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**MAERL**

An overview of dynamics and sensitivity characteristics for conservation  
management of marine SACs

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## PREFACE

The 1990s are witnessing a “call to action” for marine biodiversity conservation through wide ranging legislative fora, such as the global Convention on Biodiversity, the European Union’s “Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora” (the Habitats Directive) and more recently in developments to the Oslo and Paris Convention (OSPAR). These landmark legal instruments have in turn provided sufficient scientific rationale, legal mandate and social synergy to rally governments, NGOs, private industry and local communities into a new era of unprecedented conservation action.

Each of these initiatives identifies marine protected areas as having a key role in sustaining marine biodiversity. To manage specific habitats and species effectively there needs to be a relatively clear understanding of their present known distribution, the underpinning biology and ecology and their sensitivity to natural and anthropogenic change. From such a foundation, realistic guidance on management and monitoring can be derived and applied.

The Habitats Directive requires the maintenance and/or restoration of natural habitats and species of European interest at favourable conservation status across their biogeographical range. The designation and management of a network of Special Areas of Conservation (SACs) have a key role to play in this. The specific 'marine' habitats defined in Annex I of the Habitats Directive include:

- Sandbanks which are slightly covered by sea water all the time;
- estuaries;
- mudflats and sandflats not covered by seawater at low-tide;
- large shallow inlets and bays;
- lagoons;
- reefs;
- submerged or partly submerged sea caves;

These habitats are vast in scope and challenging to quantify in terms of favourable conservation status, so there has been increased attention to 'sub-features' of these habitats which are in effect constituent components and/or key elements of the habitats from a range of biodiversity perspectives.

One initiative now underway to help implement the Habitats Directive is the UK Marine SACs LIFE Project, involving a four year partnership (1996-2001) between English Nature (EN), Scottish Natural Heritage (SNH), the Countryside Council for Wales (CCW), Environment and Heritage Service of the Department of the Environment for Northern Ireland (DOENI), the Joint Nature Conservation Committee (JNCC), and the Scottish Association of Marine Science (SAMS). While the overall project goal is to facilitate the establishment of management schemes for 12 of the candidate SAC sites, a key component of the project assesses the sensitivity characteristics and related conservation requirements of selected sub-features of the Annex I habitats noted above. This understanding will contribute to more effective management of these habitats by guiding the detailed definition of the conservation objectives and monitoring programmes and by identifying those activities that may lead to deterioration or disturbance.

A diverse series of sub-features of the Annex I marine habitats were identified as requiring a scientific review, based on the following criteria:

- key constituent of several candidate SACs;
- important components of Annex I habitats in defining their quality and extent;
- extensive information exists requiring collating and targeting, or there is minimal knowledge needing verification and extended study.

This resulted in the compilation a nine-volume review series, each providing an "Overview of Dynamics and Sensitivity Characteristics for Conservation Management of Marine SACs" for the following sub-features:

Vol. I	Zostera Biotopes
Vol II	Intertidal Sand and Mudflats & Subtidal Mobile Sandbanks
Vol III	Sea Pens and Burrowing Megafauna
Vol. IV	Subtidal Brittlestar Beds
Vol. V	Maerl
Vol. VI	Intertidal Reef Biotopes
Vol. VII	Infralittoral Reef Biotopes with Kelp Species
Vol. VIII	Cirralittoral Faunal Turfs
Vol. IX	Biogenic Reefs.

Each report was produced initially by appropriate specialists from the wider scientific community in the respective subject. These reports have been reviewed through an extensive process involving experts from academic and research institutions and the statutory nature conservation bodies.

The results of these reviews are aimed primarily at staff in the statutory nature conservation bodies who are engaged in providing conservation objectives and monitoring advice to the marine SAC management schemes. However these reports will be a valuable resource to other relevant authorities and those involved in the broader network of coastal-marine protected areas. In order to reach out to a wider audience in the UK and Europe, a succinct 'synthesis' document will be prepared as a complement to the detailed 9-volume series. This document will summarise the main points from the individual reviews and expand on linkages between biotopes, habitats and sites and related conservation initiatives.

These reports provide a sound basis on which to make management decisions on marine SACs and also on other related initiatives through the Biodiversity Action Plans and Oslo and Paris Convention and, as a result, they will make a substantial contribution to the conservation of our important marine wildlife. Marine conservation is still in its infancy but, through the practical application of this knowledge in the management and monitoring of features, this understanding will be refined and deepened.

We commend these reports to all concerned with the sustainable use and conservation of our marine and coastal heritage.

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## EXECUTIVE SUMMARY

### Introduction

Maerl denotes loose-lying, normally non-geniculate (i.e. not jointed), coralline red algae. Depending on the terminology used, maerl refers either to a class of rhodoliths, or may be considered distinct from rhodoliths in lacking a non-algal core. Maerl beds are composed of living or dead unattached corallines forming accumulations with or without terrigenous material. Maerl develops when crust-forming coralline red algae, impregnated with calcium carbonate, become free-living due to fragmentation. Although very slow-growing, the maerl thalli (also known as rhodoliths, meaning red stones) sometimes accumulate into flat beds or large banks of maerl. These beds have considerable conservation value because of the very high diversity of organisms, some being more or less confined to the maerl habitat.

The value of maerl as a unique biotope is currently threatened by several types of human activity, such as by large-scale commercial extraction, reduction of water quality by discharges, and the use of heavy demersal fishing gear. One of the proposed solutions to these threats is the protection of candidate Special Areas of Conservation (SACs), four of which include maerl beds. Maerl is legally protected under several designations, as a habitat under both the the EC Habitats Directive 1992 and the UK Biodiversity Action Plan. The maerl-forming species *Lithothamnion corallioides* and *Phymatolithon calcareum* are both included in Annex V (b) of the EC Habitats Directive, and are on the UK Biodiversity Action Plan long list.

There are at present three main species of coralline algae known to occur free-living in the waters around the UK, with a least a further six species known to contribute to deposits in certain areas. *Phymatolithon calcareum* is the mostly widely distributed species in the British Isles and Europe generally. Most maerl species can be provisionally identified by eye, but final determination of some species requires microscopical examination of prepared sections.

Records of the presence or absence of maerl biotopes on European coasts are patchy. The United Kingdom, particularly Scotland, is home to many of the most extensive maerl beds in Europe. Maerl occurs abundantly on many west coasts, such as in Scotland, Ireland and Brittany, but it is absent from large areas of Europe, such as most of the North Sea, the Baltic, the Irish Sea and the eastern English Channel. The best known maerl bed sites are in Europe, particularly Brittany, Norway and Ireland, rather than the UK. In the UK, maerl occurs within four candidate SACs, but one of these (Strangford Lough) is poorly known. Only the Sound of Arisaig and the Fal and Helford have been studied in detail. Nine biotopes or sub-biotopes with maerl are listed in the MNCR habitat classification, and there are at least a further five biotopes in which maerl is a minor component.

### Environmental requirements and physical attributes

The ecological niches of both *Lithothamnion corallioides* and *Phymatolithon calcareum* are relatively narrow and subject to many controlling environmental factors. The most significant environmental factors affecting the distribution of maerl are currents; the interactive effects of depth and water quality; and wave action. The key physical factor affecting both the distribution of maerl and the type of maerl biotope is the occurrence of seabed currents, generated by tides, rivers, wave action or salinity differentials. Extensive maerl beds are more or less restricted to areas where there are moderate to strong currents. Where currents are lacking, the species composition of the maerl beds is atypical: small forms of *Lithothamnion corallioides* seem to

tolerate static conditions better than *Phymatolithon calcareum* does. Maerl does not occur where there is strong wave action, so it is most common in bays and inlets.

Maerl biotopes occur in a wide range of temperature regimes, from the tropics to northern Norway, but the species composition of the maerl beds is greatly influenced by temperature. The species and the proportions of living maerl thalli vary in different areas. The chemical requirements of the maerl species, including salinity and nutrient concentrations, are not known in any detail, but maerl beds in the UK are normally found in fully saline conditions.

Maerl beds can be found in association with a range of different sediments, varying in size from fine mud to coarse gravel and pebbles. Maerl-forming species are able to survive in deeper water than most seaweeds but their precise irradiance requirements (light, depth and water clarity interactions) are not known. The depth to which each maerl bed penetrates will depend on available light which is a function of water quality.

### **Biology and ecological functioning**

Two fundamentally different growth forms of *Lithothamnion corallioides*, *L. glaciale* and *Phymatolithon calcareum* occur. Plants may form crusts attached to rock, pebbles or sometimes shells, or free-living thalli, growing as nodules, rhodoliths or branched structures. In some areas, the free-living thalli originate from branches of the crustose forms, but in other areas crustose thalli are not important in the life history. Unattached *L. corallioides* and *P. calcareum* thalli in UK waters are probably almost entirely vegetatively propagated. This has important implications for management: if large quantities of living maerl are removed for any purpose, or killed (e.g. by scallop dredging) then the chances of biotope regeneration are greatly reduced. Reproductive organs are rarely found in some maerl species and frequencies of reproductive thalli vary seasonally from site to site.

