Boreal offshore muddy sand association' of Jones 1950] present in shallow (5 m to 30 m) nearshore muddy sands/muds with rich organic content and typically including the bivalve mollusc *Abra alba* and the polychaete worm *Pectinaria koreni.*
4. The Shallow *Venus* community [the 'Boreal offshore sand association' of Jones 1950] present in shallow (5 m to 40 m) nearshore sands. There are two sub-communities. The '*Tellina* sub-community' occurs in fine sands and typically includes the bivalve *Tellina* (now *Fabulina) fabula* and the polychaete *Magelona mirabilis.* The *Spisula* sub-community occurs in medium to coarse sands subject to disturbance and typically includes the bivalve *Spisula elliptica* and the polychaete *Nephtys cirrosa.*
5. The Deep *Venus* community [the 'Boreal offshore gravel association' of Jones 1950] occurs in coarse sand/gravel/shell sediments at moderate depths (40 m to 100 m) and typically includes the urchin *Spatangus purpureus* and the bivalves *Glycymeris glycymeris, Astarte sulcata* and *Venus* spp.
6. The muddy-gravel community [referred to in relation to the 'Boreal offshore muddy-gravel association' of Holme (1966)] includes very rich faunas from mixed muddy gravels.
7. The *Modiolus* community [part of the 'Boreal offshore gravel association' of Jones 1950] occurs on coarse sand/gravel or shell/stone substrata at moderate depths and typically includes the horse mussel *Modiolus modiolus* and the brittle-star *Ophiothrix fragilis* and the mussel clumps attract a rich fauna.
8. Hard substratum communities.

Mackie, Oliver & Rees (1995) describe the results of further sampling undertaken in 1989 and 1991. They conclude that the southern Irish Sea can be said to be part of the boreal zoogeographical province but with more southern lusitanian influences in area of the Celtic Deep at the southern entrance to the Irish Sea. They identify a mosaic of loose overlapping assemblages with three major types corresponding to general sediment distribution:

1. Assemblage A occurred in the deeper mud and sandy mud regions.
2. Assemblage B was found in the inshore sandy and muddy sand areas.
3. Assemblage C coincided with the offshore gravely sediments.

The frontal systems in the Irish Sea (Pingree & Griffiths 1978; Figure 7) are important areas for plankton productivity and for the marine species which

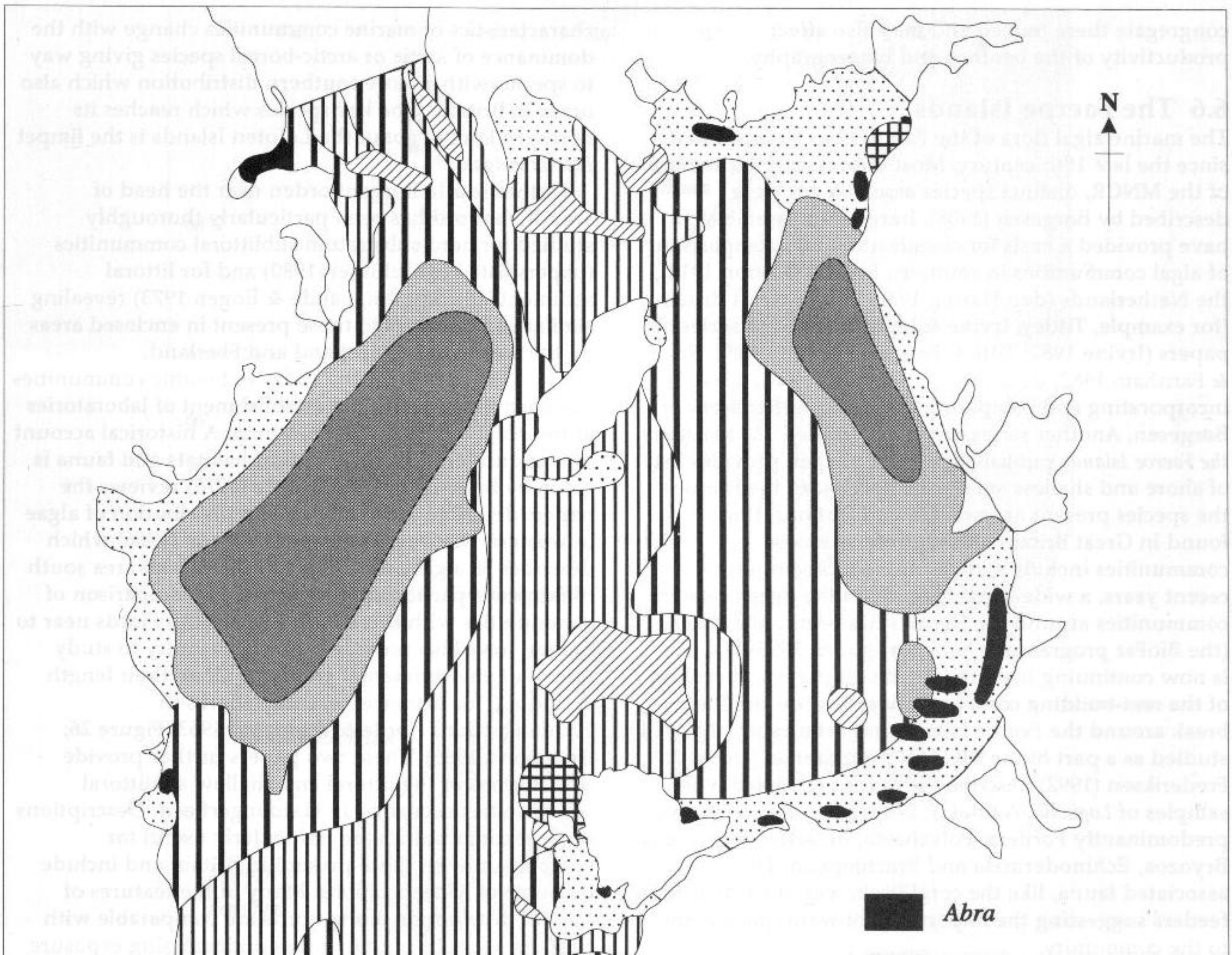


Figure 24. Generalised distribution of macrobenthic communities in the Irish Sea. (From Mackie 1990.)

congregate there to feed and may also affect productivity of the benthos and biogeography.

6.6 The Faeroe Islands

The marine algal flora of the Faeroes has been studied since the late 18th century. Most importantly for the use of the MNCR, distinct species assemblages were described by Børgesen (1908). Børgesen's assemblages have provided a basis for classification and comparison of algal communities in southern Ireland (Cotton 1912), the Netherlands (den Hartog 1959) and in Great Britain (for example, Tittley, Irvine & Jephson 1976). A series of papers (Irvine 1982; Tittley, Farnham & Gray 1982; Price & Farnham 1982) describe the seaweeds of the Faeroes incorporating and comparing the much earlier work of Børgesen. Another series of papers entitled *The zoology of the Faeroe Islands* published in Copenhagen provides lists of shore and shallow sublittoral species. In the Faeroes, the species present are, with few exceptions, those found in Great Britain although the Faeroese communities include a lower number of species. In recent years, a wide-ranging study of the deeper water communities around the Faeroes has been undertaken (the BioFar programme: Nörrevang *et al.* 1996) and this is now continuing inshore. The distribution and ecology of the reef-building coral *Lophelia pertusa* on the shelf break around the Faeroe Islands has been especially well studied as a part of the BIOFAR programme. Jensen & Frederiksen (1992) describe the fauna associated with samples of *Lophelia*. A total of 298 species was recorded, predominantly Porifera, Polychaeta, Bivalvia, Crustacea, Bryozoa, Echinodermata and Brachiopoda. The associated fauna, like the coral itself, was of suspension feeders suggesting the importance of water movement to the community.

6.7 Norway

The coastline of Norway (Figure 25) extends from about 58°N to 71°N and, at just north of 60°N, Bergen is on the same latitude as Lerwick in Shetland. Much of the coastline is exposed to very strong wave action but fjords and offshore islands create many very extensive wave-sheltered areas. Studies of marine biology in Norway extend back into the early 19th century with the pioneering work of Michael Sars. Much of this historical work is referred to in the review given by Gislén (1930) and in Brattström (1967).

Little published descriptive survey work has been undertaken between Tromsø and Trondheim along the northern part of the Norwegian coastline. However, communities recorded from a submarine gully near to Tromsø (Gulliksen 1978) are very similar to those in such gullies in Britain. Other studies by Holte & Gulliksen (1987) on sediment communities and by Jakola & Gulliksen (1987) on hard substratum communities on jetty pilings provide further comparative data from the Tromsø area. The species living in sediments are similar to those which would be encountered in similar situations in Great Britain. However, the most abundant large species found on jetty piles were arctic or arctic boreal; for instance, the ascidians *Styela rustica*, *Ascidia callosa* and *Halocynthia pyriformis*. South of Tromsø, the characteristics of marine communities change with the dominance of arctic or arctic-boreal species giving way to species with a more southern distribution which also occur in Britain. One key species which reaches its northern limit at about the Lofoten Islands is the limpet *Patella vulgata*.

Farther south, Borgenfjorden near the head of Trondheimfjord has been particularly thoroughly studied for hard substratum sublittoral communities (papers listed in Gulliksen 1980) and for littoral sediments (Strömgren, Lande & Engen 1973) revealing similar communities to those present in enclosed areas on the west coast of Scotland and Shetland.

The main centre for the study of benthic communities has been Bergen with the establishment of laboratories at the coast by the Bergen museum. A historical account of work undertaken there and of habitats and fauna is given by Brattström (1967). Jorde (1975) reviews the papers describing the ecology and distribution of algae in western Norway. The paper by Jorde (1966) which describes 38 algal associations in the coastal area south of Bergen is particularly important for comparison of communities with those found in Britain. Fjords near to Bergen have also provided the opportunity to study effects of environmental gradients along their length including, for instance, on rocky shores in Hardangerfjord (Jorde & Klavestad 1963, Figure 26; Brattegard 1966). These two papers further provide descriptions of the littoral and shallow sublittoral communities occurring in Hardangerfjord. Descriptions of algal communities are particularly useful for comparison with those present in Britain and include accounts of 25 associations. Many of the features of species distribution along fjords are comparable with those in sealochs both in terms of decreasing exposure to wave action and where large volumes of freshwater enter at the head of the inlet. Tunberg (1982) describes the communities of Raunefjorden near Bergen. The two communities (characterised by the molluscs *Thracia villosiuscula* and *Dosinia borealis* and by *Lucinoma borealis* and *Thyasira flexuosa*) described from there may be of particular interest as they do not correspond to any of those described by Thorson (1957). On the open coast here, marine communities include many more Arctic elements than in British waters at the same latitude. For example, the sea urchin *Echinus acutus* has not yet been recorded in British coastal waters but is abundant in shallow depths near Bergen and *Strongylocentrotus droebachiensis* is extremely abundant in Norway compared with the isolated populations of Shetland.

The fjords of western Norway provide opportunities for the study of deep isolated environments and Brattström (1967) comments that there must be few places where one sails inland to sample the deep-sea fauna. The communities present include ones characterised by the pogonophoran *Siboglinum ekmani* with large foramaniferans present (Brattegard 1967) as well as communities associated with the reef-forming coral *Lophelia pertusa* (Tambs-Lyche 1958). Sognfjord, with a maximum depth of 1,300 m, includes a deep sea fauna similar to that of the north-western Mediterranean (Carpine 1970). Although not occurring in inshore waters in Britain, some of these communities

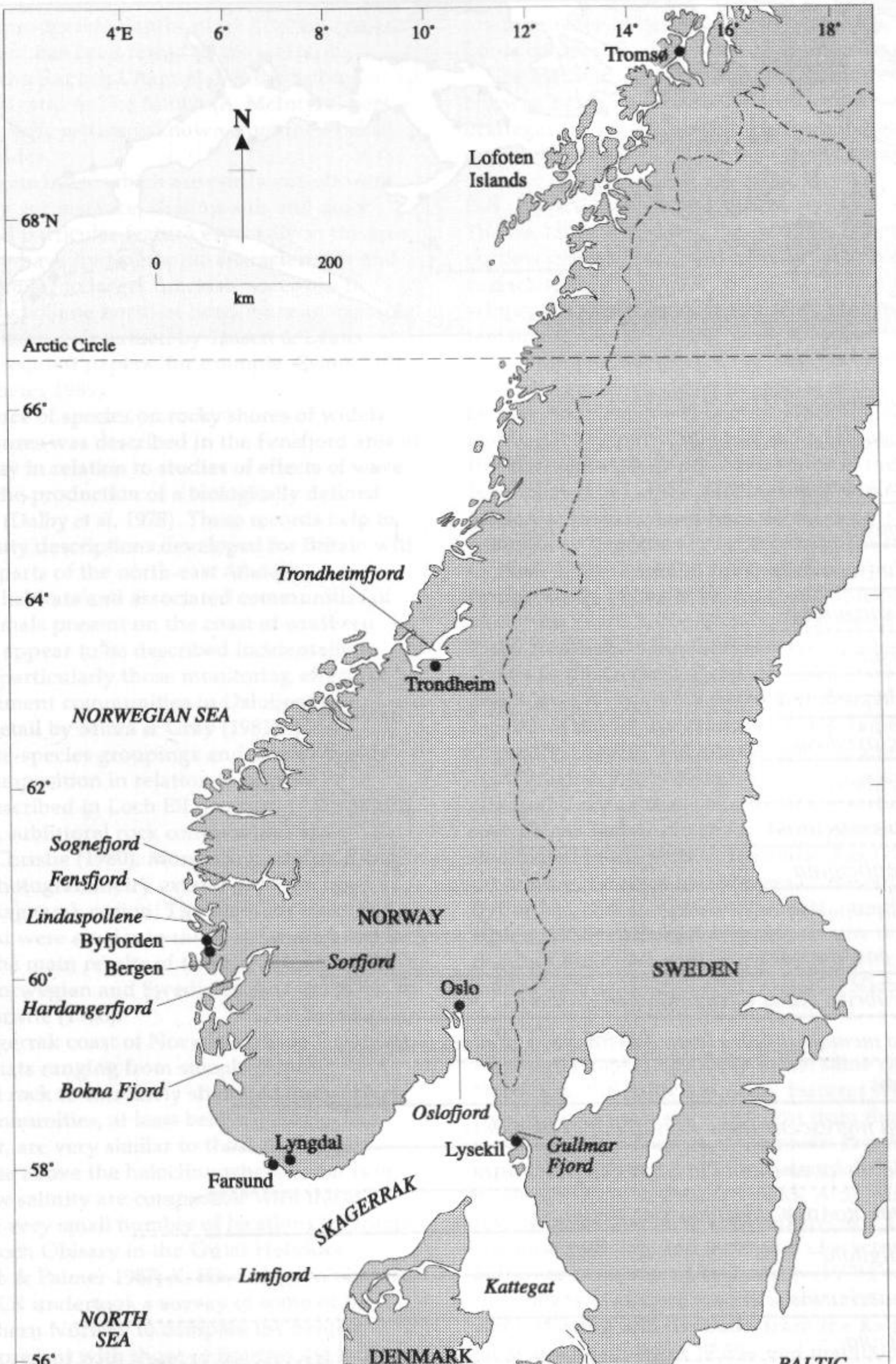


Figure 25. Norway, Sweden and Denmark, showing locations of places mentioned in the text.

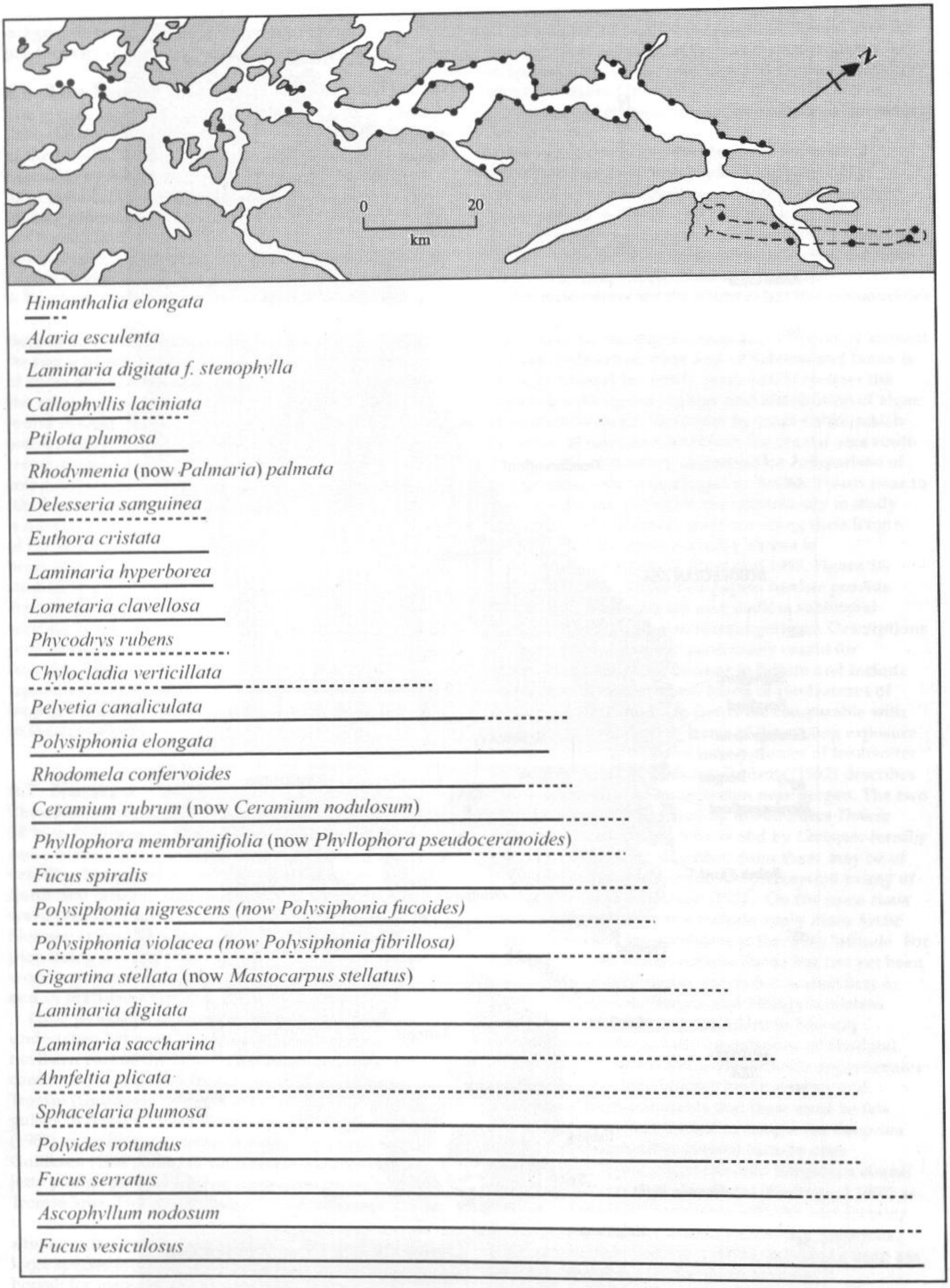


Figure 26. The horizontal distribution of selected species in Hardangerfjord and Sörfjord. (From Jorde & Klavestad 1963.)

may occur at considerable depths off the British coasts. *Siboglinum ekmani* has been found in the western approaches to the English Channel (Southward & Southward 1958) and in The Minch (A. McIntyre, pers. comm.) and *Lophelia pertusa* is known from the Rockall Bank and Hebrides.

Polls are marine inlets which are partly cut-off from the open sea by, for instance, shallow sills and are a widespread and particular feature especially in the area of Bergen. They have hydrographic characteristics and communities similar to larger brackish water obs in Scotland. Lindaspollene north of Bergen are an example of this type of habitat described by Taasen & Evans (1977) and subsequent papers (for example, Evans 1981, Taasen & Høisaeter 1989).

The abundance of species on rocky shores of widely different exposures was described in the Fensfjord area of western Norway in relation to studies of effects of wave exposure and the production of a biologically defined exposure scale (Dalby *et al.* 1978). These records help to relate community descriptions developed for Britain with those in other parts of the north-east Atlantic.

The marine habitats and associated communities of plants and animals present on the coast of southern Norway often appear to be described incidentally to other studies, particularly those monitoring effects of pollution. Sediment communities in Oslofjord are described in detail by Mirza & Gray (1981). They describe six site-species groupings and similar trends and species composition in relation to organic enrichment described in Loch Eil (Pearson 1975). Within the same area, sublittoral rock communities are described by Christie (1980). Monitoring studies using underwater photogrammetry extend onto the open coast in the Skaggerak region. The methods used and species studied were similar to those of Swedish workers and some of the main results of these studies from 22 sites on the Norwegian and Swedish coasts are given by Lundälv & Christie (1986).

On the Skagerrak coast of Norway outside Oslofjord, there are habitats ranging from steeply sloping wave-exposed rock to extremely sheltered inlets. Here, sublittoral communities, at least below the halocline where present, are very similar to those in Scottish sealochs. Those above the halocline where water is of variable or low salinity are comparable with those occurring in a very small number of locations in Britain; for instance Loch Obisary in the Outer Hebrides. (Dipper, Lumb & Palmer 1987; K. Hiscock pers. obs.). In 1991, the MNCR undertook a survey of some of the fjords in southern Norway to compare the benthic communities present with those of Scottish sea lochs (Connor 1991). Rocky intertidal communities were very restricted in extent due to small tidal range but also less rich than in Scottish sea loch most likely as a result of low salinity conditions. There were also considerable differences in sublittoral communities with bryozoans, fish, sponges and calcareous tubeworms better represented in the fjords but crustaceans, molluscs, hydroids and burrowing anemones less well represented. In general, the variety of sublittoral habitats in the fjords was less than in Scottish sea lochs mainly owing to lack of tidal currents and the predominance of bedrock habitats in the upper 50 m of fjords compared with the more varied substrata in lochs.

The distribution of marine species along the coast of Norway has been recorded and mapped (described in Brattegard & Holthe 1995) by gathering data from marine laboratories, field workers and taxonomists.

6.8 Sweden – west coast

The Swedish west coast (Figure 25) is affected by the outflow of water from the Baltic and the salinity of surface waters commonly drops to 10‰, although salinity below the halocline at 10 m to 15 m depth remains above 30‰. Rosenberg & Möller (1979) describe how sediment macrofaunal communities below the halocline are much richer in species and have a higher biomass than shallower communities subject to reduced and variable salinity. Much of the work undertaken in this part of Sweden and of relevance to the MNCR has been carried out at the Kristinebergs Marine Zoology Station at Lysekil. From here, Molander (1928) tested the community hypothesis of Petersen by his studies in the Gullmar Fjord. Later, in 1962, Molander published a further study of the sediment communities in fjords along this coast. Some of the earliest descriptions of rocky sublittoral communities were those undertaken by Gislén in the Gullmar Fjord and published in 1930. Much later, a programme aimed at describing dynamic aspects of marine communities in the same area started (Lundälv, Larsson & Axelsson 1986). Svane & Gröndahl (1988) revisited the sites surveyed by Gislén (1930) and, although finding that the downward vertical extent of macroalgae had diminished, the deeper animal-dominated fauna were very similar. Rex (1975), describing the algal assemblages in the eutrophicated Byfjorden, also compares them with samples taken by Gislén (1930) and obtained substantially different results. Other observations by diving which describe marine communities include those of Michanek (1967).

6.9 The Baltic

Although biogeographically in the same region as the North Sea, the Baltic has many features which make communities there very different from those widely encountered in the rest of the north-east Atlantic; especially with regard to low salinity and the de-oxygenation of deeper waters. A country-by-country review is not therefore undertaken here. The physical, chemical (salinity) and biological characteristics of the Baltic are summarised by Jansson (1978), who notes that the salinity of surface waters is about 6‰ to 7‰ with water flowing into the Baltic from the Kattegat having an average salinity of 17.5‰ and maintaining the salinity of deep water at about 11‰. Shallow rocky areas are dominated by filamentous algae and *Fucus vesiculosus* whereas sediment areas, particularly in the south, are extensively covered by seagrass *Zostera marina.* Jansson (1978) gives numbers of macroscopic species recorded from various parts of the Baltic and the inner limits of marine and brackish water species (summarised from Segerstråle 1957; Figure 27). Eighty-eight species are recorded in the central Baltic compared with 1,500 in the east of the Skagerrak. Andersin, Lassig & Sandler (1977) describe the sediment

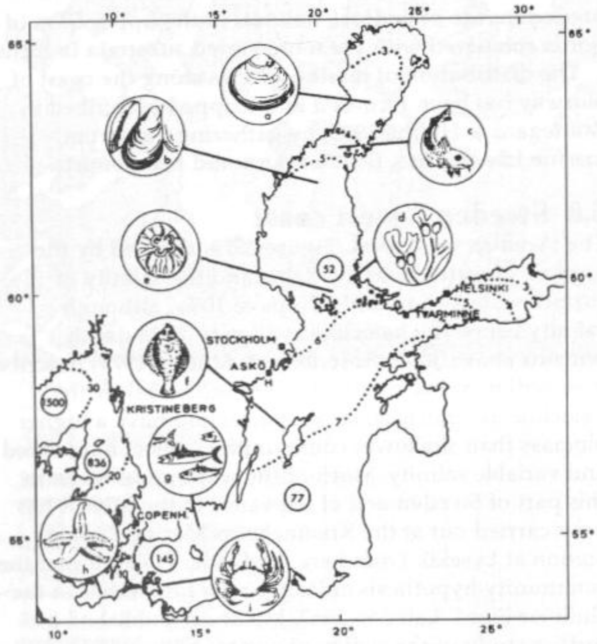


Figure 27. Numbers of macroscopic animals (in circles), salinity (dotted lines) and the innermost limit of some marine species in the Baltic. a = Baltic tellin *Macoma balthica*; b = mussel *Mytilus edulis*; c = cod *Gadus morhua*; d = bladderwrack *Fucus vesiculosus*; e = moon jellyfish *Aurelia aurita*; f = plaice *Pleuronectes platessa*; g = mackerel *Scomber scombrus*; h = common starfish *Asterias rubens*; i = shore crab *Carcinus maenas*. (From Jansson 1978.)

communities in the Baltic. In deep water, below about 60 m, the sediments switch between aerobic and anaerobic states and prolonged periods of deoxygenation occur, exacerbated by eutrophication. Inputs of pollutants to a sea where residence time of the water is 25 to 40 years is a therefore serious problem. Shallow rocky sublittoral communities in the north of the Baltic are described by Jansson & Kautsky (1977). Olenin (in press) summarises information on benthic zonation in the Baltic and describes the southern Baltic in more detail. Kiel Bay and the adjacent Lübeck Bay in the south-western Baltic are described and considered relatively rich in species compared with the rest of the Baltic (Rosenberg 1980). Lübeck Bay in the south-west was the location for the use of an underwater laboratory from which Gulliksen (1977) described the fauna of rocks and boulders. Here, rocks were dominated by the ascidian *Dendrodoa grossularia* and the polychaete worm *Polydora ciliata*, both species found in low salinity in Great Britain.

Baltic marine biologists are currently developing a marine habitat classification for HELCOM with a broadly similar structure to the MNCR classification (EC Nature 1996).

6.10 Denmark

The coast of Denmark (Figure 25) is markedly different from west to east. The west coast is predominantly sandy and, south of Esbjerg, is part of the Wadden Sea. To the east, in the Kattegat at the entrance to the Baltic, there are large and small islands virtually blocking the entrance to the Baltic. The seabed here is predominantly sedimentary and shallow areas are extensively covered by seagrass *Zostera marina*. However, areas of hard substratum occur in the form of glacial boulder dumps. The Limfjord, which cuts through Denmark from west to east, is a large (1,500 km^2) shallow inland sea connected by narrow entrances to the North Sea and Kattegat.

It was off the coast of Denmark that C.G.J. Petersen undertook his classic studies sampling the seabed to describe the communities present there (introduced in Petersen & Jensen 1911, summarised in Petersen 1915, 1918, 1924). Petersen's initial intention was to obtain samples to calculate the quantity of fish food available to bottom-living fish but he soon recognised distinct species groupings which occurred over large areas. His work was mainly in the Kattegat and detailed maps of community distribution there were presented. An '*Echinocardium–Filiformis*' community is illustrated in Figure 28.

The communities described by Petersen (1918) for areas off Denmark are listed below.

I The *Macoma* or Baltic community

II The *Abra* community

III The *Venus* community

IV The *Echinocardium–Filiformis* community

V The *Brissopsis–Chiajei* community

VI The *Brissopsis–Sarsii* community

VII The *Amphilepis–Pecten* community

VIII The *Haploops* community

[IX The deep *Venus* community]

Petersen also described the fauna associated with beds of *Zostera marina*.

The communities identified by Petersen have been described in a wide range of studies around the coast of Great Britain and the Petersen approach continues to be used today in naming sediment communities.

Petersen's work in Denmark was followed by that undertaken by Blegvad (1922, 1928, and 1930) for the southern part of the North Sea, Limfjord and the Kattegat respectively. The stations sampled by Petersen in the Kattegat in 1911–12 were sampled again using similar techniques (Pearson, Josefson & Rosenberg 1985) and significant changes attributed mainly to eutrophication are described (for instance Figure 29). Although predominantly sedimentary, the Kattegat includes 'stone reefs'; stones and boulders deposited during the ice age. These hard substrata are colonised by epibiota and the algae are described for the Tønneberg Banke by Nielsen (1991). Her records also compare the species present in the late 1980s with those collected at the same locality by Professor L.K. Rosenvinge 75 to 100 years ago. Although there were differences in species composition, species richness was similar and there was little effect from eutrophication. The predominantly remote sampling techniques used in the Kattegat missed the discovery and description of carbonate-cemented

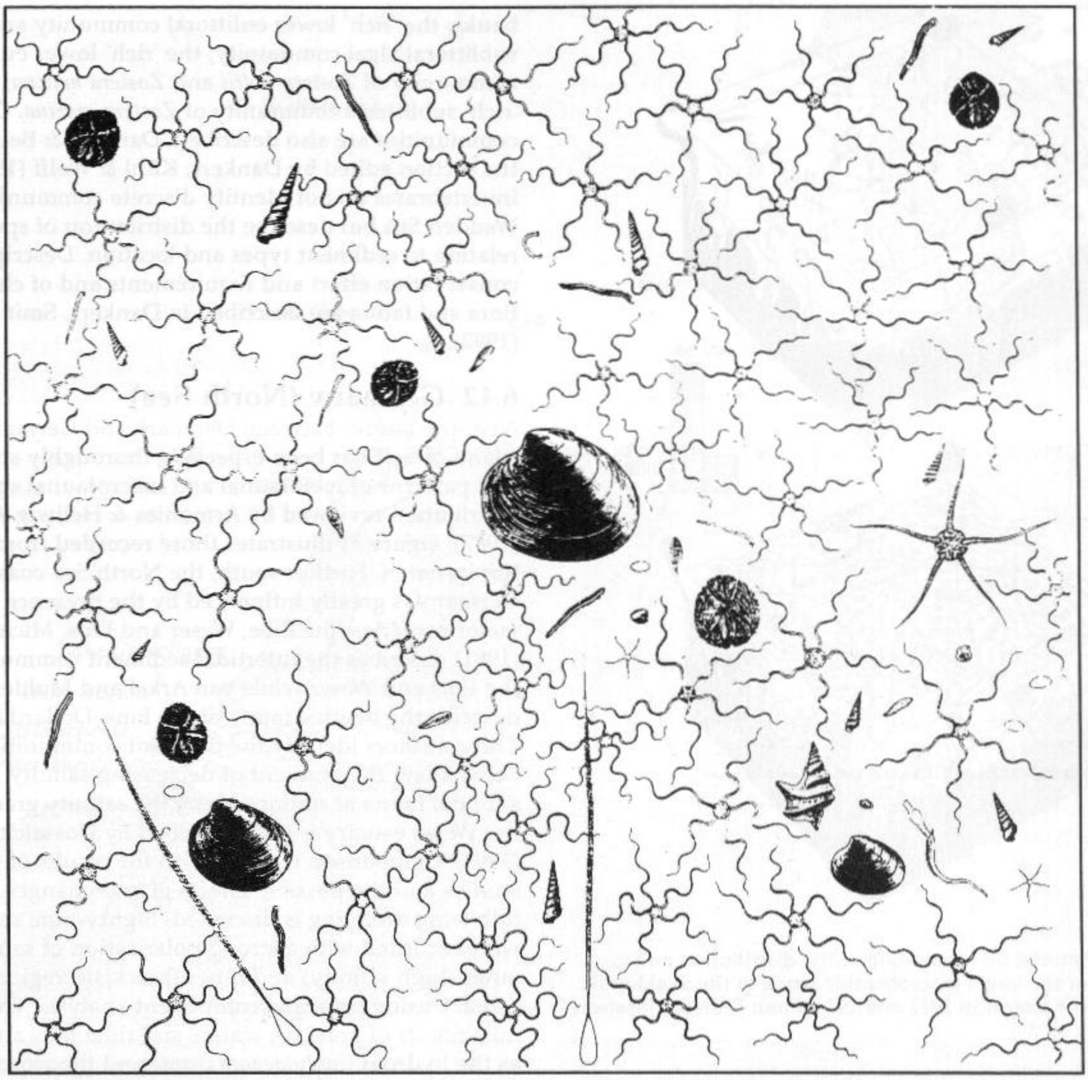


Figure 28. An *'Echinocardium – Filiformis'* community present in a 0.25 m^2 sample collected from 20 m to 22 m depth in the Kattegat. (From Petersen 1918.)

sandstone reefs including columns of carbonate rock formed as a result of methane gas seeps (Jensen *et al.* 1992). These columns, up to 4 m high and currently only known in the Kattegat, are islands for rich epifaunal communities and also attract fish. Sediments around them are very varied and therefore the range of communities in a small area is great.