Growth rates vary for different maerl species, between seasons and between sites. The result of technical difficulties involved is that growth rates have only been measured for a few species at a few sites, but the consensus from these studies is that maerl grows very slowly in comparison to most seaweeds in UK waters (up to a few mm per year), and an order of magnitude more slowly than tropical coralline algae.

Maerl biotopes often include a highly diverse community. To our knowledge there have been no overall comparisons of the diversity of maerl fauna and flora with those in equivalent samples from other biotopes, but the algal diversity on maerl in Galway Bay is similar to that in photophilic algal communities in the Mediterranean. Few of the species found in maerl biotopes are confined to those biotopes; it is the total assemblage of species within the maerl biotope that makes it unique. The few floristic and faunistic studies undertaken to date have focussed on the biodiversity aspects of maerl biotopes, rather than on interactions and community structure, although an EC MAST programme (BIOMAERL) is currently addressing these issues.

The seasonal and spatial variation in both floral and faunal composition is dramatic; the maerl species composition itself of certain maerl beds is known to change over periods of 3-30 years. Changes in the environment of the maerl biotope would affect settlement of the epiflora, possibly resulting in the dispersion of the maerl bed. The various maerl species can be regarded as keystone species within the maerl bed, as can the various creeping species which are important in stabilizing the beds. However, these species, their distributions and frequency within the different biotopes are known only for a few sites. Interactions between the flora and fauna have



not been specifically investigated. Competition for space, herbivory and changes in the biological component of the substratum have all been noted to affect the flora and fauna.

The potential importance of maerl as a habitat for the juvenile stages of demersal and pelagic species has not been specifically addressed.

### **Sensitivity to natural events**

Maerl thalli and biotopes can be classed as sensitive because maerl thalli are fragile (brittle), long-lived, recruit poorly, have poor spore dispersal, and are unable to move away. For maerl beds it is likely that the most significant natural events affecting the biotopes on an ongoing basis are storms. Resulting water movement has been found to be very important in determining the loss rates of thalli from the beds, and the turbidity that follows storms almost certainly reduces photosynthesis and thus growth rates. Disturbance caused by the passage of storm waves can result in the loss of high proportions of thalli from beds during storms.

Palaeoclimatological data may be obtainable from present-day maerl beds as well as fossil and sub-fossil maerl deposits. Dead maerl beds in some parts of the UK appear to be relicts and may indicate the effects of past climate change. Natural changes within the marine environment could have a great variety of consequences for maerl biotopes. These consequences cannot be accurately predicted on the basis of our present knowledge of the ecological interactions in coastal ecosystems. A disease such as the coralline lethal orange disease recently discovered in the Pacific could have devastating consequences for maerl beds although no such diseases are known to affect European Corallinaceae at present.

### **Sensitivity to human activities**

Information on the sensitivity of maerl biotopes to human activities is scarce but informed speculations can be made about potential impacts. Commercial dredging of maerl deposits is particularly destructive since this removes the productive surface layer and dumps sediment on any plants which escape dredging, inhibiting habitat recovery.

Other commercial activities that may be seriously damaging to maerl biotopes are related to fishing and fishfarming. Both finfish and shellfish aquaculture can result in degradation of maerl beds. Scallop dredging results in the removal of the living maerl thalli from the biotope surface, the loss of the stabilising algae and the disruption of the structure of the maerl bed, and can potentially change the trophic structure of maerl communities. One of the biggest threats to live and dead maerl beds is suction dredging for large burrowing bivalves such as *Ensis* and *Venerupis* species. There is insufficient information available on the relationships between species in maerl biotopes to attempt any more than a broad speculation as to the effects of predator removal, but these could be serious.

Coastal construction, landfill and channel dredging are all likely to result in increased sediment load, resulting in the smothering of maerl biotopes, but specific information is lacking. Coastal alterations such as the construction of sea defences may alter the depositional patterns with the same consequences to maerl biotopes as dredging. If the underlying substratum is altered, it is unlikely that maerl will be able to re-establish itself at that site. As a result of changes in agricultural practices, increased sediment is carried into the coastal waters by rivers - eutrophication of coastal waters might result in the excessive growth of ephemeral species of macroalgae.

Anthropogenic global warming could affect maerl distribution, due to different temperature requirements for each species. Changed weather patterns and storms, and changes in sea level, could have serious consequences for the survival of the finely balanced maerl biotopes.

### **Monitoring and surveillance options**

There are many difficulties involved in monitoring maerl biotopes. Numerous methods of sampling maerl biotopes have been used in the past, each of which has advantages for particular organismal groups in particular situations. The methods of choice for monitoring will therefore depend on the questions that need to be answered for each area. Methods of monitoring various different aspects of the maerl biotopes are currently under review and development. Different methods are appropriate for achieving particular conservation objectives.

In order to determine the extent of the maerl biotope complex, there are several types of surveillance that can realistically be carried out. In particular, the demonstration that maerl can be mapped remotely using *RoxAnn*<sup>TM</sup> processors shows that basic information on the distribution of maerl beds could be obtained relatively cheaply. A combination of Admiralty charts and remote sensing could provide rough estimates of extent of maerl biotopes. Sampling methods include towed dredges and trawls and direct diver observation are appropriate to identify maerl biotopes for biotope inventory.

For quantitative sampling of maerl biotopes, the numbers and sizes of samples and the frequency of sampling the biotope for monitoring purposes all need to be established. Suggestions can be made, however, based on statistical evaluation of the numerical variability of the organisms being studied in each maerl bed. Different sampling methods will have to be used for different objectives. For example, infauna cannot be assessed either qualitatively or quantitatively by non-destructive techniques. Appropriate sampling methods for different types of organisms are:

- sampling directly by divers using quadrats and/or cores *in situ*.
- deployment of a variety of indirect sampling gears from ships (grabs, box corers).
- Quantitative sampling of large and conspicuous species can be carried out by divers with quadrats or on towed sledges

Methods of monitoring various different aspects of the maerl biotopes are under continual review and development. The search for sentinel species that are particularly sensitive to particular impacts is continuing as part of the BIOMAERL research programme. Extrapolation from data obtained over the last few years on other marine biotopes suggests that evaluation of samples using a lower level of taxonomic expertise, e.g. to genus level only, may provide sufficient information to determine the health of the biotope.

### **Gaps and requirements for further research**

There are many gaps in our present knowledge of maerl beds, ranging from simple questions such as where the maerl beds occur, to complex problems such as the effect of environmental change on the structure of maerl communities. Although some gaps in knowledge require long-term or detailed research programmes, others can be addressed relatively simply. The demonstration that maerl can be mapped acoustically by remote sensing shows that basic information on the distribution of maerl beds could be obtained relatively cheaply.

One of the most serious questions with regard to management of maerl as a resource as well as a biotope concerns growth rates of maerl species and longevity of maerl beds. Research into the growth rates of different maerl-forming coralline algae under different conditions should be regarded as a priority.

More specific information on the use of maerl beds as nursery areas for commercially harvested species might be very useful in gaining support from the public and other users of SACs for maerl conservation.

### **Synthesis and application of information for conservation management relevant to marine SACs**

As maerl is one of the slowest-growing plant life forms, at least some monitoring should be designed to be very long-term. Short periods of monitoring, of growth rates for example, might give misleading results. Given that our understanding of the biology and ecology of maerl species and maerl biotopes is poor, management plans and monitoring programmes designed for their conservation must be robust then fine-tuned as our understanding of these systems increases. Maerl biotopes require intensive and extensive research in order to permit efficient management plans and monitoring programmes to be refined.

Some cheaper options, such as acoustic surveys, are appropriate for some maerl beds. Selected maerl beds or maerl biotopes, particularly those in SACs, should be monitored at a higher resolution. This would include faunal and flora surveys, with population monitoring of species selected for their likely importance to community structure. To achieve some conservation objectives, quantitative studies of maerl biotope species diversity and abundances, requiring intensive and time-consuming research, are necessary.

A pan-European approach to maerl bed conservation is advocated by the BIOMAERL programme. An index based on various biotic and abiotic measures would represent the overall biodiversity status of a particular maerl bed. Such an index would be capable of being monitored over time to provide a check on environmental change, especially any deterioration. It would also supply a mappable, objectively-derived descriptor that, by virtue of being independent of species composition, would be capable of direct comparison at a pan-European scale.



## I. INTRODUCTION

### A. STUDY AIMS

The goal of the present paper is to provide a scientific review of maerl biotopes, based on existing literature and current expert opinion, which will inform marine practitioners involved in the process of establishing and protecting marine SACs. The review is therefore targeted at fundamental environmental and biological attributes; sensitivity considerations for both natural and anthropogenic influences; monitoring and surveillance options; and applications for conservation management relevant to marine SACs.

### B. NATURE AND IMPORTANCE OF MAERL BEDS

#### 1. *What maerl is and why it is important*

##### a. **Maerl**

Maerl develops when coralline red algae, which have a hard calcium carbonate skeleton, become free-living due to fragmentation. Large maerl thalli are amongst the oldest marine plants in Europe. Although they are very slow-growing, the maerl thalli sometimes accumulate into flat beds, ripples or large banks of live and dead maerl, or dead maerl only. The three-dimensional structure of maerl thalli forms an interlocking lattice that provides a wide range of niches for infaunal and epifaunal invertebrates. Therefore these beds can harbour a very high diversity of organisms, some of which are more or less confined to the maerl habitat. Maerl beds are also an important source of calcium carbonate grains for other coastal habitats, especially beaches and dunes. Maerl species are very slow-growing algae, and some maerl beds are estimated to be about 8000 years old.