The Limfjord includes extensive shallow water communities but about 22% of the bottom is influenced by annual oxygen depletion in late summer (Rosenberg 1980). Studies of the Limfjord figure greatly in the Reports of the Danish Biological Station including a special note in Petersen (1918). Communities there were later described by Blegvad (1928) and by Jørgensen (1980), who notes the presence of a typical *Macoma* community in shallow water and a *Syndosmya* (now *Abra*) community in the soft muds. Farther south, on the North Sea coast, Ringkøbing Fjord is a very extensive shallow area of brackish water behind a coastal land strip. Its history during this century has been one of considerable change in saltwater influence (Johansen, Blegvad & Spärck 1933-1936).

The brackish water habitats of the shallow fjords on the east coast were extensively surveyed by Muus (1967), who concluded that they were dominated by a *Cardium lamarki* (now *Cerastoderma glaucum*) – *Hydrobia ventrosa* community. The most recent description of benthic communities there (Spärck 1936) compares the fauna with other brackish north European waters. The situation today is doubtless different again as a new opening to the sea has been made in recent years (H. Christensen pers. comm.).

In the Wadden Sea area of Denmark, studies were undertaken by Thamdrup (1935) and Smidt (1951) in the brackish inshore waters. Thamdrup describes a seaward zone with *Arenicola marina*, *Cerastoderma edule* and *Macoma balthica*, and a zone closer inshore with *Hydrobia ulvae*, *Pygospio elegans* and *Corophium volutator*. Smidt also describes the epifauna of *Zostera* (presumably *Zostera marina*), *Mytilus edulis*, *Ostrea edulis* and *Sabellaria spinulosa* as well as mobile fauna.

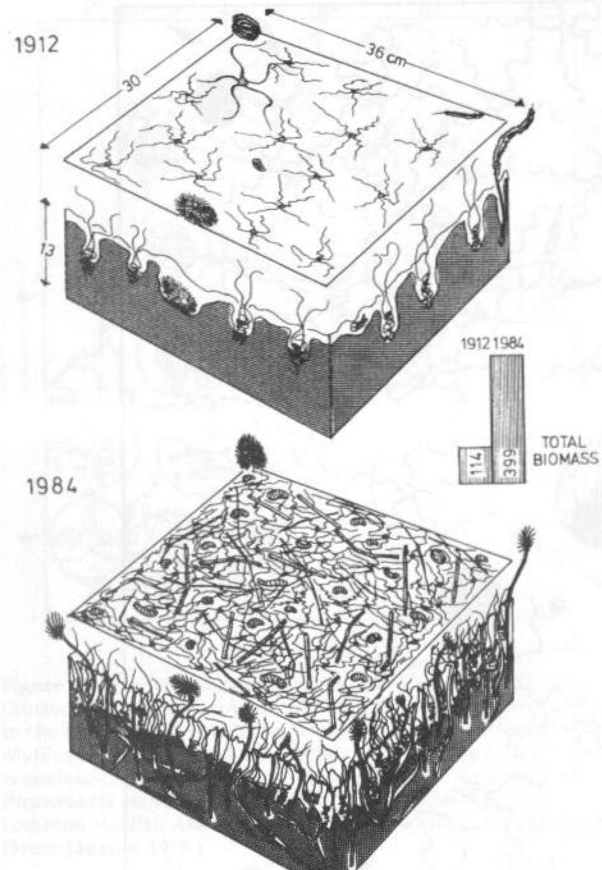


Figure 29. Pictorial representation of the distribution and abundance of the larger macrobenthic fauna in the Skaldervik, southeastern Kattegat in 1912 and 1984. From Pearson, Josefson & Rosenberg (1985).

6.11 The Wadden Sea

The 'Wadden Sea' ('Waddenzee' in the Netherlands, 'Wattenmeer' in Germany and 'Vadehavet' in Denmark) extends along the western and northern coasts of Denmark, Germany and the Netherlands (Figure 30). It is bounded on the open coast by 17 large barrier islands as well as many small islands and sand banks. The Rivers Ems, Weser and Elbe empty into the Wadden Sea which occupies about 10,000 km^2 making it the largest estuarine area in Europe (Wolff 1979). Studies of the Wadden Sea have mostly been carried out within country boundaries but brought together by the Wadden Sea Working Group. The work carried out is summarised in Wolff (1983). Accounts of work undertaken solely within the political boundaries of a particular country are noted in the country descriptions. Volume 1, parts 3 and 4 of the series *The ecology of the Wadden Sea* edited by Wolff (1983) are very useful summaries. Hoek *et al.* (1983) describe seven macrophyte communities from the Wadden Sea: the upper eulittoral *Enteromorpha* community; the lower eulittoral *Enteromorpha-Ulva* community; the lower eulittoral community of *Zostera noltii, Zostera marina, Enteromorpha* and *Ulva*; the lower eulittoral community of *Fucus vesiculosus* on *Mytilus* banks; the 'rich' lower eulittoral community and upper sublittoral algal community; the 'rich' lower eulittoral community of *Zostera noltii* and *Zostera marina*; and the 'rich' sublittoral community of *Zostera marina*. Diatom communities are also described. Dankers & Beukema in the section edited by Dankers, Kühl & Wolff (1983) on invertebrates do not identify discrete communities in the Wadden Sea but describe the distribution of species in relation to sediment types and location. Descriptions of conservation effort and requirements and of changes in flora and fauna are described in Dankers, Smit & Scholl (1992).

6.12 Germany (North Sea)

Near the border between Denmark and Germany, the island of Sylt has been especially thoroughly studied and patterns of meiofaunal and macrofaunal species distribution reviewed by Armonies & Hellwig-Armonies (1987). Figure 31 illustrates those recorded from Konigshafen. Further south, the North Sea coast of Germany is greatly influenced by the presence of three major estuaries: the Elbe, Weser and Ems. Michaelis (1981) describes the intertidal sediment communities of the Ems and Weser while van Arkel and Mulder (1982) describe the benthic fauna of the Ems–Dollard estuary. These authors identify the different communities that occur along the gradient of decreasing salinity. The subtidal fauna at stations along the salinity gradient in the Weser estuary is also described by Gosselck *et al.* (1993). Comparison is made with the results of previous studies and the possible effects of and changes in fauna following dredging is discussed. Eighty-nine species were recorded with a strong polarisation of samples to outer (high salinity) and inner (brackish) regions of the estuary using principal component analysis. The typical inhabitants of brackish waters and tidal flats are noted as the hydroid *Cordylophora caspia* and the worms *Streblospio shrubsoli* and *Manayunkia aestuarina*. Differences in the estuarine fauna between 1967 and 1991 are accounted for partly by man-made deepening of the Weser and by eutrophication but also rapid proliferation of non-native species (for instance, the worm *Marenzelleria viridis* and the bivalve *Ensis directus*).

Other parts of the inshore intertidal areas especially thoroughly studied include the area of Norderney (Dörjes 1992) and a portion of the tidal flats behind barrier islands on the north coast (Hertweck 1995) where the distribution of eight intertidal assemblages and distinctive shore types has been surveyed and mapped. Jade Bay, adjacent to Wilhelmshaven, has also been extensively studied for both intertidal assemblages (for instance, Hertweck 1994; Figure 32) and the biota of subtidal channels (Dörjes 1992).

Descriptions of the marine communities present off the North Sea coast of Germany (the German Bight) include the work of Hagmeir (1925), Remane (1940), Stripp (1969a, 1969b), Reineck *et al.* (1968) and Salzwedel, Rachor & Gerdes (1985) for the level seabed. Reise & Bartsch (1990) characterise epifaunal communities for the German Wadden Sea and offshore areas in the German Bight. These constituted two separate regions in terms of species composition, with the main dominant species in the Wadden Sea being

Figure 30. The German Bight, Wadden Sea and the Low Countries, showing locations of places mentioned in the text.

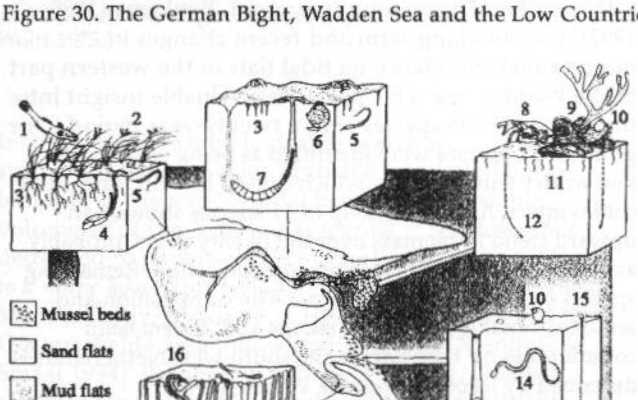


Figure 31. Benthic communities in Konigshafen on the island of Sylt, Wadden Sea. (From Reise 1985.) 1. *Pomatoschistus microps*, 2. *Hydrobia ulvae*, 3. *Pygospio elegans*, 4. *Macoma balthica*, 5. *Scoloplos armiger*, 6. *Cerastoderma edule*, 7. *Arenicola marina*, 8. *Carcinus maenas*, 9. *Mytilus edulis*, 10. *Littorina littorea*, 11. *Tubificoides benedeni*, 12. *Heteromastus filiformis*, 13. *Mya arenaria*, 14. *Nephtys hombergii*, 15. *Lanice conchilega*, 16. *Nereis* (now *Hediste*) *diversicolor*, 17. *Corophium volutator*.

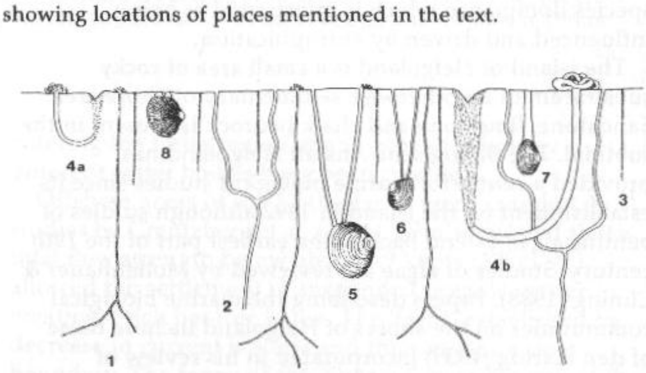


Figure 32. Typical assemblage of endobenthos and lebensspuren [architectural patterns in the sediment typical of certain species] in the transitional zone between the mudflat and mixed flat in the Jade area near Wilhelmshaven. 1. *Heteromastus filiformis*; 2. *Nereis* (now *Hediste*) *diversicolor*; 3. *Pygospio elegans*; 4. *Arenicola marina*, a) juvenile, b) half adult size; 5. *Scrobicularia plana*; 6. *Macoma balthica*; 7. *Mya arenaria*, juvenile; 8. *Cerastoderma edule*. (From Hertweck 1994.)

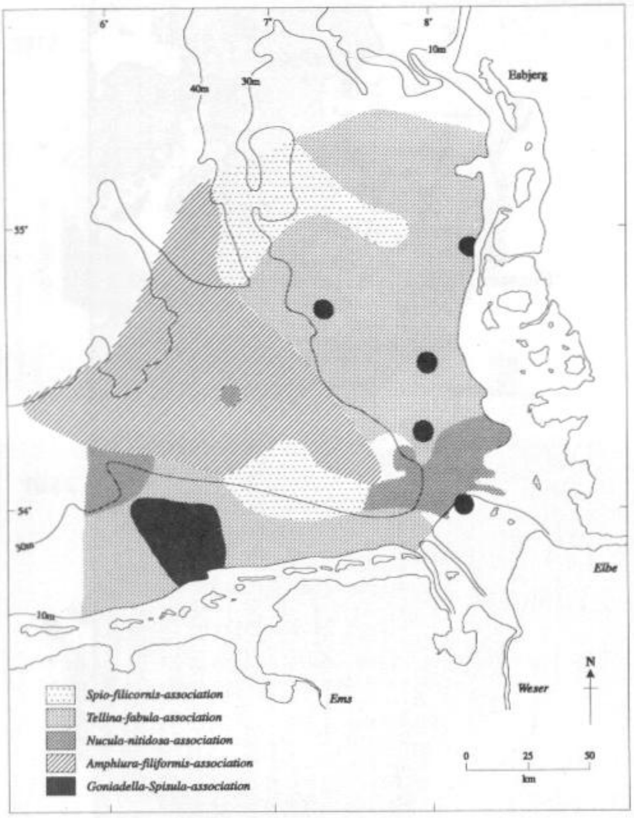


Figure 33. The distribution of deeper sublittoral communities in the German Bight and adjacent areas. (From Salzwedel, Rachor & Gerdes 1985.)

decapod crustaceans and in the North Sea echinoderms. Five communities are listed for the German Bight in Salzwedel, Rachor & Gerdes (1985) and their distribution is illustrated in Figure 33. Changes in the sublittoral zoobenthos of the German Bight over 60 years based on published data are described by Rachor (1990). He suggests an overall increase in biomass and change in species dominance which is interpreted as being influenced and driven by eutrophication.

The island of Helgoland is a small area of rocky substratum in an otherwise sedimentary offshore area. Sandstone, limestone and chalk bedrock is present in the subtidal. The Biologische Anstalt Helgoland has provided a centre for marine biological studies since its establishment on the island in 1892 although studies of benthic algae extend back to the earliest part of the 19th century. Studies of algae are reviewed by Mollenhauer & Lüning (1988). Papers describing the marine biological communities on the shores of Helgoland include those of den Hartog (1959) incorporated in his review of Netherlands algal communities, Munda & Markham (1982), who describe littoral algal communities and seasonal change, and Janke (1986), who describes littoral animal populations, and later (Janke 1990), biological interactions on the shores. The sandstone shores of Helgoland are dominated by the fucoid alga *Fucus serratus* with lesser amounts of *Fucus spiralis* and *Fucus vesiculosus* and a small number of other species. *Pelvetia canaliculata*, which is usually abundant on fucoid dominated European shores, is absent on Helgoland. Munda & Markham (1982) note that the winter and early spring flora of Helgoland shows several resemblances to the summer flora of Scandinavia. Animal communities on Helgoland shores are notable for the absence of *Patella* species and for the high abundances of rock-boring polychaetes *Polydora ciliata* and *Fabricia sabella* in the soft sandstone rock. The noted absence of some other common rocky shore species (the gastropods *Monodonta lineata, Gibbula umbilicalis* and *Littorina* (now *Melarhaphe*) *neritoides*) is to be expected in the cold North Sea. The distribution of macroscopic algae is described by Lüning (1970). *Laminaria digitata* and *Laminaria saccharina* occur between 0.5 m and 1.5 m below mean low water of spring tides followed by a *Laminaria hyperborea* forest to 4 m. The deepest algae (encrusting species) were recorded at 15 m. The development of a subtidal hard substratum community is described by Anger (1978). Recently, several mostly unpublished studies have investigated the fauna of hard substrata. Schultze *et al.* (1990) describe the macrofauna and macroflora of kelp plants. De Kluijver (1991) describes analysis of samples from 80 stations at 14 locations around Helgoland. Nine communities are identified.

6.13 The Netherlands

The coast of the Netherlands is long and indented with many important features for comparison with Britain. The intertidal algal communities on hard substrata (mainly artificial surfaces) are thoroughly described and classified by den Hartog (1959) and by Nienhuis (1976). Communities colonising brackish waters are also described, often in relation to major coastal protection or land claim works. For instance, Kroon, de Jong & Verhoeven (1985) list the macrofauna of ponds, ditches and drainage channels on the island of Texel identifying those which are euryhaline fresh water, 'true' brackish water, euryhaline marine and holeurhaline species with a general distribution over the whole salinity range.

The fauna of tidal flats in the Dutch Wadden Sea is described by Beukema (1976), who found predominantly a *Macoma balthica* community present. Beukema (1989, 1992) describes long-term and recent changes in macrofaunal abundance on tidal flats in the western part of the Wadden Sea. This provides a valuable insight into the changes in 29 species over a twenty-year period. One group of 12 species were identified as being sensitive to low winter temperatures, which caused low densities after cold winters. A further group of 11 species showed an upward trend in biomass over the twenty years, probably as a consequence of increasing eutrophication. Remaining species showed no specific trend. The composition and seasonal variation of *Zostera marina* and *Zostera noltii* communities on tidal flats in the south-west Netherlands is described by Jacobs, Hegger & Willens (1983).

Farther south and to the Belgian border, is the Delta Region where three major European rivers, the Rhine, Meuse and Scheldt (which separates into the Western and Eastern Scheldt) enter the sea. This was previously an extensive estuarine area but, following disastrous floods in 1953, the Netherlands government decided to close-off three of the four main estuaries, a decision which would have created huge brackish or freshwater lakes. However, environmental considerations led to only a partial implementation of the plan. The Delta

<table>
<tr><th>A
North Sea</th><th>B
Lower reaches of estuaries</th><th>C
Middle reaches of estuaries</th><th>D
Upper reaches of estuaries</th><th>E
Rivers</th></tr>
<tr><td>Very stable, high salinity
Exposed</td><td>Stable, high salinity
Sheltered</td><td>Unstable, medium salinity
Sheltered</td><td>Stable, low stability
Sheltered</td><td>Stable, low stability
Sheltered</td></tr>
<tr><td>Restricted to A
(types 1, 2)
44 species</td><td>Restricted to B
(type 4)
17 species</td><td rowspan="2">Restricted to C
(type 6)
Boccardia ligerica
Rhithropanopeus harrisii
Cyathura carinata
Leptocheirus pilosus
Corophium multisetosum</td><td rowspan="2">Restricted to D
(type 8)
Perforatella rubiginosa
Erpobdella monstriata
Haemopsis sanguisuga
Glossiphonia heteroclita</td><td rowspan="2">Restricted to E
(type 9)
4 species</td></tr>
<tr><td colspan="2">Restricted to A and B (types 2, 3, 4)
104 species</td></tr>
<tr><td>(Talitrus saltator)
(Talorchestia deshayesii)</td><td colspan="2">Restricted to A, B and C (type 5)
Macoma balthica
Mya arenaria
Eteone longa
Heteromastus filiformus
Crangon crangon
Carcinus maenas</td><td colspan="2">Restricted to D and E (type 9)
22 species</td></tr>
<tr><td></td><td>Restricted to B and C (types 5, 6)
Nereis succinea
Polydora ligni
Pygospio elegans
(Orchestia gammarella)</td><td>Assiminea grayana
Limapontia depressa
Alderia modesta
Streplospio shrubsolii
Manayunkia aestuarina
Neomyosis integer
Sphaeroma rugicauda
Gammarus salinus
Corophium volutator</td><td colspan="2"></td></tr>
<tr><td></td><td colspan="3">Restricted to B, C and D (type 7)
Nereis diversicolor</td><td></td></tr>
<tr><td></td><td></td><td colspan="2">Restricted to C and D (type 7)
Gammarus zaddachi
Pseudamnicola confusa</td><td></td></tr>
<tr><td></td><td></td><td colspan="3">Restricted to C, D and E (types 7, 8)
Potamopyrgus jenkinsi
Limnaea peregra
Trocheta bykowskii
(Orchestia cavimana)</td></tr>
<tr><td colspan="5">Migrating species (type 10)
Eriocheir sinensis</td></tr>
</table>

Figure 34. The distribution of sediment benthos species over the salinity gradient from the North Sea to the Rivers Rhine, Meuse and Scheldt. The large number of species characteristic of the North Sea and lower reaches of the estuaries are not shown. (From Wolff 1973.)

Institute for Hydrobiological Research was founded to study the changes which occurred in relation to the building of the various tidal barriers (for example, volume 18 of the *Netherlands Journal of Sea Research* is dedicated to papers on *Lake Grevelingen: from an estuary to a saline lake* (Hummel, Brummelhuis & de Wolf 1986)). More recently, a volume of *Hydrobiologia* described the Oosterschelde area following its closure (Nienhuis & Smaal 1994). Before these changes started, detailed studies were undertaken and are reported in Wolff (1973), who concentrates on describing and comparing brackish water faunas. Figure 34 illustrates the distribution of soft-bottom animal species over the salinity gradient from the North Sea to the rivers. Changes to the Rhine, Meuse and Scheldt estuaries as a result of tidal barrier construction were described by Heip (1989), who suggests that only the Western Scheldt remains a true unchanged estuary. He points out that, from the original situation of four comparable estuaries entering the Delta region, many ecologically very different water bodies have been created.

Offshore areas of the Netherlands were sampled in studies by Creutzberg *et al.* (1984), who suggested that a tidal flow strength below about 0.9 knots (1.8 m s^{-1}) allowed the settlement of suspended organic matter creating a rich benthic fauna. The 'front' established by decrease in current is static and thus creates a clear boundary. The fauna of the 'Oyster Ground' north of the Dutch Wadden Sea is described by de Wilde, Berghuis & Kok (1984) and by Cadée (1984). Here, there was a southern sandy area in which communities resembled the *Venus* (now *Chamelea*) *gallina* community of Petersen and a northern rich *Amphiura filiformis* community with spatangids, *Chaetopterus variopedatus*, callianassids, *Arctica islandica* and amphiuroids on a muddy seabed in depths of about 30 m to 50 m (Figure 35). The distributionn of meiobenthic and macrobenthic species and identification of species groupings (using

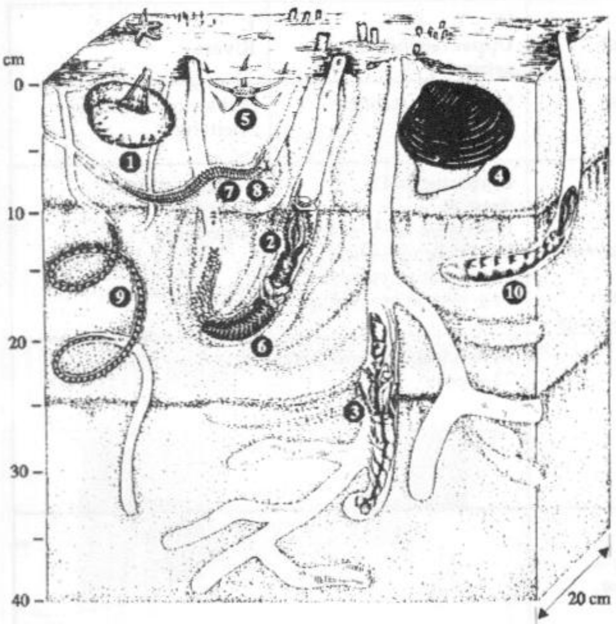


Figure 35. The community present on the Oyster Ground. (From de Wilde, Berghuis & Kok 1984.) 1. Spatangids (includes *Echinocardium cordatum, Echinocardium flavescens, Brissopsis lyrifera*). 2. *Chaetopterus variopedatus*. 3. Callianassids (includes *Callianassa subterranea, Upogebia deltaura*). 4. *Arctica islandica*. 5. Ophiuroids (includes *Amphiura filiformis, Amphiura chiajei*). 6. *Gattyana cirrosa*. 7. *Glycera rouxi, Glycera alba*. 8. *Nereis* (now *Hediste*) and *Nephtys* spp. 9. *Notomastus latericeus*. 10. *Echiurus echiurus*.

TWINSPAN) off the north coast of the Netherlands is described by van Scheppingen & Groenewold (1990) and by Holtmann & Groenewold (1994). Their results are described in terms of the indicator species and groupings identified by TWINSPAN analyses. The offshore macrobenthic assemblages are described as:

north of the 30 m depth line

- an *Amphiura filifomis, Callianassa subterranea* and *Mysella bidentata* assemblage;
- a *Callianassa subterranea, Cultellus pellucidus, Lumbrinereis latrelli, Magelona papillicornis* and *Nephtys hombergii* assemblage.

south of the 30 m depth line

- a *Chaetozone setosa, Magelona papillicornis* and *Spiophanes bombyx* assemblage;
- a *Nepthys cirrhosa* and *Scoloplos armiger* assemblage.

Off the south coast of the Netherlands, in the Southern Bight of the North Sea, benthic communities were sampled by Govaere *et al.* (1980). They describe a nearshore *Abra* community, a transition zone and an offshore *Venus* community.

Extensive studies of macrobenthos continue off the Netherlands; they include a long-term monitoring programme described by Holtmann *et al.* (1995) and publication of an atlas of zoobenthos of the Dutch continental shelf (Holtmann *et al.* in press). The paper by Holtmann *et al.* (1995) suggests, as before, four station clusters although they are distributed differently. Analysis of data from 1991 to 1994 showed no major change in benthos over the years.

6.14 Belgium

The coast of Belgium is about 65 km long and is sandy beach backed by dunes. Due to the influence of the nearby Scheldt estuary, the eastern section is much more silty than to the west. The intertidal coast is described by Warmoes, Backeljau & de Bruyn (1988), who studied the littorinid molluscs found there. Dykes for coastal defence are constructed along about 40 km of coastline but are only rarely within the littoral zone. However, large numbers of breakwaters built at right angles to the coast, together with piers and harbours, provide littoral hard substrata. Below low water, the seabed is very gradually sloping sand which only reaches 10 m depth between 3 km and 10 km offshore. The seabed off the Belgium coast was one of the first to be sampled systematically (Gilson 1907). The area offshore from the eastern part of the coast was included in the sampling of benthic communities described by Govaere *et al.* 1980. A few kilometres offshore, the western half is characterised by the Flemish Banks; sandbanks set obliquely to the shore. Locally coarse sandy sediments are found with a rich interstitial fauna (Rappé 1978; Vanosmael *et al.* 1982). A monitoring programme sampling sublittoral sediments off the coast has been under way for several years but results are not yet published (A. Catrysse pers. comm.).

6.15 Channel Islands

The Channel Islands were especially mentioned by Forbes & Godwin-Austen (1859) as peculiar for the presence of many Lusitanean species not only absent from south-western coasts of England but also from the nearby western coast of France. Crisp & Southward (1958) included the Channel Islands in their study of the distribution of intertidal organisms along the coasts of the English Channel. Holme (1966) included sample sites in the region of the Channel Islands in his survey of benthic communities in the English Channel (Section 5.2.5). However, remarkably little information describing marine biological communities around the islands has been found. The marine algae of Guernsey were described by Lyle (1920) although recent studies (Dr C. Maggs pers. comm.) have revealed a great increase in non-native species, which now dominate some areas. The littoral fish of Guernsey were listed by Wheeler (1970). Surveys of the species living in a wide variety of habitats, particularly in the littoral, at Portelet Bay and some other locations in Jersey were reported by Culley *et al.* (1983), Thomas & Culley (1987) and Culley, Thomas & Thorp (1988). Their studies do not include identification of community types but descriptions from habitats rarely sampled in Great Britain, including rockpools and crevices, and are useful for comparative purposes. Crisp & Southward noted the presence of the topshell *Gibbula pennanti* and the ormer *Haliotis tuberculata*, which are not found in Great Britain. This was mentioned again by Culley, Thomas & Thorp (1988) along with several species of algae that are rarely encountered or not found in Great Britain.

6.16 Isle of Man

Some of the earliest studies of marine biology in the first half of the 19th century were undertaken by Edward Forbes off the Isle of Man (Figure 36)(for example, Forbes 1835a&b). However, it was following the move of the Liverpool Marine Biology Committee's interests to the Isle of Man in 1892 and later by the establishment of the Liverpool University Marine Biology Laboratory at Port Erin that marine research became firmly established there. Since then, much ecological work has been undertaken, although this has been almost entirely around the southern part of the island. The algae of the Isle of Man are listed in Knight & Parke (1931) and the marine fauna together with descriptions of the main collecting grounds in Bruce, Colman & Jones (1963). Jones (1951) describes the bottom fauna off the south end of the Isle of Man where he identified four communities in relation to sediment types: 'the offshore gravel community'; 'the offshore fine sand community'; 'the offshore muddy sand community' and 'the offshore mud community'. Further descriptions of seabed communities are given in Eggleston (1963) and Ward (1988), who concentrate on assemblages of Bryozoa. Some of the communities in littoral sediments are described in Southward (1953). One of the early studies using self-contained underwater breathing apparatus to survey areas of rocky seabed is published in Kain (1960). She sampled algae at intervals of approximately 1 m depth from low water to the depth to which rock was present at ten different locations around the south coast. In addition, mobile hard substrata were sampled at four sites. A study of seasonal change on the breakwater at Port Erin was described in the same paper.

Much of the work undertaken from the Isle of Man has been experimental rather than descriptive in nature and has added considerably to our knowledge of the ecology and dynamics of marine ecosystems. Of special note are the studies of limpet grazing (reviewed in Southward 1953 and in Hartnoll & Hawkins 1985), sea urchin grazing (Jones & Kain 1967) and the ecology of kelp (reviewed in Kain 1979). There are several unpublished reports describing rocky sublittoral communities and a great deal of local knowledge, mainly about the southern area of the island, is held by marine station staff. Most recently, Geffen, Hawkins & Fisher (1990) have characterised the shores of the Isle of Man and mapped the occurrence of marine habitats and communities based on those defined by the MNCR. The biota is distinctly northern or cold-water with the absence of several southern species most probably compounded by the isolation of the Isle of Man from possible mainland sources of larvae. The southernmost records on the west coast of Britain for the red alga *Odonthalia dentata* occur off the Isle of Man.

6.17 Ireland

6.17.1 Introduction

The coast of Ireland (Figure 36) is predominantly rocky and encompasses a western seaboard bathed by the warm waters of the North-East Atlantic Drift around to the much colder waters of the enclosed Irish Sea. Differences in seawater temperature around Ireland result in a distinctive geographical distribution of species (for example, of littoral species: Southward & Crisp 1954). Communities on the west coast include a rich mixture of lusitanean elements and those characteristic of enclosed inlets within such areas as Galway Bay.

Recorded studies of marine biology in Ireland extend back to the beginning of the 19th century but useful comparative information is found in more recent reports. Northern Ireland's sublittoral and littoral areas were thoroughly surveyed in exercises similar to the MNCR (Erwin *et al.* 1986, 1990; Wilkinson *et al.* 1988). The littoral and inshore sublittoral areas of the Republic of Ireland have been surveyed since 1993 as a part of the European Commission Life-funded *BioMar* programme (Costello & Mills 1996). MNCR are partners in the programme and the BioMar team based in Dublin used MNCR methods and entered data to the MNCR database.

Papers describing the marine ecology of Ireland and published in the *Irish Naturalists Journal* are listed in Kelly *et al.* (1996).

6.17.2 Republic of Ireland

The Clare Island Survey which was undertaken in the early part of the 20th century under the auspices of the Royal Irish Academy was a 'model' descriptive survey encompassing studies of hydrology, sedimentology and the relationships between various communities and their environment. The results of this survey are summarised in Southern (1915). The descriptions of algal communities (Cotton 1912) and animal communities (Southern 1915) are easily compared with the work of the MNCR. Fifteen algal 'associations' (although some are described by habitat type rather than species) are described for exposed rocky littoral areas while ten are described for sheltered rocky shores. Further associations are described for sublittoral regions, littoral and sublittoral sediments, saltmarshes, river mouths and brackish bays. Southern (1915) provides a hierarchical classification of habitat types and characterising animal species and notes 15 sediment types and associated species and 11 hard substratum types and associated species for both littoral and sublittoral areas. Petersen (1918) commented on Southern's communities and suggested the presence of '*Macoma*' and '*Venus*' communities and something approaching the '*Echinocardium – Filiformis*' community.