##### b. **Economic importance**

Maerl has traditionally been harvested on a small scale in Europe by dredging for use as a soil conditioner or for various other purposes such as a treatment for acid drinking water. Industrial extraction as an animal food additive and to replace lime as an agricultural soil conditioner reached c. 600,000 tonnes of maerl per annum in the 1970s in France alone. Maerl extraction forms a major part of the French seaweed industry, both in terms of tonnage and value of harvest. In the UK up to 30,000 tonnes p. a. of maerl were harvested commercially in the Fal from 1975 to 1991.

##### c. **Scientific importance**

Within the United Kingdom, Scotland is home to many of the most extensive maerl beds in Europe. Maerl biotopes have high species diversity, which matches that in other marine biotopes studied by similar methods. There is a small group of species that appear to be confined to maerl biotopes; many other invertebrates and algae are found predominantly on maerl. The biotopes are fragile according to most recognized categories of fragility.

It should be emphasized that records of the presence or absence of maerl biotopes on European coasts are patchy. Within Europe, detailed studies of maerl biotopes have been undertaken only in the past 40 years and at only a handful of locations. In general, maerl beds have been better studied in Europe, particularly N. France, Norway and Ireland, than in the UK. Large, historically accessible maerl banks are relatively well recorded as a result of commercial

interests. The locations of other maerl sites are known from the results of grab and dredge sampling during scientific research cruises. In more recent times, reports of maerl banks have been made by scuba divers. However, the extent of a maerl bed at any given location, its species composition, and the species associated with it, remain largely unknown.

#### **d. Conservation significance**

The value of maerl beds as a unique assemblage of biotopes is currently threatened by several types of human activity, e.g. large-scale commercial extraction, reduction of water quality by discharges, and the use of heavy demersal fishing gear. Part of the process designed to mitigate threats to these habitats is the designation of candidate Special Areas of Conservation (SACs). The maerl biotope complex has been selected as one of the biotope complexes to be reviewed scientifically in the UK Marine SACs Project for the reasons included in the list below. Assessment of the conservation value of maerl beds has previously been discussed by Hall-Spencer (1995a), who proposed most of the following points that must be taken into account:

- Maerl beds have considerable conservation value because although maerl is confined to a very small proportion of European shallow sublittoral waters, each of the beds studied to date has been found to harbour a disproportionately high diversity and abundance of associated organisms in comparison with surrounding biotopes; some of these species are confined to the maerl habitat or rarely found elsewhere.
- Some of the organisms that live within maerl beds are rare, unusual or poorly known.
- Maerl biotopes, which are relatively scarce, are currently threatened by several types of human activity. The effects of habitat removal through offshore construction activities or the commercial extraction of maerl are irreversible over timescales relevant to humans. Other severe threats to maerl habitats include poor water quality and the use of demersal fishing gear such as scallop dredges.
- The coralline algae that form the maerl are amongst the slowest-growing species in the North Atlantic so that any damage to the maerl beds may take decades to repair.
- Large beds of free-living, unsegmented, coralline algae have occurred since the Miocene in diverse environments on continental shelves around the world. Since the coralline algae contain calcium carbonate, they fossilize fairly well and can be used as stratigraphic markers and as indicators of paleoenvironmental conditions (Foster *et al.*, 1997).
- Coralline algae may be one of the largest stores of carbon in the biosphere. All plants take up carbon during photosynthesis, but coralline algae deposit large amounts of carbon in their cell walls in the form of calcium carbonate.
- Two of the more common maerl-forming species, *Lithothamnion corallioides* Crouan frat. and *Phymatolithon calcareum* (Pallas) W. Adey & McKibbin, are included in Annex V (b) of the EC Habitats Directive, 1992.
- As part of the UK's response to the European Union Habitats Directive to protect habitats, maerl is identified in the JNCC interpretation of the EC Habitats Directive as a key habitat within the Annex I category 'sand banks which are slightly covered by seawater at all times'.

- Both *Lithothamnion corallioides* and *Phymatolithon calcareum* are on the long list of species in the UK Biodiversity Steering Group Report (Anon., 1995).
- Maerl is the subject of a Habitat Action Plan under the UK Biodiversity Action Plan.
- Maerl beds occur in three demonstration SACs within the UK (**Table 3**), while the Fal and Helford (Cornwall) candidate SAC includes the largest maerl bed in England.

## 2. Definitions

We provide here some definitions of the terms that will be used in this review.

A **biotope** is defined as ‘the **habitat** (i.e. the environment’s physical and chemical characteristics) together with its recurring associated **community** of species, operating together at a particular scale’ (Connor *et al.*, 1997). The habitat encompasses the substratum and the particular conditions of wave exposure and other factors which contribute to the overall nature of the location. The term community refers to a similar association of species which regularly recurs in widely separated geographical locations.

A **biotope complex** (sometimes known in Europe as a ‘biocoenosis’) is a group of biotopes with similar overall character that should be relatively easy to identify by non-specialists or by remote/rapid sensing methods (Connor *et al.*, 1997).

**Maerl** is a Breton word (sometimes written **maërl**), and refers to loose-lying, normally non-geniculate (i.e. unsegmented because they lack decalcified joints), coralline red algae. Attempts have been made to distinguish between branched, twig-like forms (maerl in the most frequently used sense) and nodules or rhodoliths (see below), which may or may not have a non-algal core.

**Maerl beds** are composed of living or dead unattached corallines forming accumulations, with or without terrigenous material. This is the term most commonly used in the British Isles, although Irvine & Chamberlain (1994) refer to them as maerl-rhodolith beds. Elsewhere in the world, such beds are often called rhodolith beds (e.g. Steller & Foster, 1995). Dead maerl beds are often called **maerl deposits**.

**Rhodolith** (meaning red stone) is a general term covering nodules and unattached growths composed principally or entirely of coralline algae (Bosence, 1983a, 1983b). In this geological terminology, maerl is therefore a type of rhodolith. In biological usage in the British Isles, the term rhodolith is often reserved for corallines with a non-algal core (the plant may have grown to cover the shell or pebble originally colonised), but this terminology is not in accordance with that of Bosence (1983a, 1983b). There are intergrades between entirely algal growths and those those with non-algal cores, in both appearance and mode of formation, and strict definitions are probably not practical (Irvine & Chamberlain, 1994, p. 14). As noted above, in many parts of the world usage of the word rhodolith means that it can be read as a synonym for maerl in the British, biological, sense.

A **thallus** is the ‘body’ of a seaweed.

## C. SYNOPSIS OF MAERL DISTRIBUTION IN EUROPE AND IN THE UK

### 1. Maerl-forming species

There are a large number of seaweeds that deposit calcium salts within their tissues - many of these are crust-forming members of the Rhodophyceae. Of these crust-forming red algae, a proportion of the species may also be found free-living as maerl, not attached to the rock or pebble substratum. Coralline species contributing to maerl beds seem to be those capable of growing on lightweight, mobile substrata and/or continuing to grow as mobile portions of thallus after becoming detached (Irvine & Chamberlain, 1994). Several species in several genera can form maerl beds; these are differentially distributed, as summarised in **Table 1** below. Under appropriate conditions live, branched maerl can build up to 2 (-10) m above the surrounding sea floor (J. Hall-Spencer, pers. comm.), sometimes occupying thousands of square metres (Irvine

& Chamberlain, 1994). Deposits of unattached coralline algae are found in both tropical and temperate seas of the world (Bosence, 1983b).

Three main species of free-living coralline algae are reported to occur in European waters, with at least a further six (to eight) species known to contribute to deposits in certain areas (**Table 1**). *Phymatolithon calcareum* is often the most abundant maerl species, with other species usually found only as minor elements of the maerl bed.

**Table 1. Maerl-forming species in European waters** (Irvine & Chamberlain, 1994; J. Hall-Spencer, pers. comm.). See Appendix 1 for further details.

Name	Geographical range within Europe
<b>Major maerl-forming species</b>	
<i>Lithothamnion corallioides</i> (P. & H. Crouan) P. & H. Crouan	Forms maerl from Ireland and the southern British Isles to the Mediterranean
<i>Lithothamnion glaciale</i> Kjellman	Forms maerl from Arctic Russia, N. Norway and W. Baltic to northern British Isles
<i>Phymatolithon calcareum</i> (Pallas) W. Adey & McKibbin	Forms maerl from S. Norway and W. Baltic to the Mediterranean
<b>Minor maerl-forming species</b>	
<i>Corallina officinalis</i> L.	Attached thalli from Mediterranean to Norway (Finnmark); records as maerl in Brittany, Scotland and Norway
<i>Lithophyllum dentatum</i> (Kützing) Foslie	Species status and limits uncertain; records from Ireland
<i>Lithophyllum racemus</i> (Lamarck) Foslie (including British records of <i>L. duckeri</i> Woelkerling)	Limits uncertain; now thought to be a Mediterranean endemic with erroneous records from S. England and Ireland
<i>Lithophyllum fasciculatum</i> (Lamarck) Foslie	Ireland, UK and Brittany
<i>Lithophyllum hibernicum</i> Foslie	Species status uncertain; Ireland
<i>Lithothamnion lemoineae</i> Adey	Distribution unclear; encrusting plants reported from Northumberland but known as maerl only from Orkney
<i>Lithothamnion sonderi</i> Hauck	Encrusting thalli from Mediterranean to W. Baltic and Norway (Nordland) but reported as maerl only in Scotland
<i>Phymatolithon purpureum</i> (P. & H. Crouan) Woelkerling & L. Irvine	Encrusting thalli from Arctic Russia, N. Norway and W. Baltic to S. Spain; records as maerl in Brittany, Scotland and Norway

*Lithophyllum incrustans* can also occur as a maerl component, and the spectacular large *Lithophyllum* thalli found in western Ireland (e.g. Irvine & Chamberlain, 1994: fig. 23) may be attributable to this species. Recently Basso (e.g. 1995a, 1995b) has begun a taxonomic investigation of maerl-forming species in the Mediterranean. Varieties of *L. corallioides* have previously been recognized (Cabioc, 1969) but are now considered taxonomically superfluous (although they may have ecological significance).

## 2. Characteristic features of most common maerl species

Classification of maerl biotopes requires that the physical descriptors of the site (water depth, substratum composition, wave exposure regime, salinity and tidal currents) are known as well as the species of maerl-forming algae. The main species of maerl-forming algae can be difficult to tell apart without extensive experience of identification of coralline algae. The characteristic features of the three most common species of maerl in the British Isles, abstracted from Irvine & Chamberlain (1994) are summarised below (**Table 2**, with further details given in Appendix 2).



**Table 2. Comparison of morphological features of the three most common maerl species in the British Isles**

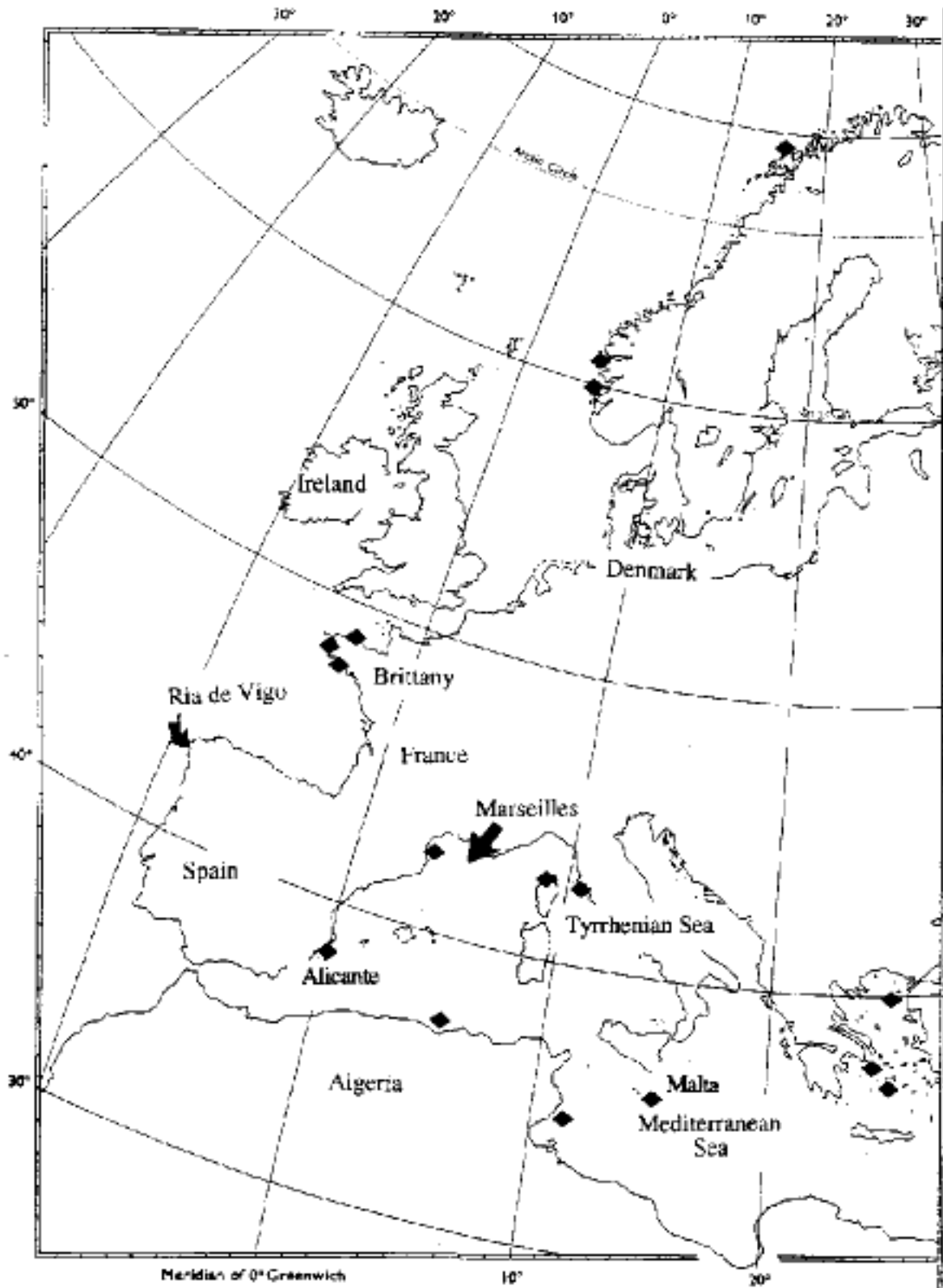
Character	<i>Lithothamnion corallioides</i>	<i>Lithothamnion glaciale</i>	<i>Phymatolithon calcareum</i>
Colour tendency (fresh)	Brownish pink	Reddish to deep pink with violet tinge	Mauvish brown
Thallus surface	Covered with low mounds	Mainly smooth, some scattered low mounds	Some lowish mounds, frequently flaky areas
Thallus texture	Slightly glossy	Matt	Somewhat chalky
Branch hardness	Brittle	Hard	Quite hard
Branch size	Mainly <1 mm diameter	Variable	Mainly >1 mm diameter

In practice, a combination of the surface texture (glossy for *L. corallioides* only) and the colour is most useful, and distinguishes quite well between *L. corallioides* and *P. calcareum*, although it is problematic for discriminating between *L. glaciale* and *P. calcareum*. The chalky surface of *P. calcareum* may be diagnostic in cases for which these latter two species are likely to be confused. To be certain, one must examine sterile thalli microscopically as identification by eye is unreliable.

### 3. *Distribution*

#### a. **European**

Distribution of European maerl species is currently being reviewed as part of the EC MAST-funded BIOMAERL programme (J. Hall-Spencer, pers. comm.). Although patchily distributed, maerl beds are found throughout the Mediterranean Sea, with important beds in Algeria (Feldmann, 1943), at Marseilles (Huvé, 1956), in Corsica and Sardinia, and in the Aegean (Jacquotte, 1962). Maerl is common on the Atlantic coasts, from Norway and Denmark in the north to Portugal in the south (extending to Morocco and Mauritania on the African coast). It is particularly abundant in Brittany



**Figure 1.** The main sites where maerl has been studied in Europe. Studies referred to are as follows: N. Norway (Freiwald, 1995); S. Norway (Foslie, 1894); Brittany, France (J. Cabioc, 1968-1983; L. Cabioc, 1968; Hily *et al.*, 1992); Ria de Vigo (Adey & McKibbin, 1970), Alicante, Spain (BIOMAERL project); Marseilles, France (Huvé, 1956); Corsica (Jacquotte, 1962); Algeria (Feldmann, 1943); Tyrrhenian Sea, Tuscany, Italy (Basso, 1995a, 1995b); Malta (BIOMAERL project).

(see J. Cabioch, 1966, 1969, 1970). Spanish maerl deposits are confined mainly to the Ria de Vigo and Ria de Arosa (Galicia, NW Spain) (Adey & McKibbin, 1970; J. Hall-Spencer, pers. comm.). In Ireland, maerl is widely distributed in the south and south-west (e.g. Galway Bay, Bantry Bay, Roaringwater Bay). *Phymatolithon calcareum* is the most widespread maerl species in Europe. Maerl is absent from large areas of Europe, such as most of the North Sea, the Baltic, the Irish Sea and eastern English Channel, presumably due to environmental constraints.

**Figure 1** shows the main sites where maerl has been studied in Europe.

## b. UK

Maerl beds are patchily distributed around the coasts of the UK. They are nearly all on exposed west coasts of Britain, where there are no major rivers carrying large quantities of suspended sediment. The dominant coastal rocks are crystalline (T. Scoffin, pers. comm.), especially in west Scotland and west Ireland, so that weathered fine terrigenous sediments are generally absent (with the exception of reworked glacial deposits). Maerl beds are typically associated with sounds or estuaries with currents but protection from strong waves.