The series of papers entitled *The ecology of Lough Ine* published since 1948 have greatly enhanced our knowledge of littoral and shallow sublittoral ecology. Lough Ine (now called Lough Hyne) is a deep enclosed marine basin in south-west Ireland. The lough has been studied since the late 1920s (Renouf 1931) and later by J.A. Kitching and his co-workers (early papers are summarised in Kitching & Ebling 1967 and updated in Kitching 1987). Those studies have included descriptions of the distribution of marine species in different habitats and particularly in relation to environmental conditions including wave exposure, tidal current velocity, siltation, light and deoxygenation. Few studies list species in terms of communities. Nevertheless, several are particularly useful for comparative purposes including

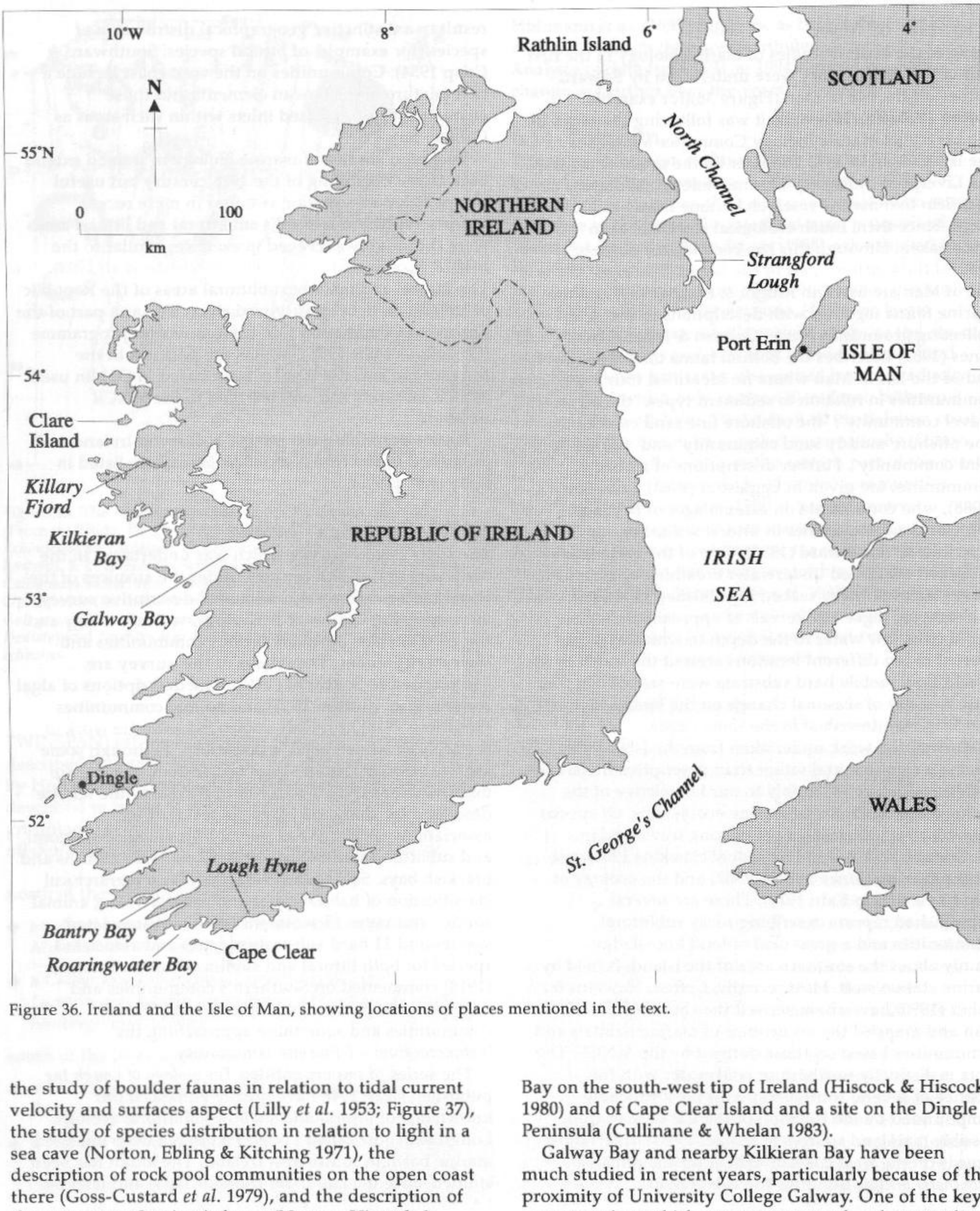


Figure 36. Ireland and the Isle of Man, showing locations of places mentioned in the text.

the study of boulder faunas in relation to tidal current velocity and surfaces aspect (Lilly *et al.* 1953; Figure 37), the study of species distribution in relation to light in a sea cave (Norton, Ebling & Kitching 1971), the description of rock pool communities on the open coast there (Goss-Custard *et al.* 1979), and the description of the open coast *Laminaria* forest (Norton, Hiscock & Kitching 1977). Hiscock (1976) described the animal communities of underwater cliffs on the open coast, just within the Lough and in the most sheltered part of the Lough (Figure 38). Other studies undertaken in south-western Ireland include the description of rocky shore communities in Bantry Bay (Crapp 1973), the survey of Killary Fjord (Mathers 1975), of Roaringwater Bay on the south-west tip of Ireland (Hiscock & Hiscock 1980) and of Cape Clear Island and a site on the Dingle Peninsula (Cullinane & Whelan 1983).

Galway Bay and nearby Kilkieran Bay have been much studied in recent years, particularly because of the proximity of University College Galway. One of the key papers against which we compare results of our studies in Great Britain is the work of Könnecker (1977) which described rocky sublittoral marine communities and their distribution in relation to temperature stability as follows:

I. Stenohaline, stenothermal, offshore
   (a) *Tethyopsilla – Tetilla* association (below 40 m)

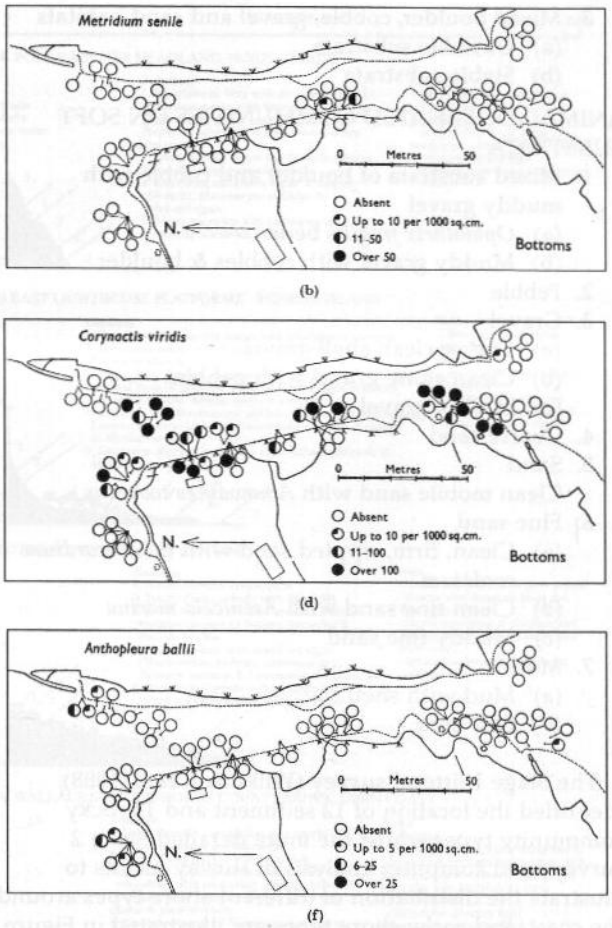


Figure 37. Studies at Lough Ine (now Lough Hyne) have demonstrated the relationship between environmental factors and species distributions. Here, the distribution of three species of sea anemone in relation to tidal current velocity is illustrated for the rapids area. (From Lilly *et al.* 1953.)

(b) *Axinella dissimilis* (now *A. polypoides*) association (25 m to 40 m)

II. Stenohaline, eurythermal, offshore-inshore
- (a) Upper *Laminaria hyperborea* association (0 m to 15 m)
- (b) Lower *Laminaria hyperborea* association (15 m to lower limit of *Laminaria*)

III. Euryhaline, eurythermal, inshore
- (a) *Lithothamnium* association (0 m to 20 m)
- (b) *Laminaria saccharina* association (0 m to 10 m)
- (c) *Raspailia – Stelligera* association (below 10 m)
- (d) *Musculus discors* association (no depth limits, strong currents)

A later paper (Könnecker & Keegan 1983) expands these descriptions.

The fauna of extensive beds of maerl in Galway Bay and nearby Kilkieran Bay were described by Keegan most recently in 1974. Keegan (1974) describes six maerl or predominantly maerl substrata and associated communities providing a basis, with the work of Cabioch (1968) in Brittany, for comparison of communities associated with this particular substratum. Similarly, the work of Maggs (1986) on the algae attached to maerl in Galway Bay provides a comparison

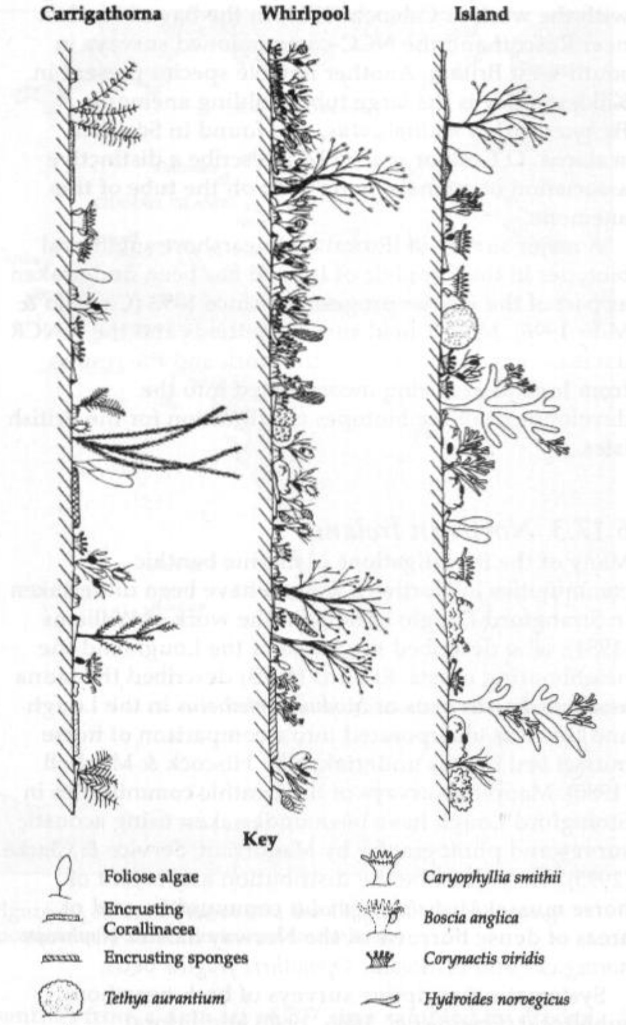


Figure 38. Illustration of the sessile species colonising cliffs at a depth of 15 m on the wave exposed open coast outside of Lough Hyne, the tidal stream exposed area just within the lough and the extremely sheltered area in the western basin of the lough. (The key is re-drawn and current names used.) (From Hiscock 1976.)

with the work of Cabioch (1969) in the Bay of Morlaix near Roscoff and the NCC-commissioned surveys in south-west Britain. Another notable species present in Kilkieran Bay is the large tube-building anemone *Pachycerianthus multiplicatus*, also found in Scottish sealochs. O'Connor *et al.* (1977) describe a distinctive association of animals living in or on the tube of this anemone.

A major survey of littoral and nearshore sublittoral biotopes in the Republic of Ireland has been undertaken as part of the *BioMar* programme since 1993 (Costello & Mills 1996). MNCR field survey methods and the MNCR database have been used in the work and the results from Ireland are being incorporated into the development of the biotopes classification for the British Isles.

6.17.3 *Northern Ireland*

Many of the investigations of marine benthic communities in Northern Ireland have been undertaken in Strangford Lough; notably in the work of Williams (1954), who described the fauna of the Lough and the neighbouring coasts. Roberts (1975) described the fauna associated with beds of *Modiolus modiolus* in the Lough and this was incorporated into a comparison of horse mussel bed faunas undertaken by Hiscock & Mitchell (1980). Mapping surveys of the benthic communities in Strangford Lough have been undertaken using acoustic survey and photography by Magorrian, Service & Clarke (1995). They describe the distribution and extent of horse mussel *Modiolus modiolus* communities and of areas of dense burrows of the Norway lobster *Nephrops norvegicus* and brittlestar *Ophiothrix fragilis* beds.

Systematic descriptive surveys of both nearshore sublittoral (Erwin *et al.* 1986, 1990) and littoral (Wilkinson *et al.* 1988; Fuller *et al.* 1991) benthic communities were undertaken in Northern Ireland by the Department of Environment (NI). The sublittoral survey describes communities in the following habitats (from Erwin *et al.* 1986):

PLANT-DOMINATED COMMUNITIES

1. Bedrock & boulder: *Laminaria hyperborea*
2. Bedrock & boulders: *Laminaria saccharina*
3. Sand covered rock
4. Sand scoured rock
5. Mobile cobbles
6. Pebble & gravel
7. *Phymatolithon calcareum* (maerl)
8. Very sheltered conditions
9. *Zostera marina*

ANIMAL-DOMINATED COMMUNITIES ON HARD SUBSTRATA

1. Bedrock
   - (a) Species composition (= ubiquitous species)
   - (b) Sand scoured rock
   - (c) *Sabellaria spinulosa* reefs
   - (d) Terraced bedrock
   - (e) Caves & fissures
   - (f) Surge gullies
2. Boulder
3. Mixed boulder, cobble, gravel and sand habitats
   - (a) Unstable substrata
   - (b) Stable substrata

ANIMAL-DOMINATED COMMUNITIES ON SOFT SUBSTRATA

1. Mixed substrata of boulder and cobble with muddy gravel
   - (a) *Ophiothrix fragilis* beds
   - (b) Muddy gravel with cobbles & boulder
2. Pebble
3. Gravel
   - (a) Coarse clean shell gravel
   - (b) Clean stone gravel with pebbles
   - (c) Muddy gravel
4. Coarse sand
5. Sand
   Clean mobile sand with *Ammodytes tobianus*
6. Fine sand
   - (a) Clean, firm, rippled sand with *Echinocardium cordatum*
   - (b) Clean fine sand with *Arenicola marina*
   - (c) Muddy fine sand
7. Mud
   - (a) Mud with shell
   - (b) Soft mud

The Stage 1 littoral survey (Wilkinson *et al.* 1988) identified the location of 12 sediment and 13 rocky community types whilst the more detailed Stage 2 survey used computer analysis of survey results to illustrate the distribution of different shore types around the coast, and rocky shore types are illustrated in Figure 39. Interpretation of the biological results suggested that geographical location, wave exposure and sedimentological features were mainly responsible for determining the distribution of sites with similar species assemblages.

The results of both surveys were summarised and the community descriptions interpreted to the MNCR habitat/community types for purposes of mapping their distribution (Baxter & Boaden 1990); 24 littoral and 19 sublittoral habitat/community types in 12 major site types are described.

6.18 Atlantic France

The Atlantic coast of France (Figure 40) extends from its North Sea border in the east where conditions are dominated by sedimentary coasts and turbid cold waters past the mainly rocky coasts of Normandy and Brittany bathed in clearer and warmer waters to the sedimentary coasts of the Bay of Biscay to the south. The results of a wide range of studies undertaken on sedimentary and rocky habitats on the French Atlantic coast are available for comparison with MNCR work. Those studies have also been brought together to compile a classification of benthic communities in Dauvin (1994), providing a particularly valuable comparison with the MNCR biotopes classification.

The widest ranging studies offshore are those for the whole of the English Channel undertaken by Cabioch *et al.* (1977) investigating the distribution of species from mobile hard substrata (Figure 23). Descriptions of

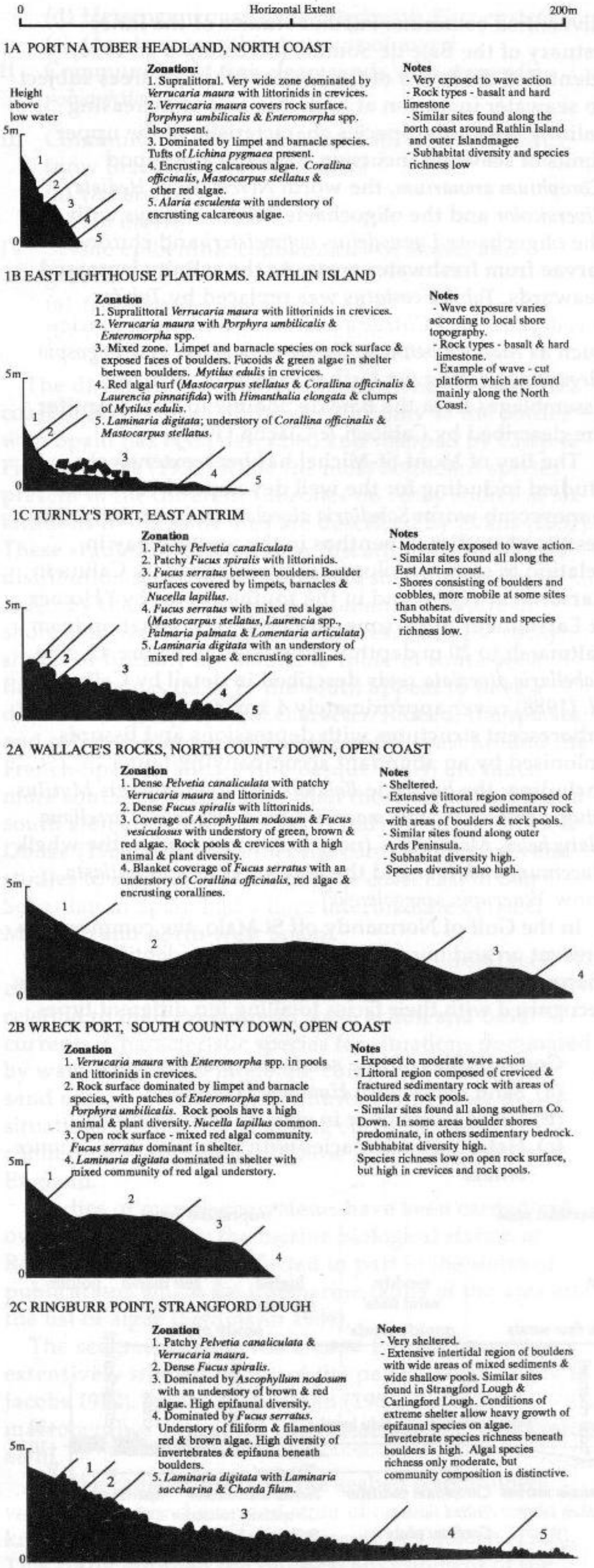


Figure 39. Characterising species for major rocky shore types in Northern Ireland. (From Fuller *et al.* 1991.)

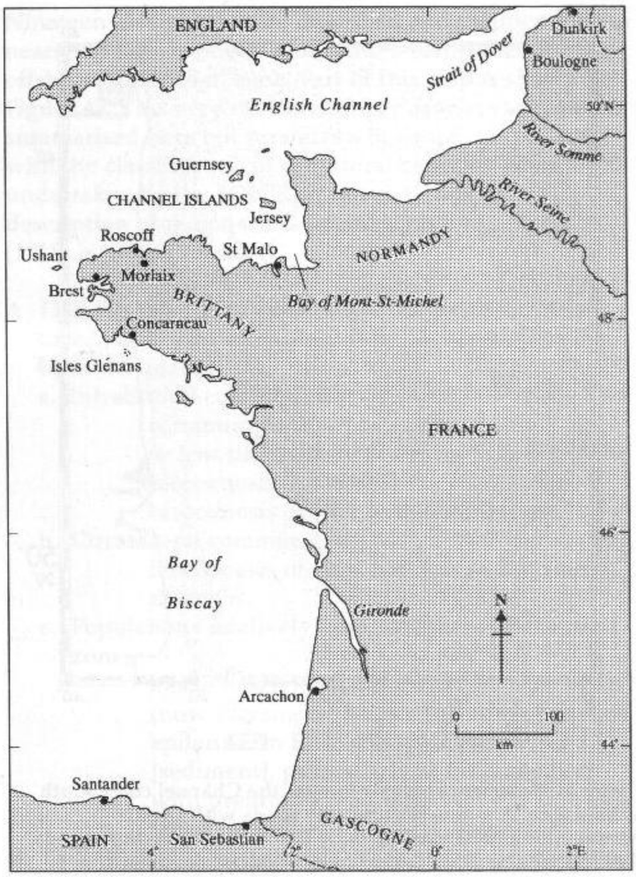


Figure 40. Atlantic France and the Channel Isles, showing locations of places mentioned in the text.

benthos from a data set of 707 sites sampled by dredge between 1971 and 1975 and extending from Belgium to Normandy in France and across the Channel to the south-east coast of England will be published in Sanvicente-Añorve & Leprêtre (in press.).

The sediment communities along the North Sea and English Channel coast between Belgium and Cape Gris-Nez have been extensively sampled and seven groups identified and mapped (Davoult *et al.* 1988). These are:

- ◆ Pebbles with sessile epifauna community
- ◆ *Modiolus modiolus* facies
- ◆ Gravel with *Amphioxus* (now *Branchiostoma*) *lanceolatus* community
- ◆ Muddy heterogeneous sediment community
- ◆ Fine to medium clean sand with *Ophelia borealis* community
- ◆ Muddy fine sand with *Abra alba* community
- ◆ Soft intertidal sediment communities

Farther south along the open coast, Cabioch & Glaçon (1975) describe and map five benthic communities [termed "peuplements" in the French text and translated here as "communities"] south of Boulogne to the estuary of the Somme (Figure 41). Desprez, Ducrotoy & Sylvand

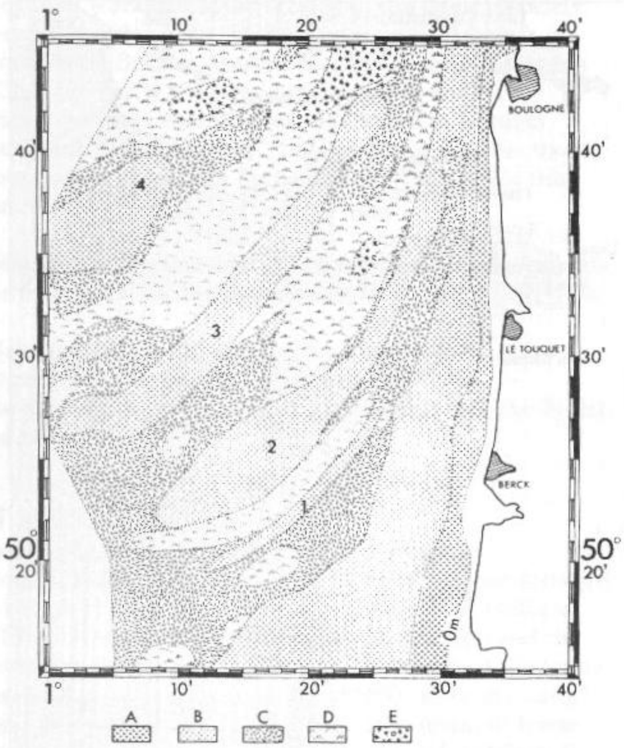


Figure 41. Sediment communities on the Channel coast south of Boulogne. A = fine slightly silty sands with *Donax vittatus-Abra alba-Macoma balthica*; B = fine and medium sands characterised by *Ophelia bicornis*; C = coarse sediments with *Amphioxus* (now *Branchiostoma*) *lanceolatus-Spatangus purpureus*; D-E = Community of pebbles and gravel with sessile epibiota (E = *Ophiothrix fragilis* facies). 1–4 = principal sand banks. (From Cabioch & Glaçon 1975.)

(1986) describe the fauna of three estuarine bays: the Baie de Somme, the Seine and the Baie de Veys and temporal change in benthic communities. The Baie de Somme was studied particularly in relation to salinity gradients and in comparison with the Baie des Veys (Ducrotoy & Sylvand 1991). Six major assemblage types were identified: marine; marine under estuarine influence; composite estuarine; transitional estuarine; link communities with the terrestrial environment, and diversified estuarine. Further studies of the inner estuary of the Baie de Somme (McLusky *et al.* 1994) identified the fauna of freshwater areas, of areas subject to seawater incursion at high tide and of increasing salinity seawards. Species characteristic of the upper limits of seawater incursion were the amphipod *Corophium arenarium*, the worm *Nereis* (now *Hediste*) *diversicolor* and the oligochaete *Tubifex costatus* with only the oligochaete *Limnodrilus hoffmeisteri* and chironomid larvae from freshwater areas. As the salinity increased seawards, *Tubifex costatus* was replaced by *Tubifex pseudogaster* and *Clitello arenarius* with marine species such as *Macoma balthica*, *Bathyporeia pilosa* and *Pygospio elegans* appearing yet farther seawards. Benthic assemblages from the Baie de Somme to Cap d'Antifer are described by Cabioch & Glaçon (1977).

The Bay of Mont-St-Michel has been extensively studied including for the well developed beds of the honeycomb worm *Sabellaria alveolata* present there. The results of studies of benthos in the western bay in relation to sedimentology are summarised by Caline in Larsonneur (1994) and in the southern part by l'Homer & Larsonneur in Larsonneur (1994). The zonation from saltmarsh to 20 m depth is illustrated in Figure 42. The *Sabellaria alveolata* reefs described in detail by Caline *et al.* (1988) cover approximately 4 km^2 forming arborescent structures with depressions and fissures colonised by an abundant accompanying fauna including: the barnacle *Balanus crenatus*; mussels *Mytilus edulis*; crabs *Carcinus maenas*, *Cancer pagurus*, *Porcellana platycheles*, *Macropipus* (now *Liocarcinus*) *puber*; the whelk *Buccinum undatum* and the bivalve *Venerupis pullasta* (now *Venerupis senegalensis*).

In the Gulf of Normandy off St Malo, the communities present on and in mobile substrata were identified and mapped by Retière (1975). Four different communities are recognised with their facies totalling ten different types.

I Communities of fine sands more or less silty
- (a) Sand facies with *Hyalinoecia bilineata*
- (b) Silted facies poor in species with *Abra alba*
- (c) Heterogeneous facies with *Sthenelais boa* – *Eunice vittata*

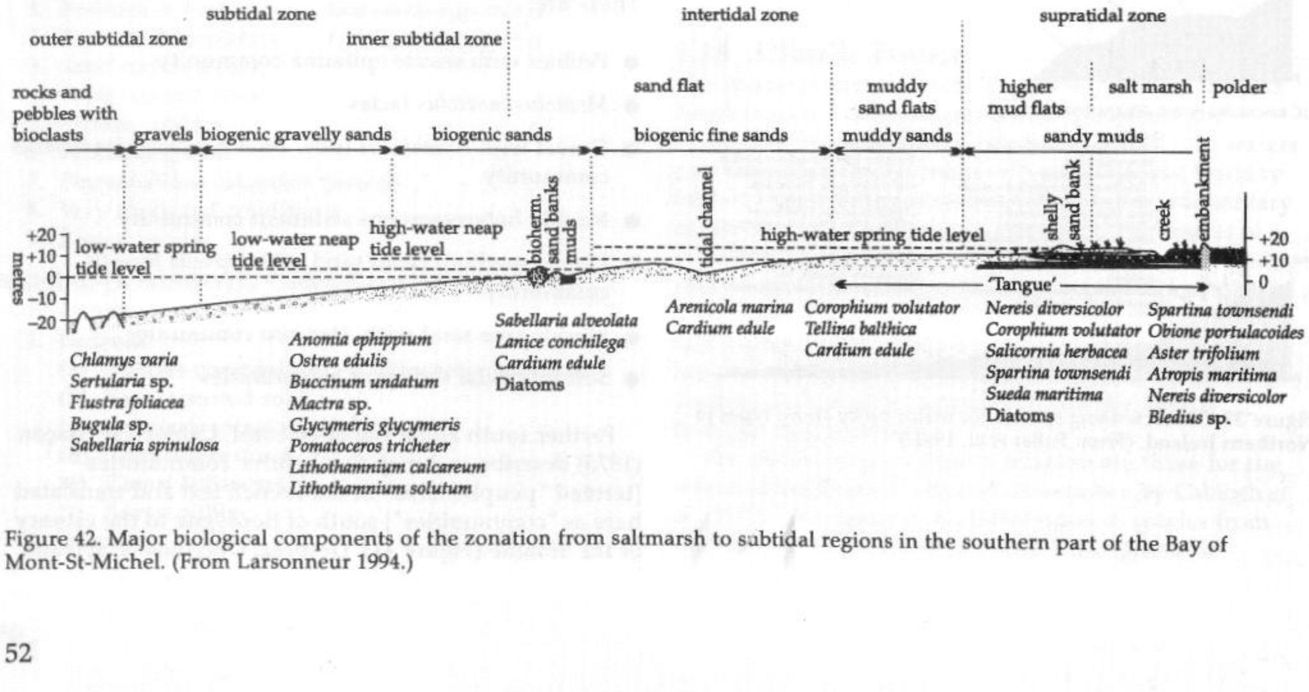


Figure 42. Major biological components of the zonation from saltmarsh to subtidal regions in the southern part of the Bay of Mont-St-Michel. (From Larsonneur 1994.)

(d) Heterogeneous facies silted with *Pista cristata*
(e) (As above), within bottoms of maerl

II Communities of fine clean sands with *Armandia polyophthalma*

III Communities of coarse sediments with *Amphioxus* (now *Branchiostoma*) *lanceolatus*
(a) (As above)
(b) (In maerl)

IV Sessile epibenthic communities of stones and gravels
(a) (As above)
(b) Facies with *Ophiothrix fragilis*

The distribution of shore animals along the Atlantic coast of France from north-west Brittany to the border with Spain has been described and mapped by Crisp & Fischer-Piette (1959) while the most abundant species present in the different subzones on rocky shores at six locations in the same area are described by Evans (1957). These studies revealed a clear discontinuity in species distribution south of the Gironde estuary, doubtless aided by the almost entirely sedimentary nature of shores for over a hundred kilometres. Thus the rocky shores of Brittany are similar to those of south-west Britain whereas those to the south appear to have a different biogeographical character. Indeed, the species and communities present on the rocky coast around the French-Spanish border (the Basque coast) are much more southern in character than those farther west and south along the Spanish coast. Studying algae, Hoek & Donze (1966) drew together the conclusions of several studies to suggest that the Basque coast east of San Sebastian in Spain had a flora intermediate between Morocco and north-west Spain.

Castric Fey (in press) describes the sublittoral rock communities near to Trébeurden in eastern Brittany in relation to their exposure to wave action and tidal currents. Characteristic species for situations dominated by wave action and moderate currents where coarse sand occurs on rocks are contrasted with those of situations dominated by strong currents. These communities are similar to those found in south-west England.

Studies of marine ecosystems have been carried out over many years by the marine biological station at Roscoff. This work is reflected in part in the series of publications which list the marine fauna of the area and the list of algae (Feldmann 1954).

The seagrass beds of the area of Roscoff have been extensively studied (many of the papers are included in Jacobs 1982). Jacobs & Huisman (1982) described macrobenthos associated with *Zostera marina* and *Zostera noltii*.

Off the coast of Brittany, the seabed communities were defined and mapped from about 84 km west to 48 km east and 60 km north of Roscoff by Cabioch (1968). This study outlined the physical environment of the English Channel, described the distribution of species in relation to depth, substratum, current and longitude, and described the biocenoses, communities (as "peuplements") and facies of communities present. Many of the species listed are hard substratum epifauna. Nineteen assemblages are described and mapped for the nearshore 'frontolittoral' zone and a further ten for the offshore 'prelittoral' zone. Part of this map is shown in Figure 43. This very extensive study cannot easily be summarised here but provides a basis for comparison with the classification of sublittoral biotopes being undertaken by the MNCR. A translation of the description of regions and assemblages by Cabioch (1968) is given below.

A THE FRONTOLITTORAL REGION [with irregular topography and extending from tidal regions to the Channel 'plain']

a. Infralittoral communities:
communities composed of fine sands more or less silty with *Abra alba* and *Corbula gibba*;
biocoenosis of maerl;
biocoenosis of rock with laminarians.

b. Circalittoral communities:
biocoenosis of hard bottoms with *Axinella dissimilis*.

c. Populations relatively independent of the vertical zones:
biocoenosis of coarse sediments with *Venus* (now *Clausinella*) *fasciata* including facies of epifauna on *Sabellaria spinulosa* bound [sediment], particularly at the transition with prelittoral populations;
facies on rock with *Musculus discors*.

B THE PRELITTORAL REGION [flat plains, the greatest part of the western basin of the Channel]
biocoenosis of hard bottoms with *Axinella dissimilis*;
biocoenosis of stones and gravels of the coastal prelittoral;
biocoenoses of stones and gravels in the wider prelittoral;
biocoenosis of coarse sediments with *Venus* (now *Clausinella*) *fasciata*, facies with *Echinocardium pennatifidum*.
(The above include a number of facies.)

The studies undertaken by Cabioch used remote sampling techniques but diving has also been used on the Brittany coast. Drach undertook a series of observations using SCUBA during the late 1940s and early 1950s on the Atlantic coast of France summarised in Drach (1952). These were followed by those of Ernst (1955) studying algae.