In southern Britain, maerl beds consist of *Phymatolithon calcareum* and *Lithothamnion corallioides*. *Lithothamnion corallioides* is replaced in Scotland by *L. glaciale* (Hall-Spencer, 1995b). *Phymatolithon calcareum* is both the most widely distributed and the most abundant maerl species in the UK.

- In **Scotland**, maerl is widespread along the west coasts, in the Western Isles and Orkney and Shetland. It is known from the north coast (Loch Eriboll) but is absent from east coasts.



In **Wales** it is restricted to a small area of Milford Haven and small patches around the Pembrokeshire Islands and Lleyn peninsula.

- In **England** also maerl is rare. Living maerl (including *L. corallioides*) grows on the St Mawes Bank in the Fal Estuary, the largest known area of the biotope in England. Maerl has also been reported from the mouth of the Helford River. Deep deposits of dead plants (described as sub-fossil) are known in other parts of Carrick Roads and in Falmouth Bay and these show that maerl formerly covered a much wider area. Maerl beds are also reported from Dorset (*Phymatolithon calcareum*; Irvine & Chamberlain, 1994) and small amounts occur in the Isles of Scilly and Lundy.
- In **Northern Ireland**, extensive maerl beds are found on the north-east coasts at Garron Point and Ballygalley Head, whilst scattered maerl has been recorded from a number of sites including Church Bay, Ringfad Point, Cushendun Bay and Carlingford Lough. A thin maerl bed of small extent is present in Strangford Lough but it has not been investigated in detail (Erwin *et al.*, 1986). On the open coast maerl is found from approximately 10 m to 35 m, with dense beds at 15-25 m, whilst in Carlingford Lough it is in 2-5 m. In both cases the tidal streams are 2-4 knots. Morton (1994) cites a 19th century record of *Lithothamnion corallioides* from Belfast Lough but this is unlikely to be present now due to subsequent industrial development, the dredging of navigational channels and recent levels of sewage pollution (see Brown *et al.*, 1997).



**Figure 2.** The main sites where maerl has been studied in the UK and Ireland, and the locations of other maerl beds relevant to marine conservation (Loch Eriboll, Loch Sween, Strangford Lough, Milford Haven, Bantry Bay). Studies referred to are as follows: Shetland Is. (MNCr database); Orkney Is. (Foster-Smith & Davies, 1993); Sound of Arisaig (Davies & Hall-Spencer, 1996); Clyde Sea Area (Hall-Spencer, 1995); Galway Bay and Connemara (Bosence, 1976, 1980; Keegan, 1974; Konnecker & Keegan, 1983; Maggs, 1983a, 1983b); Roaringwater Bay (Hiscock & Hiscock, 1980).

**Figure 2** shows the main sites where maerl has been studied in the UK and Ireland. In the UK, maerl beds occur in three of the 12 project demonstration site candidate SACs, and in the Fal and Helford candidate SAC (**Table 3**). Of these sites the best studied are the Sound of Arisaig and the Fal and Helford. The extensive maerl beds in the Sound of Arisaig have been mapped by acoustic remote sensing, and sampled biologically by diving and diver-operated corers (e.g. Howson, 1994; Davies & Hall-Spencer, 1996). The Fal and Helford maerl bed on St Mawes bank has a long history of biological study, principally by a group from Portsmouth University (e.g. Blunden *et al.*, 1981, 1997; Farnham & Jephson, 1977; Farnham & Bishop, 1985) and by the NCC (Rostron, 1985) and English Nature (Davies & Sotheran, 1995). The extent of the relatively small live bed and the very extensive dead beds have been surveyed, and both fauna and flora investigated by divers. The maerl has been chemically characterised. As noted above, the Strangford Lough maerl beds have not been studied in detail and the only published work concerns the molluscan fauna (Nunn, 1992).

**Table 3. UK candidate SACs containing maerl beds**

SAC	EU habitat designations
Loch nam Madadh (Loch Maddy)	shallow inlets and bays, lagoons
Sound of Arisaig	sandbanks
Strangford Lough	shallow inlets and bays
Fal and Helford	sandbanks, mud and sand flats, large shallow inlets and bays

## D. RELEVANCE TO MNCR BIOTOPE CLASSIFICATION

### 1. Introduction

There are at present nine biotopes or sub-biotopes with maerl listed in the MNCR habitat classification (Connor *et al.*, 1997), as follows:

Code	Description
IGS.Phy	<i>Phymatolithon calcareum</i> maerl beds in infralittoral clean gravel or coarse sand
IGS.Phy.R	<i>Phymatolithon calcareum</i> maerl beds with red seaweeds in shallow infralittoral clean gravel or coarse sand
IGS.Phy.HEc	<i>Phymatolithon calcareum</i> maerl beds with hydroids and echinoderms in deeper infralittoral clean gravel or coarse sand
IGS.Lgla	<i>Lithothamnion glaciale</i> maerl beds in tide-swept variable salinity infralittoral gravel
IGS.HalEdw	<i>Halocampa chrysanthellum</i> and <i>Edwardsia timida</i> on sublittoral clean stone gravel
CGS.Ven.Neo	<i>Neopentadactyla mixta</i> and venerid bivalves in circalittoral shell gravel or coarse sand
IMX.Lcor	<i>Lithothamnion corallioides</i> maerl beds on infralittoral muddy gravel
IMX.Lfas	<i>Lithophyllum fasciculatum</i> maerl beds with <i>Chlamys varia</i> on infralittoral sandy mud or mud
IMX.Lden	<i>Lithophyllum dentatum</i> maerl beds on infralittoral muddy sediment.

All of these biotopes except for CGS.Ven.Neo (which is common) are regarded as uncommon or scarce in Britain. In Ireland, five additional biotopes with maerl have been recorded by the Biomar survey (Costello *et al.*, 1997). They also occur in the MNCR classification but maerl is not a key component in them. These are:

<b>Code</b>	<b>Description</b>
IMS.Zmar.Bv	<i>Zostera marina</i> and bivalves in sheltered infralittoral fine sand and mud
CGS.NcoBv	<i>Neopentadactyla mixta</i> and venerid bivalves in circalittoral gravel and coarse sand
IMX.An	Burrowing anemones in sublittoral muddy gravel
IMX.Ost	<i>Ostrea edulis</i> beds in shallow sublittoral muddy fine sand and shell
IGS.Lhia	<i>Limaria hians</i> nests on infralittoral medium to muddy sand

As more maerl beds are described in biological detail, spatial and temporal patchiness is increasingly being recognized. Although it is possible that more maerl biotopes will be recognized, because there are relatively few species 'faithful' to (i.e. found almost exclusively in) maerl biotopes it is probable that the species present at a particular location are a reflection of the unique environmental conditions at that site.

#### KEY POINTS

- Maerl denotes loose-lying, normally non-geniculate (i.e. not jointed), coralline red algae. Depending on the terminology used, maerl refers either to a class of rhodoliths, or may be considered distinct from rhodoliths in lacking a non-algal core.
- Maerl beds are composed of living or dead unattached corallines forming accumulations with or without terrigenous material. They can harbour a very high diversity of organisms, some of which are more or less confined to the maerl habitat. Maerl beds are also an important source of calcium carbonate grains for other coastal habitats, especially beaches and dunes. Maerl species are very slow-growing algae, and some maerl beds are estimated to be about 8000 years old.
- Maerl is legally protected under several designations, as a habitat under both the EC Habitats Directive 1992 and the UK Biodiversity Action Plan, under the habitat designations ‘shallow inlets and bays’, ‘lagoons’, ‘sandbanks’, ‘mud and sand flats’. The maerl-forming species *Lithothamnion corallioides* and *Phymatolithon calcareum* are both included in Annex V (b) of the EC Habitats Directive, and are on the UK Biodiversity Action Plan long list.
- Three main species of coralline algae are known to occur free-living in the waters around the UK, with at least a further six species known to contribute to deposits in certain areas. *Phymatolithon calcareum* is the mostly widely distributed species in the British Isles and Europe generally.
- Most maerl species can be provisionally identified by eye, but final determination of some species requires microscopical examination of prepared sections.
- Records of the presence or absence of maerl biotopes on European coasts are patchy. Maerl occurs abundantly on many west coasts, such as in Scotland, Ireland and Brittany, but it is absent from large areas of Europe, such as most of the North Sea, the Baltic, the Irish Sea and the eastern English Channel.
- The best known maerl bed sites are in Europe, particularly Brittany, Norway and Ireland, rather than the UK.
- In the UK, maerl occurs within four candidate SACs, but in one of these (Strangford Lough) it is very poorly known, while Loch Na Madadh maerl beds have been surveyed on a broad scale only. The Sound of Arisaig and the Fal and Helford maerl beds have been studied in detail.
- Nine biotopes or sub-biotopes with maerl are listed in the MNCR habitat classification, and there are at least a further five biotopes in which maerl is a minor component.
- At any given location, the extent and species composition of maerl beds and the diversity and identity of other associated species within a maerl bed are still poorly known.





## II. ENVIRONMENTAL REQUIREMENTS AND PHYSICAL ATTRIBUTES

### A. INTRODUCTION

This chapter presents an overview of the ecological requirements and physical attributes for maerl, all of which affect its distribution. Different environmental factors may influence maerl distribution interactively or synergistically - for example the interaction between water clarity and the presence of fine sediments. Although few studies have been made of the environmental requirements of maerl beds in the UK, the environmental factors leading to the observed distribution patterns of maerl beds in Europe have previously been discussed by Jacquotte (1962), L. Cabioch (1968), J. Cabioch (1969, 1970) and Bosence (1976). Bosence (1976) carried out a valuable study of some environmental aspects of the ecology of maerl in Mannin Bay, County Galway.

Detailed measurements of environmental data are current being made at several European maerl beds as part of the BIOMAERL programme. These include comprehensive sampling not only of the benthic environment of each maerl ground (including bathymetry, macro- and micro-architecture of the maerl surface, granulometry, calcimetry, organic matter content, pH and Eh profile), but also of the water column overlying the BIOMAERL study sites (including measurements of seawater temperature, salinity, Secchi disc transparency, seston content, current speed as well as chlorophyll and photosynthetically active radiation on occasion). Edaphic measurements have been collected seasonally over one to two years. Preliminary results of these studies are in broad agreement with data presented here.

We suggest that the ecological niche of both *Lithothamnion corallioides* and *Phymatolithon calcareum* is relatively narrow and subject to many controlling environmental factors. Moderate current and wave action on the one hand, but moderate turbidity and sedimentation on the other, are antagonistic conditions which help to explain the limited spatial distribution of these species in shallow coastal temperate waters.

The most significant environmental factors affecting the distribution of maerl are water movement - both currents and wave action - and the interactive effects of depth and water quality. On a geographical scale, the distribution of maerl species is strongly influenced by the temperature regime. Other physical factors, such as water chemistry, are of relatively minor importance. Maerl beds are found on a very broad range of underlying substrata.

### B. WATER MOVEMENT

#### 1. Introduction

A key physical environmental factor affecting the distribution of maerl and the biotope type is the occurrence of currents. These can be the result of tides, river influence or due to density differences arising from variation in salinity in the virtually tide-less Mediterranean, as well as the ripple-forming bottom currents resulting from wave action. In the bay of Morlaix (L. Cabioch, 1968) maerl deposits are often confined to areas where current speeds are increased by passing over rocky outcrops or sills. In areas where the maerl beds are subjected to strong tidal currents or wave oscillation they may develop into a large scale ripple pattern, with differential distributions of live and dead thalli (and of epiflora and epifauna) between the tops of the ridges and the bottoms of the gullies. These maerl megaripples have been described and illustrated by Bosence (1976) and Hall-Spencer (1995a).

## 2. Tidal characteristics

The upper limit of the living maerl is generally defined by the astronomical low-water mark since maerl thalli cannot survive desiccation. Unlike many seaweeds, maerl-forming species have a very poor ability to withstand emersion, probably only for a few minutes. It is also possible that a coincidence of the lowest tides, clearest water and mid-day sunshine could allow sub-surface irradiances which are above the tolerance limit for the maerl species or the consolidating epiphytes of the maerl bed. Tidal regime, in combination with the local water clarity, may likewise affect the lower limit of maerl by its effect on irradiance (i.e. large tidal amplitude decreases irradiance by increasing the depth of water at high tide). Currents induced by tidal movements are likely to be very important in influencing maerl distribution, in terms of the maerl biotope complex in general and the particular species present. In Galway Bay, where there are extensive live maerl beds in three main areas, only one area (in the Inner Bay) lacks moderate or strong currents. Tidal flow rates at spring tides on maerl beds in Greatman's Bay, Galway, were measured at over  $10 \text{ cm s}^{-1}$  at the surface of the maerl bed (Maggs, 1983a). Silt-free deposits of *Phymatolithon calcareum* are found at 20-30 m inshore from the Aran Islands, where the tide flow between the islands results in fairly strong bottom currents. At the only known site where large maerl banks occur intertidally, in western Ireland (Muckinish, Co. Clare), very strong tidal currents keep the maerl mobile, as large maerl waves, so that no individual maerl thallus is emersed more than briefly at low water.

## 3. Wave action

In Mannin Bay, Bosence (1976) found that dense maerl beds were restricted to less wave-exposed parts of the bay. In moderately wave-exposed and sheltered areas, different morphological forms of maerl develop under different degrees of wave action. Bosence (1976, 1983b) showed that branching of maerl is a sensitive indicator of hydraulic conditions: more stable (discoid) forms were found in areas with higher exposure to water movement whereas ellipsoid forms were less stable and occurred where there was less water movement. Wave action, like currents, can create flat areas of maerl or, more often, small ridges or megaripples in a ridge and furrow system.

Wave exposure has effects on species composition also. In Galway Bay, maerl deposits on the wave-exposed northern shore of the bay are dominated by *Phymatolithon calcareum*, while in the inner bay, the silty beds sheltered from tidal streams and wave action are formed mostly of *Lithothamnion corallioides*.

## C. LIGHT, DEPTH AND WATER CLARITY

In general, the coralline red algae are the deepest living of any of the marine algae, having been seen growing at depths in excess of 300 m (from a submersible) in the clear waters of the Caribbean (Littler *et al.*, 1986, 1991). Free-living coralline algae (rhodoliths) in tropical waters can usually be found at depths below the range of the reef-binding coralline algae associated with coral reefs. At the other extreme of the habitat range, at a few sites in western Ireland (e.g. Mannin Bay, part of Killary Harbour, and Muckinish), Brittany and elsewhere (Norway, Scotland and amongst seagrasses in the Mediterranean), maerl occurs intertidally, generally only near the extreme low-water mark.

### **Table 4. Depth range of living maerl beds in the British Isles, Europe and elsewhere**

Location	Depth range (m below chart datum)	Reference
<b>British Isles</b>		
Skye	to 20	MNCR database
Orkney	to 25	MNCR database
Clyde Sea Area	6 - 18	Hall-Spencer, 1995a
Falmouth	0-10	Blunden <i>et al.</i> , 1981
Mannin Bay	0 - 16	Bosence, 1976
Galway Bay:     outer inner	20 - 30 5 - 8	Maggs, 1983a
<b>Europe &amp; Mediterranean</b>		
Rade de Brest	0-5	Hily <i>et al.</i> , 1992
Ria de Vigo, Spain	6	Adey & McKibbin, 1970
Baie de Morlaix	6 - 17	Cabioch, 1969
Marseilles	40 - 45	Huvé, 1956
Algeria	20 - 40	Feldmann, 1943
Madeira	45	Cabioch, 1974
Cyclades, Aegean Sea	45 - 100	Jacquotte, 1962
Malta	10 - 130	BIOMAERL, unpublished
<b>Elsewhere</b>		
California	2 - 12	Foster <i>et al.</i> , 1997

The light levels under which maerl can thrive are suggested by the depth ranges in which it grows (**Table 4**), in areas where it is subject to a particular water clarity (**Figure 3**). In the Mediterranean, where water is of oceanic quality, some maerl beds are found below 100 m (Jacquotte, 1962). The Outer Galway Bay, where maerl grows down to 30 m, receives warm, high salinity southern water of North Atlantic Drift (and occasionally Lusitanian) origin (O'Brien, 1977; O'Connor *et al.*, 1993). In Mannin Bay (where water clarity is much reduced compared to the Outer Galway Bay due to the occurrence of coastal water), Bosence (1976) found that dense maerl beds were restricted to less than 8 m depth by light penetration. He reported that light was the limiting factor for maerl growth in Mannin Bay. Growth was best at 1-8 m, and ceased below 16 m at 12-13°C. In the British Isles, maerl beds have been recorded to 27 m (Irvine & Chamberlain, 1994), but are most frequently reported at depths of 1-10 m. On the Channel and Atlantic coasts of France, few maerl beds are deeper than 20 m, probably due to the turbidity of the coastal waters (Giraud & Cabioch, 1979).