Algal communities surveyed by diving in the Bay of Morlaix east of Roscoff are described by L'Hardy-Halos (1972). Earlier studies there had described the flora of the extensive beds of maerl occurring on the shallow seabed (Cabioch 1969) providing a basis for comparison of maerl communities in NCC-commissioned studies in south-west Britain (for example, Little & Hiscock 1987). At the time of the *Amoco Cadiz* oil spill in 1978, several studies of sediment benthos had been started in the area of the Bay of Morlaix near Roscoff. These studies rapidly became surveys of the effects of oil pollution providing much useful information on the response of sediment benthos communities. Dauvin (1988) mentions three species groupings in the area:

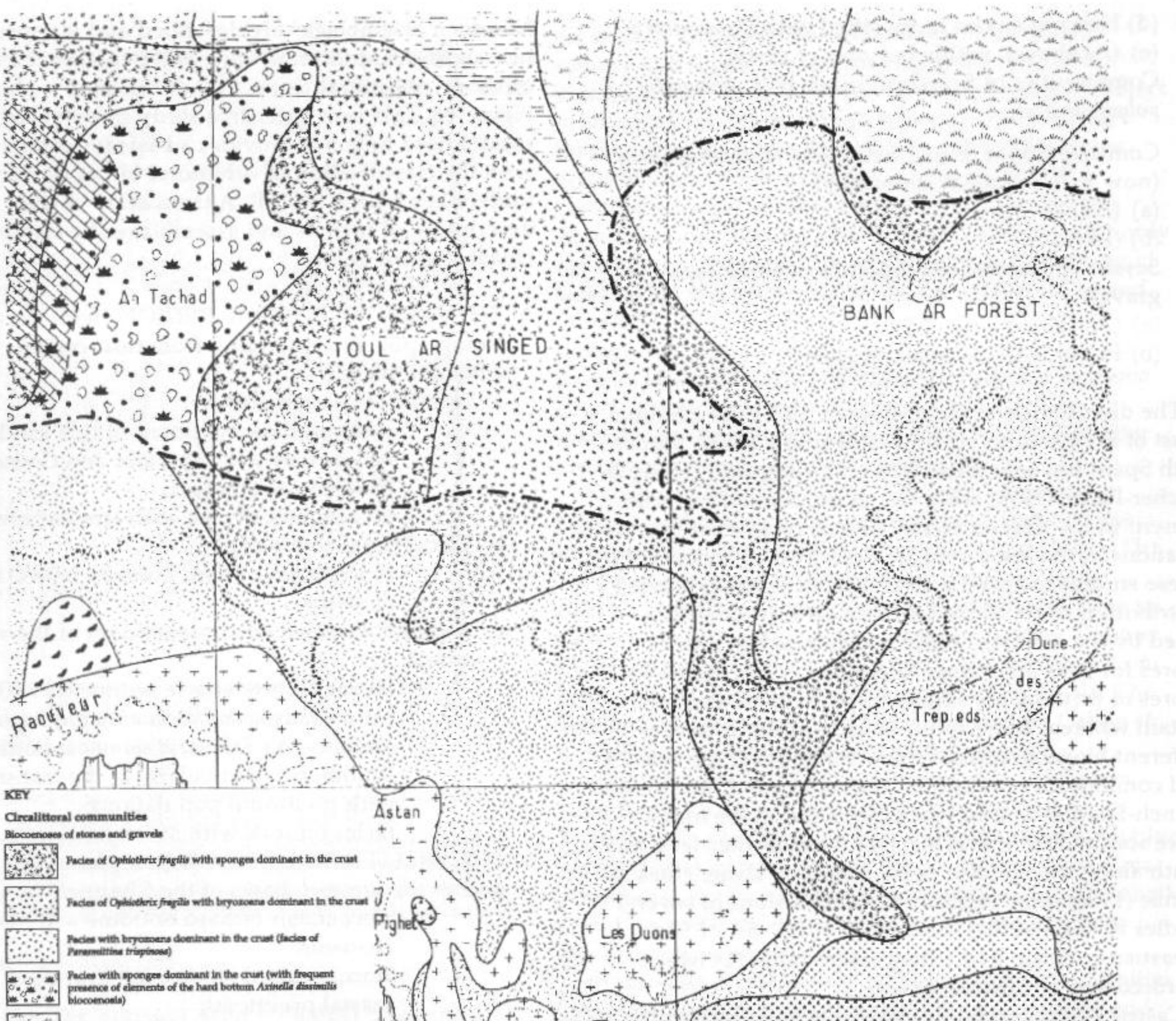


Figure 43. Seabed biocoenoses, communities and facies of communities off the Bay of Morlaix. Part of a much larger map of inshore (frontolittoral) region of the north coast of Brittany. (From Cabioch 1968.)

1. community of fine sands with little silt with *Abra alba* – *Hyalinoecia bilineata;*
2. community of muddy sands with *Abra alba – Melinna palmata;*
3. community of coarse sand with *Amphioxus* (now *Branchiostoma*) *lanceolatus – Venus* (now *Clausinella*) *fasciata.*

There appears to be no published description of hard substratum sublittoral communities present in the marine inlets and coast adjacent to Roscoff except for a brief report of an expedition by British divers in 1985 (Ackers 1986). This study revealed communities basically similar to those found in south-west Britain but enriched by many southern species not recorded in British waters including, most conspicuously, the sponge *Ulosa digitata*, the fan worm *Sabella spallanzanii*, the starfish *Echinaster sepositus* and the ascidian *Polysyncraton lacazei*. Some species, for example the sea fan *Eunicella verrucosa*, were much more abundant in Brittany than off the British coast although some others such as the alga *Carpomitra costata*, the cup coral *Leptopsammia pruvoti*, the anemones *Aiptasia mutabilis* and *Parazoanthus axinellae* and soft coral *Alcyonium glomeratum* were much less abundant than might have been expected farther south than Great Britain. Some northern species were not recorded (*Nemertesia ramosa* and *Flustra foliacea*) or were present in low numbers (*Alcyonium digitatum, Urticina felina, Asterias rubens, Echinus esculentus*).

Studies using diving techniques in the Glénan archipelago by L'Hardy-Hales *et al.* (1973) and by Castric-Fey *et al.* (1973) provide a description of the composition and distribution of rocky sublittoral communities very similar to those occurring off south-western Britain. Castric-Fey *et al.* (1973) described four distinct zonal communities (Figure 44):

1. Upper infralittoral community characterised by *Laminaria digitata* extending from 0 m to 6 m on horizontal surfaces and +0.5 m to 3 m on vertical surfaces.
2. Lower infralittoral community characterised by dense *Laminaria hyperborea* with rich algae and animals to 18 m followed by more sparse *Laminaria hyperborea* (to a maximum depth of 26 m) and a monotonous community predominantly of the algae *Delesseria sanguinea, Bonnemaisonia asparagoides* and *Dictyopteris membranacea.*
3. Upper circalittoral community characterised by Axinellidae and brachiopods from 30 m to 55 m.
4. Lower circalittoral community characterised by *Dendrophyllia cornigera* and *Swiftia rosea* below 55 m.

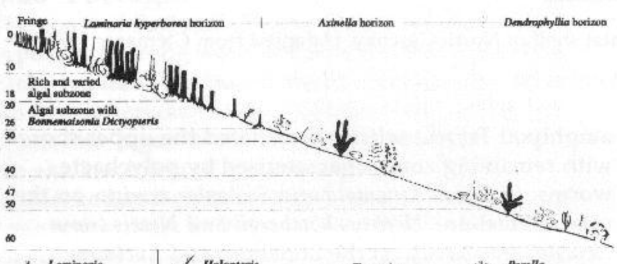


Figure 44. Schematic profile of the seabed showing zonation of the main characterising species for rocky substrata in the Glénan archipelago. (From Castric-Fey *et al.* 1973.)

A later paper (Castric-Fey, Girard-Descatoire & Lafargue 1978) expanded these descriptions by including faunal lists and noting species present in caves, fissures and other habitats. The uppermost zone is described as the infralittoral fringe in the later paper.

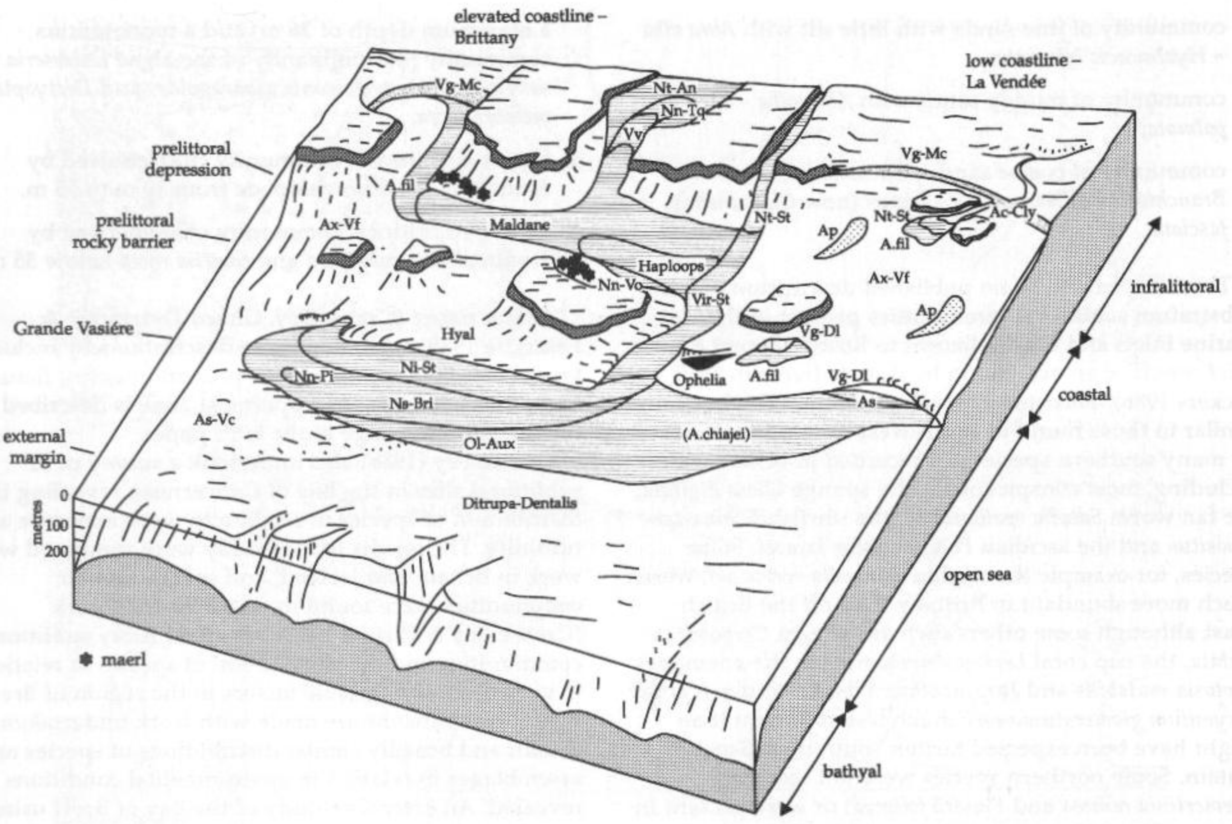
Castric-Fey (1988) also undertook a survey of 21 sublittoral sites in the Bay of Concarneau revealing the distribution of species in relation to wave exposure and turbidity. The results of that study were compared with work in Britain and Ireland, and several similar communities were found to occur. Further work (Castric-Fey & Chassé 1991) described rocky sublittoral communities and the distribution of species in relation to various environmental factors in the region of Brest. Again, comparisons are made with work undertaken in Britain and broadly similar distributions of species and assemblages in relation to environmental conditions revealed. An extensive study of the Bay of Brest using mainly underwater video by Hily (1989) provided a classification which defined 17 different habitat types in five major groups with their associated assemblages of species.

Farther south, off the northern Gascony coast, Glémarec (1973) describes 19 sediment communities present from shallow to deep water divided into infralittoral, coastal, and open sea étages (Figure 45). Glémarec (1973) also reviews work undertaken to the north of Gascony and around Britain. The communities are further described and incorporated with ones for the English Channel in Glémarec (1995). Sediment types and characterising species are used and the communities can be matched to those described elsewhere in the literature and provide a basis for comparison with those present around Great Britain. Infaunal sediment communities off south Gascony are described by Cornet *et al.* (1983) whilst epifaunal sediment communities are described in Sorbe (1989).

(A significant publication, Dauvin (1997), which describes marine biocoenoses of Atlantic France, was received after completion of this section but is not reviewed here.)

6.19 Atlantic Spain

The north-western and northern coasts of Spain (Figure 46) are predominantly rocky and were the subject of a detailed study of littoral communities by Fischer-Piette (1955), who records species present and their distribution along the coast. Littoral fish are recorded by Ibanez *et al.* (1989). These studies, together with the work of Hoek & Donze (1966), emphasise the increasingly southern character of fauna and flora eastwards along the northern coast of Spain. Various



Infralittoral étage		Coastal étage		Open sea étage	
Vg-Mc	The fine sands of *Venus gallina–Mactra corallina*	Vg-Dl	The fine sands of *Venus gallina–Dosinia lupina*	Ditruppa-Dentalis	The sands of *Ditrupa arietina–Dentalium entalis*
Ac-Cly	The muddy sands of *Acrocnida brachiata–Clymene oerstedi*	A.fil	The muddy sands of *Amphiura filiformis–Tellina serrata*	Ol-Aux	The muddy sands of *Onuphis lepta–Auchenoplax crinita*
Nt-An	The sandy muds of *Nucula turgida–Melinna palmata–Abra nitida*	Maldane	The sandy muds of *Maldane glebifex–Clymene modesta*	Ns-Bri	The sandy muds of *Nucula sulcata–Brissopsis lyrifera*
Nt-St	The muds of *Nucula turgida–Abra alba–Sternaspis scutata*	Vir-St	The muds of *Virgularia* spp.–*Sternaspis scutata*	Ni-St	The muds of *Ninoe armoricana–Sternaspis scutata*
Nn-Ta	The mixed sediments of *Nucula nucleus–Tapes aureus*	Nn-Vo	The mixed sediments of *Nucula nucleus–Venus ovata*	Nn-Pi	The mixed sediments of *Nucula nucleus–Pitar rudis*
Vv	The mixed sediments of *Venus verrucosa*	Ax-Vf	The gravels of *Branchiostoma lanceolatum–Venus fasciata* or *Amphioxus* gravels	As-Vc	The gravels of *Astarte sulcata–Venus casina*
		Hyal	*Hyalinoecia bilineata*		

Figure 45. The distribution of sediment communities on the continental shelf of North Gascony. (Adapted from Glémarec 1973.)

papers referred to in Hoek & Donze (1966) also point to the dynamic nature of fucoid cover along the northern coast in which fucoids had become increasingly rare in the first half of the 19th century but had increased in abundance since 1950. However, the general sparsity of fucoids greatly affects the appearance of shores and Hoek & Donze (1966) note that the marine vegetation of north-west Spain is intermediate in appearance between that of north-west Brittany and the Basque coast referred to above. Papers by López-Cotelo Viéitez & Diaz-Pineda (1982) and Vilas (1986) include descriptions of sandy beach fauna in north-west Spain. Here, the amphipod *Talitrus saltator* dominated the upper shore with remaining zones characterised by polychaete worms: *Scolelepis squamata* and *Scoloplos armiger* on the upper midshore, *Nephtys hombergii* and *Nereis* (now *Hediste) diversicolor* on the midshore and *Euclmene oerstedii*, *Pectinaria koreni* and *Nephtys hombergii* lower down. Studies of sublittoral communities appear few. López-Cotelo, Viéitez & Diaz-Pineda (1982) include a description of polychaete and mollusc communities in sublittoral sediments for areas offshore of Santander. Here, a boreal-lusitanean *Tellina* community in which the polychaete worm *Nephtys cirrosa* was most abundant and a reduced *Macoma balthica* community in which the bivalve molluscs *Cerastoderma edule* and *Scrobicularia plana* with the polychaete worm *Nephtys hombergii* were characteristic. Fine sediments were characterised by a heterogeneous community including the worms *Glycera unicornis, Euclymene oerstedi, Polydora ciliata* and *Pectinaria koreni*. Within Santander Bay, Lastra *et al.* (1990) distinguished two major communities: an *Abra alba* community in the inner area of the bay and a sandy community characterised by the hermit crab *Diogenes pugilator*, the cumacean *Iphinoe trispinosa* and the polychaete *Nephtys cirrosa* in the open bay.