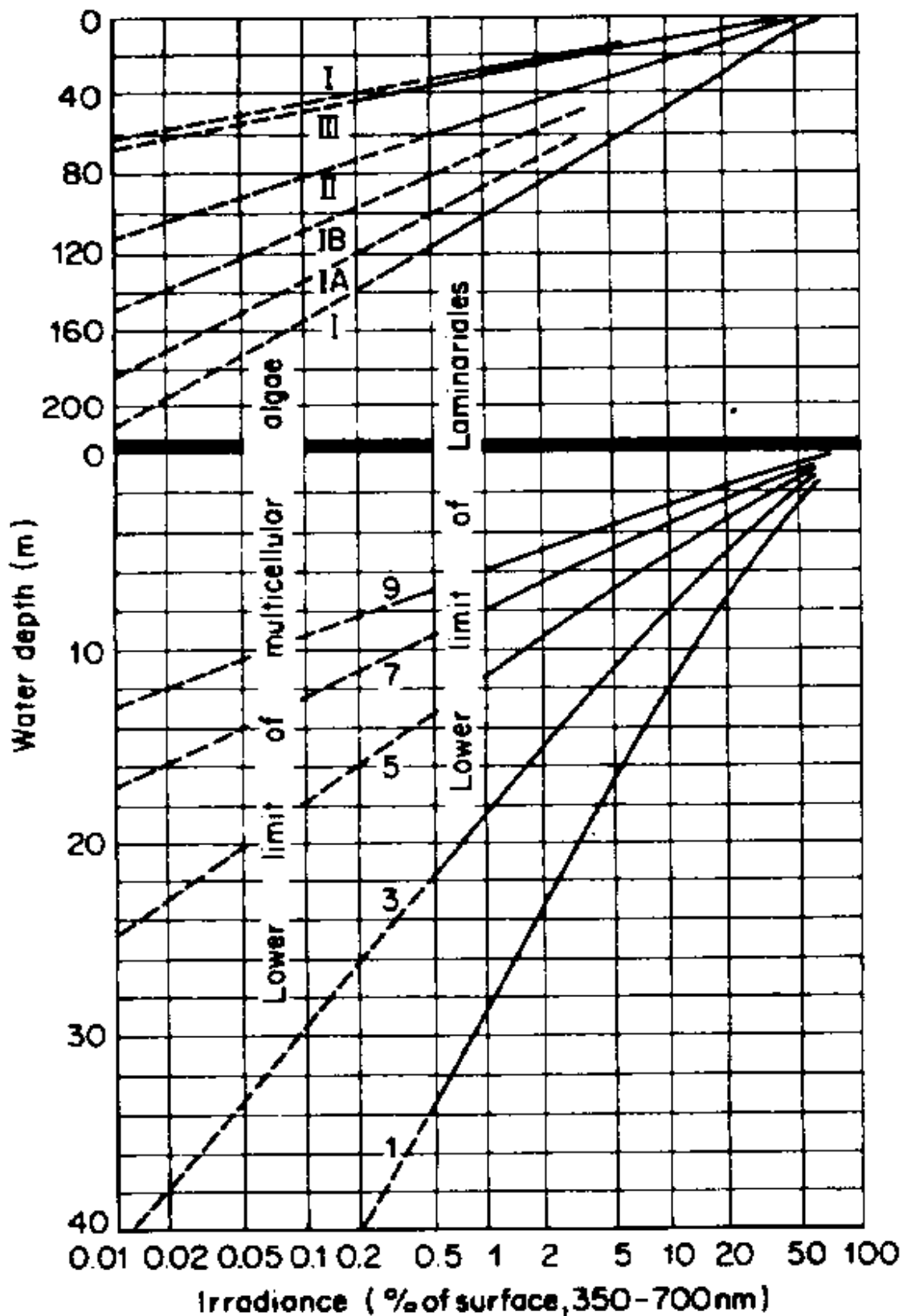


Figure 3 .

The total penetration of photosynthetically active radiation (i.e. light useful for plant growth) to depth depends on the water type. The numbered lines show the % of surface irradiance that penetrates to different depths for water of oceanic types I-III (above heavy line) and for coastal waters of types 1-9 (below heavy line). Lower limit of multicellular algae = lower limit of crustose corallines. For example, in Coastal 7 water, this would occur at 14 m, whereas in Oceanic I water the lower limit of crustose corallines is at c. 160 m. (From Dring, 1982.)

## D. TEMPERATURE

Temperature has long been known to be the primary determinant of species composition on a geographical scale, because the boundaries of biogeographical regions are associated with isotherms (Lüning, 1990). Maerl biotopes occur in a wide range of temperature regimes, from the tropics to northern Norway, but the species composition of the maerl beds is greatly influenced by temperature. Adey & Adey (1973) showed that the distribution of coralline algal species in the North Atlantic could be correlated with temperature/habitat boundaries. An obvious temperature-related maerl phenomenon in the UK is the absence of *Lithothamnion corallioides* from Scotland, either because winter temperatures occasionally drop below the minimum survival temperature of this species (between 2 and 5°C) or because temperatures do not remain high enough for long enough to support sufficient annual growth (Appendix 4). Laboratory studies on Spanish maerl (Appendix 4) showed that *Phymatolithon calcareum* survived down to 2°C, dying at 0.4°C, and the optimum temperature for growth was 15°C. *L. corallioides* had a higher minimum survival temperature, dying at 2°C, and surviving without growth at 5°C. Temperature also appears to confine *Lithothamnion glaciale* to northern parts of the British Isles. Hall-Spencer (1994) showed that *L. glaciale* only produced reproductive conceptacles in winter when water temperatures were below 9°C.

## E. CHEMISTRY

### 1. Introduction

Several aspects of water chemistry may influence the development of maerl beds. Although in the past low salinity was thought to favour maerl, this idea has been superseded by the results of salinity measurements made near the maerl surface, which show that maerl beds grow in fully saline waters and do not tolerate strongly reduced salinity. Elevated nutrient levels do not appear to affect maerl beds, and high calcium is advantageous for maerl.

### 2. Salinity

It was previously thought that the occurrence of maerl beds was related to depression of salinity, since maerl beds were commonly found near estuaries (e.g. Joubin, 1910). However, Jacquotte (1962), L. Cabioch (1968), J. Cabioch (1969, 1970) and Bosence (1976) showed that although the surface salinity in the vicinity of maerl beds in France and Ireland is often low, the bottom water is generally fully saline. In Galway Bay, the maerl beds are subject to fully saline water for most of the year, bottom salinity being measured as between 34.4 psu (practical salinity units ~ ppt) and 34.8 psu, but reduced to about 30.0 psu in February and April (Maggs, 1983a). King & Schramm (1982) found that growth of some maerl species is impaired at salinities below 24 psu.

*Lithothamnion glaciale* differs from the other maerl species, in that it can tolerate variable salinities in Scottish sealochs, where the biotope IGS.Lgl is found (Connor *et al.*, 1997). Actual salinity measurements at the biotope surface are not available.

### 3. Nutrients

Tolerance of elevated nutrient levels has been suggested by J. Cabioch (1969) on the basis of field observations of maerl distribution in Brittany, but experimental studies are still sparse. Recently, Grall & Glémarec (1997) have shown that maerl beds in the bay of Brest are

functionally intact, in terms of diversity and species richness, under eutrophicated conditions, although growth of ephemeral algae is promoted.

#### 4. Calcium

King & Schramm (1982) reported that the salient factor affecting growth of maerl in culture experiments using various salinity growth media was the calcium ionic concentration, rather than the salinity *per se*. They found an optimum uptake of calcium carbonate at 30 psu.

#### F. SUBSTRATUM

Substratum nature is an important factor in the spatial distribution of algal and faunal assemblages in general (Hily *et al.*, 1992). Maerl beds can be found in association with a range of different sediments, varying in size from fine mud to coarse gravel and pebbles (as shown in the MNCR biotopes classification in the previous chapter, and in Appendix 2). Jacquotte (1962), L. Cabioch (1968), J. Cabioch (1969, 1970) and Bosence (1976) all considered that the importance of sediments with a low proportion of fine sands and muds had previously been overestimated; in the Mediterranean maerl is often mixed with fine mud. On the contrary, some maerl species or morphological forms show a preference for finer substrata (J. Cabioch, 1969).

The density at which numbers of living thalli are to be found on different underlying substrata has apparently not been investigated in detail. In the sound of Iona (Cucci, 1979) estimated that about 22,000 thalli m<sup>2</sup> were present in the surface layer of the maerl bed, but that the proportion of living thalli varied in different areas of the sound. Keegan (1974) reported that animals associated with maerl differed according to whether it was on a soft bottom, supporting burrowing animals e.g. *Mya arenaria*, or hard, dominated by brittlestars and crinoids. Some of the underlying substratum may be mixed with maerl, or there may be no obviously terrigenous material present, the maerl bank consisting solely of living maerl overlying deposits of dead maerl.

## KEY POINTS

### Introduction

- The ecological niches of both *Lithothamnion corallioides* and *Phymatolithon calcareum* are relatively narrow and subject to many controlling environmental factors.

### Water movement

- A key physical factor affecting the type of maerl biotope and the distribution of maerl is the occurrence of seabed currents. Extensive maerl beds are more or less restricted to areas where there are moderate to strong currents. Where currents are lacking, the species composition of the maerl beds is atypical: small forms of *Lithothamnion corallioides* seem to tolerate static conditions better than *Phymatolithon calcareum* does. Maerl does not occur where there is strong wave action, so it is most common in bays and inlets.

### Depth and water quality

- Maerl-forming species are able to survive in deeper water than most seaweeds but their precise irradiance requirements are not known. The depth to which maerl penetrates depends on available light, which results from a complex interaction between light at the surface (increases at lower latitudes), tidal regime (large tidal amplitude increases mean depth of water) and average water clarity, which is related to geographical location. In the British Isles, maerl can occur to 30 m but beds are larger and deeper at depths of 15 m or less. In the clear waters of the Mediterranean, where water is of Oceanic light-absorbing quality, maerl grows to more than 100 m.

### Temperature

- Maerl biotopes occur in a wide range of temperature regimes, from the tropics to northern Norway, but the species composition of the maerl beds is greatly influenced by temperature. The species and the proportions of living maerl thalli vary in different areas. This is exemplified in the British Isles by the distribution of *L. corallioides* (restricted to southern coasts and absent from Scotland) and *Lithothamnion glaciale* (particularly abundant in Scotland).