The north-west and west-facing coast is rocky and highly indented including several rias. The sediment communities of those inlets are described in a series of papers by López-Jamar (1978, 1981, 1982 and López-Jamar & Mejuto 1985). López-Jamar & Mejuto (1985) describe sediment communities in the ría of Corunna and found a *Tellina* community dominant. Donze (1968) records the marine algal vegetation of the Ría de Arosa in north-west Spain, and López-Jamar (1982) the infaunal communities. He records two major communities: a *Spiochaetopterus costarum* community inhabiting anoxic sediments with high organic content, and a *Sternaspis scutata – Tharyx marioni* community inhabiting muddy sediments that are not anoxic. In the outer part and partially off the northern shore, there are more sandy bottoms with three further infaunal assemblages identified. The rias are extensively used for mariculture and Sanjurjo (1981) describes the fauna of mussel ropes in the Ría de Arosa whilst Tenore, Corral & González (1985) assess effects of this intense cultivation. Most southerly along the Spanish coast are the rias of Pontevedra and Vigo. Sandy beach communities here are described by Vieitez (1982), who reports the presence of a reduced *Macoma* community and a boreal lusitanean *Tellina* community (*sensu* Thorson 1957). The fauna of sandy littoral and shallow sublittoral substrata in two areas outside of the Ría de El Barquero is described in a detailed study by Mazé, Laborda & Luis (1990). They found a boreal lusitanean *Tellina* community on the Bancos Arenosus, an offshore bank, and a clear zonation of fauna consisting mostly of species also found on sandy beaches in Great Britain, on the sandy beach fringing the coast (the Area Longa beach).

6.20 Portugal

The coast of Portugal (Figure 46) is predominantly exposed to strong wave action with both sandy and rocky habitats. Studies of marine communities have been mainly undertaken in the sheltered inlets along the coast. The 'lagoons' of western and southern Portugal are shallow inlets of the sea, some of which are landlocked and some of which have channels connecting them to the sea. Quintino, Rodrigues & Gentil (1989) describe the benthic species in the lagoon of Obidos in western Portugal and conclude that species characteristic of both Atlantic and Mediterranean lagoons were present. The lagoon of Albufeira is essentially marine with a maximum depth exceeding 13 m. Dredge and grab samples of fauna were analysed by Quintino *et al.* (1987) using correspondence analysis to identify the communities illustrated in Figure 47. They concluded that the overall faunistic composition can be related to the Atlantic and Mediterranean fauna of coastal or lagoonal systems. They identify their coarse clean sand assemblage (AI) precisely with the 'biocenose des sables grossiers et fins graviers sous l'influence hydrodynamique' described by Pérès & Picard (1964). Their transition group (AII) includes several species characteristic of the biocenosis 'sables à *Amphioxus*' (now *Branchiostoma*) (Pérès & Picard 1964; Bellan 1964). The third group, which covered about 90% of the lagoon floor, was considered typical of coastal lagoons both for the Atlantic and Mediterranean and is related to the 'biocenose lagunaire euryhaline et eurytherme' of Pérès & Picard (1964) and Bellan (1964). The Ría de Aveiro is described by Moriera *et al.* (1993). The 'ria' extends as the Canal de Mira along which is a salinity gradient from 35 to 0‰ providing a typical longitudinal estuarine gradient. Analysis of biological samples identified three major groupings representing subtidal stations in the outer channel (separated into three groups), intertidal stations in the middle and outer reaches and inner stations. The numerically dominant species in these groups (the polychaetes *Hediste diversicolor, Amages adspersa, Streblospio dekuyzeni, Pygospio elegans, Tharyx marioni* and *Heteromastus filiformis*, the crustaceans *Urothoe brevicornis, Cyathura carinata* and *Corophium multisetosum*, the prosobranchs *Hydrobia ulvae* and *Potamopyrgus jenkensi*, and the bivalves *Scrobicularia plana, Cerastoderma edule* and *Venerupis pullastra*) are mostly species which would characterise similar habitats in Britain. Studies have also been undertaken in the 'ria' of Alvor on the southern coast of Portugal (for instance, Rodrigues & Dauvin 1987). Communities are described according to the hydrosedimentary gradient as: a medium clean sand community near the mouth, an intermediate community and a landward community on sandy mud. The fauna was considered typical of European coastal lagoons.

The lagoon of St Andre is a landlocked system. Benthic and fish communities were described by da Fonseca, Costa & Bernardo (1989). There is a marked change in the fauna through the year in relation to changes in salinity, and the species (most of which also occur in Britain) characteristic of the different salinity regimes are listed. The Ría Formosa is a large area of enclosed coast with four openings into the Atlantic. Austen, Warwick & Rosado (1989) note that the benthic ecology of the area is not very well known. Their work included the sampling of macro-and meiofauna along a gradient of sewage pollution identifying organisms generally to family level. Thus, no comparison with communities elsewhere is possible although it is notable that they conclude digging for shellfish disturbs macrobenthic communities well beyond any influence from sewage.

For the open coast, Dexter (1988, 1990) describes the sandy beach fauna from 60 locations. The zonation she described was of: the talitrid *Talitrus saltator* and the oniscid *Tylos europeus* isopods in the supralittoral fringe; cirolanid isopods especially *Eurydice affinis* in the 'retention' zone (see McLachlane & Jaramillo 1995 for terminology); *Spio filiformis, Nephtys cirrosa*, haustoriid, urothoid, oedicerotid and pontoporinid amphipods and

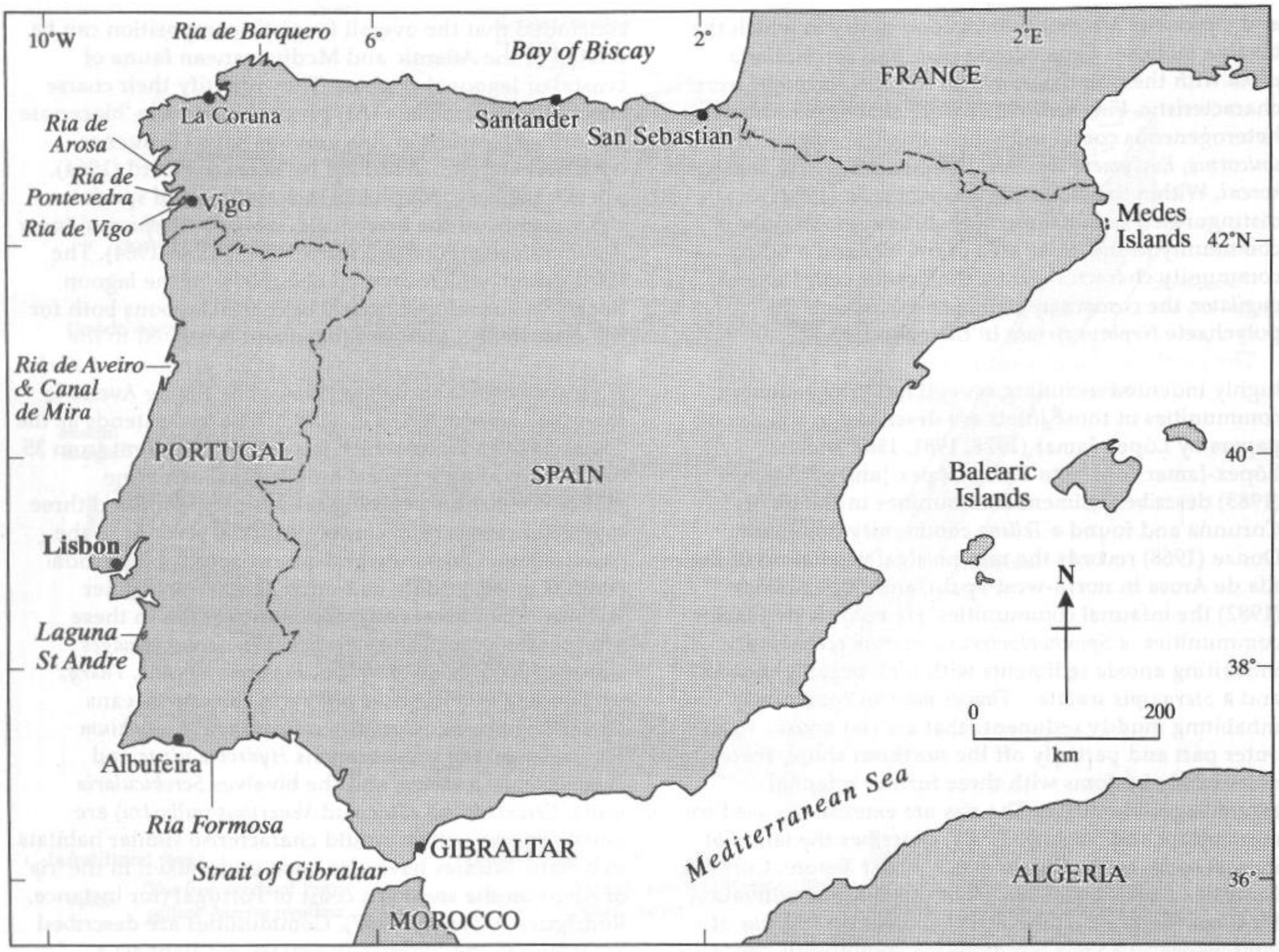


Figure 46. Spain, Portugal and Mediterranean France, showing locations of places mentioned in the text.

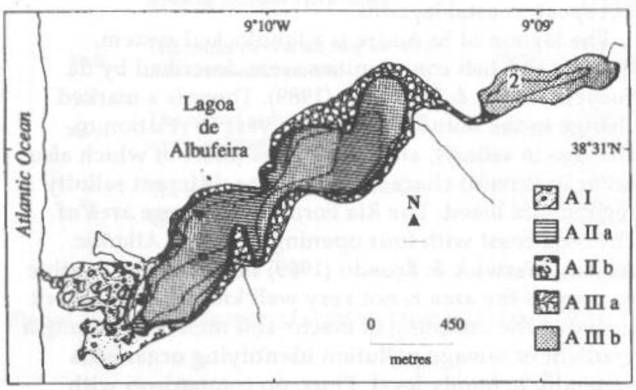


Figure 47. Distribution of macrobenthic communities in the lagoon at Albufeira. AI = marine assemblage of *Saccocirrus papillocercus, Nephtys cirrosa* and *Spisula ovalis*; AII = transition assemblage; AIIa = high richness group; AIIb = medium sands with *Spio martinensis*; AIII = lagoon assemblage; AIIIa = sandy mud mainly of *Abra ovata* and *Heteromastus filiformis*; AIIIb = impoverished muds with *Phoronis psammophila*. (From Quintino *et al*. 1987.)

the isopods *Spaeroma rugicauda* and *Spaeroma hookeri* in the resurgence zone and *Donax trunculus, Tellina tenuis, Gastrosaccus sanctus* and the crab *Portumnus latipes* in the saturation zone.

6.21 The Mediterranean

The Mediterranean Sea includes many species and features in common with the Atlantic but also many species and features not found west and north of the Straits of Gibraltar. Similarities with the Atlantic as well as species richness generally decreases with increasing distance eastwards. Much marine biological work has been carried out in the Mediterranean. This contributes to our knowledge of the taxonomy and ecology of marine species, to the sampling techniques that can be used to record and separate marine communities and to the identification of biotopes. The absence of an extensive littoral zone and the warmer waters in the Mediterranean encouraged the study of sublittoral areas using diving techniques much earlier than in the north-east Atlantic. A remarkable early study that provides much information on the ecology of hard substratum sublittoral species and communities is the work by Riedl (1966) *Biologie der Meereshöhlen*. However, the many studies undertaken on specifically Mediterranean systems are not described here but attention is given to work aimed at classifying benthic marine habitats and communities, mainly undertaken on the French and Spanish coasts, which provides important reference for MNCR studies.

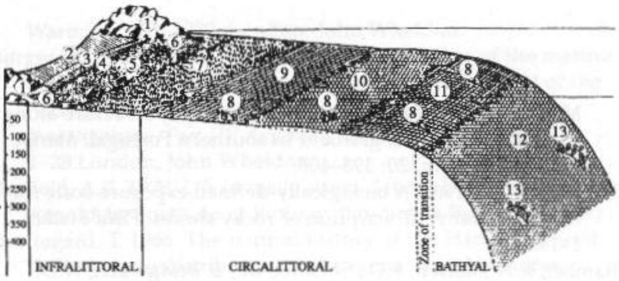


Figure 48. General scheme of the distribution of the main biocoenoses on the French coast of the Mediterranean: 1, rocky points; 2, alluvial area; 3, high and middle beach (supralittoral and mediolittoral sandy biocoenoses); 4, biocoenoses of the fine sands in very shallow waters; 5, biocoenosis of the well sorted sands; 6, biocoenosis of the photophilous algae on rocky substratum; 7, biocoenosis of the *Posidonia* meadows; 8, coralligenous biocoenosis; 9, biocoenosis of the coastal detritic; 10, biocoenosis of the terrigenous mud; 11, biocoenosis of the shelf-edge detritic; 12, biocoenosis of the bathyal mud; 13, biocoenosis of the deep sea corals. (From Pérès 1967.)

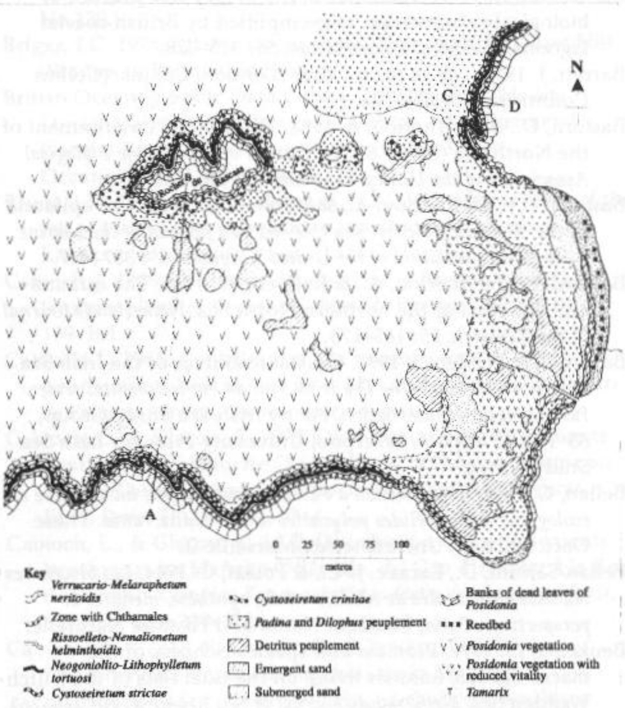


Figure 49. Marine benthic biocoenoses in the Bay of La Palu, Port-Cros National Park, France. (From Augier & Boudouresque 1967.)

The work of Pérès & Molinier (1957) provides the basis for defining zonation of epibenthic communities in the sublittoral which, although mainly based on the Mediterranean coast, is easily converted to work in north-east Atlantic ecosystems at a broad scale (Hiscock & Mitchell 1980). Pérès & Picard (1964) extended the zonal classification to one for the major assemblages of species in the Mediterranean benthos in their *Nouveau manuel de bionomie benthique de la Méditerranée*. Their conclusions are largely repeated, in English, in Pérès (1967), where the extent and depths of the major zones are illustrated (Figure 48). Augier (1982) provides an inventory and classification of marine benthic biocoenoses of the Mediterranean derived greatly from the work of Pérès & Picard (1964) and which reviews the major works. Bellan-Santini, Lacaze & Poizat (1994) give an up-to-date summary of the marine biocoenoses and threats to them in the Mediterranean. The system of classification for benthic communities established now since 1957 in the Mediterranean has provided the opportunity to map the extent of distinctive habitats and communities as a tool in management for nature conservation. For example, Augier & Boudouresque (1967) map marine benthic biocoenoses in the Port-Cros National Park (Figure 49). The studies of marine benthic habitats and communities undertaken in the Medes Islands off the north-east coast of Spain (Ros, Olivella & Gili 1984) also followed the classification system first established by Pérès & Picard (1964) and the inventory with detailed descriptions of species richness and the distribution of communities thus provided is the basis for their proposal of protected status for the islands.

It is the high proportion of the species present in the Mediterranean which do not occur or do not occur in abundance on the Atlantic coast of Europe (in shallow waters at least – below a depth of about 200 m, Carpine (1970) records communities with many species similar to those of muddy substrata in the north-east Atlantic including a close similarity between the Mediterranean bathyal communities and those from the deep water in Sognfjord in Norway) and the great differences in dominant species of particular habitats which makes direct comparison or integration of classifications at a detailed level difficult between the Mediterranean and Atlantic coasts of Europe. Nevertheless, the framework for a classification which can be applied across Europe should be the same for all of the north temperate Atlantic area.

7 Acknowledgements

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