### Water chemistry

- The chemical requirements of the maerl species, including salinity and nutrient concentrations, are not known in any detail, but maerl beds in the UK are normally found in fully saline conditions. The growth of most maerl species is reduced below 24 psu, although *L. glaciale* forms maerl beds in lagoons and sealochs subject to variable salinity. Elevated nutrient conditions do not appear to affect maerl.

### Substratum

- Maerl beds can be found in association with a range of different sediments, varying in size from fine mud to coarse gravel and pebbles, as indicated by the recognition of maerl biotopes on substrata ranging from mud to shell gravel and pebbles.





### III. BIOLOGY AND ECOLOGICAL FUNCTIONING

#### A. INTRODUCTION

This section draws together information from diverse sources on the biology and ecology of maerl species and maerl biotopes in order to provide a background for the design of efficient management plans and monitoring programmes for maerl conservation. The numbers of species and the biological variety of the species which may form part of the maerl biotopes are extensive (see appendices). For the majority of the living components of a maerl bed, not only are the interactions between different species unknown, but the basic biology of many of the component species is also unknown. Emphasis here is on the biology and ecology, as presently known, of the main maerl-forming coralline algae in UK waters, *Lithothamnion corallioides*, *L. glaciale* and *Phymatolithon calcareum*. In interpreting the results of laboratory studies on biological characteristics of these species, it must be stressed that, while maerl beds are usually composed of a combination of *L. corallioides*, *L. glaciale* and *P. calcareum*, the proportions in which the species are present may vary widely between adjacent sites and over time, and may include other, rarer, maerl-forming species.

#### B. BIOLOGICAL CHARACTERISTICS

##### 1. Introduction

Two fundamentally different growth forms of *L. corallioides*, *L. glaciale* and *P. calcareum* can be found. The plants may form crusts attached to rock, pebbles or sometimes shells, or they may be free-living, growing as nodules, rhodoliths or as branched structures resembling “jacks” or caltrops. Only two crustose plants of *L. corallioides* have been recorded from UK waters (Dorset and Devon; Irvine & Chamberlain, 1994) and none of *P. calcareum*. *L. glaciale* on the other hand is commonly found both in the free-living and attached forms although it has frequently been misidentified as *L. corallioides* in the more northerly parts of the British Isles (Hall-Spencer, 1995b). Maerl beds are usually composed of one of a combination of *L. corallioides* and *P. calcareum* or, in Scotland, *L. glaciale* and *P. calcareum*. The proportions in which the species are present may vary widely spatially and temporally.

##### 2. Life history

Jacquotte (1962) and Cabioch (1969, 1970) reported that juvenile plants of the maerl species grow as crusts on pebble or shell substrata. Erect branches formed by these crusts break off and give rise to maerl thalli. Thus two growth forms of *Lithothamnion corallioides*, *L. glaciale* and *Phymatolithon calcareum* occur: encrusting or free-living.

In Brittany, recruitment to free-living maerl populations was predominantly from branches shed from crustose plants; vegetative propagation from unattached plants was rare (Cabioch, 1969). Freiwald (1995) likewise found that free-living *L. glaciale* maerl in N. Norway originates from branched attached crusts. Huvé (1956), by contrast, reported that fragmentation of free-living maerl thalli was the main method of reproduction in the maerl beds near Marseilles. Propagation from branches shed from crustose plants may also occur in Madeira and Tenerife, where crustose plants are frequent, but in UK waters, as noted above, crustose plants of *L. corallioides* and *P. calcareum* are extremely rare or unknown (Irvine & Chamberlain, 1994). Unattached plants of these species must therefore be almost entirely vegetatively propagated. *Lithothamnion glaciale*, on the other hand, is commonly found in both the free-living and attached forms.

### 3. *Reproduction*

Most authors working on the taxonomy or ecology of maerl species comment that reproductive organs are rarely found. During a 2-year-long monthly sampling sequence in maerl beds in Galway Bay, Maggs (1983a) did not find any fertile thalli of *L. corallioides*. Only one fertile plant of *L. corallioides* has been reported for the British Isles, an epilithic plant from the south coast of England. In Galway Bay, only tetrasporangial conceptacles were found for *P. calcareum*. At one site, these varied between an average of 1 and 3 thalli per sample (except during May and June when none were found), representing less than 1% of thalli. At a second site nearby, an average of 1 to 14 fertile thalli were found per sample, with a mid-summer maximum, although fertile plants were found throughout the year. Many hundreds of specimens of *P. calcareum* and *L. corallioides* were collected in the Ria de Vigo (Adey & McKibbin, 1970) of which only 24 and 3 plants respectively showed evidence of conceptacles. Of these, only about 6 plants (all *P. calcareum* collected in March-April) had developing conceptacles, all the others being mature or degenerate.

In the baie de Morlaix, Brittany, Cabioch found *P. calcareum* with tetrasporangial conceptacles in the winter and *L. corallioides* with tetrasporangial conceptacles mainly in the winter; she suggested that phasic reproduction occurred, reaching a peak perhaps once in 6-8 years (Cabioch, 1969). This may explain the observed variations in the continually changing proportions of the different maerl species forming a maerl bed (Cabioch, 1969). Depending on the length of time since the most recent reproductive event and the relative success of the settlement and colonisation, one species may become dominant within an area of maerl in terms of numbers of live plants. This dominance may decline with time as the plants die and another species becomes reproductive. Dominance cycles with periods of about 30 years have been recorded on some of the maerl beds of northern Brittany.

By contrast, *Lithothamnion glaciale* plants have reproductive conceptacles all year in Greenland and Sweden (Rosenvinge, 1917; Suneson, 1943). In Scotland, however, although conceptacles are common in winter, the thalli are sterile in summer (Hall-Spencer, 1994).

### 4. *Growth rates*

#### a. **Introduction**

Very few experiments to measure the growth rates of coralline algae have been attempted, due to the technical difficulties of working on these organisms, particularly the maerl morphologies. Results reported to date suggest that there are wide variations (between species, between geographical areas, and seasonally) in growth rates of maerl whether measured as gross calcium carbonate production, or as apical extension of maerl branches. Further work is currently ongoing to determine 'typical' growth rates for maerl (Fazakerley, 1997; Fazakerley & Guiry, 1998; Hall-Spencer, pers. comm.).

#### b. **Calcium carbonate accumulation**

Gross measurements of calcium carbonate accumulation have been made for some maerl beds; these show a high degree of variation. *Lithothamnion corallioides* and *Phymatolithon calcareum* accumulated over 400 g CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup> in Ireland (Bosence, 1980). On the basis of buoyant density measurements of baskets of live maerl, *L. corallioides* was estimated to produce 876±292 g CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup> at a shallow site in the rade de Brest (Potin *et al.*, 1990). On the Mallorca-Menorca shelf most of the modern algal carbonate production occurs at depths of less

than 85-90 m, which is the lower limit of the coralligenous and maerl communities (Canals & Ballesteros, 1997). Maerl beds in moderately deep waters (40-85 m) formed  $210 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ . These growth rates are similar to those for the temperate crustose species *Lithophyllum incrustans* of  $379 \text{ g m}^{-2} \text{ yr}^{-1}$  (Edyvean & Ford, 1987) but an order of magnitude lower than that of the tropical reef coralline genus *Porolithon* ( $3120 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) measured by Johansen (1981). Much lower estimates of only 16-41  $\text{g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  were made by Cucci (1979) for maerl deposits in the Sound of Iona, perhaps indicating less than optimal environmental conditions.

### c. **Thallus growth rates**

Field growth rate measurements were made by Adey & McKibbin (1970) on numerous individual rhodoliths of *P. calcareum* and *L. corallioides* in the Ria de Vigo (Appendix 4). The study was conducted on maerl beds at a depth of 5-6 m below low water. Using repeated photographs as well as physical measurements, they determined that the growth rates of branch tips on the rhodoliths were very slow. Little or no growth was recorded during the winter months (less than  $1 \mu\text{m d}^{-1}$  between October and March) with maximum growth occurring in June and July. In total their estimates indicate an annual growth rate of  $0.55 \text{ mm yr}^{-1}$  for branch tips of *P. calcareum* and  $0.10 \text{ mm yr}^{-1}$  for *L. corallioides*. According to their calculations based on ambient temperatures and irradiance, mean yearly growth in the south-western British Isles would be less than 1 mm per year. Böhm *et al.* (1978), however, calculated apical branch elongation of Baltic plants of *P. calcareum* as 0.5-2.7 mm per year. Potin *et al.* (1990) likewise found the maximum growth rate of *L. corallioides* in Brittany (0.26% per day) to occur in July, and the minimum in February, but the rates cannot be compared directly with those recorded by Adey & McKibbin (1970) due to different methodology.

More recently, Fazakerley (1997) and Fazakerley & Guiry (1998) have carried out pilot studies on the growth rates of *Lithophyllum dentatum*, *Lithophyllum fasciculatum* and *Lithothamnion corallioides* in Kingstown Bay, Connemara, by tagging 20 individuals of each in very shallow water. Mean growth of the three species over the 30-week period was  $5.93 \mu\text{m d}^{-1}$ ,  $5.14 \mu\text{m d}^{-1}$ , and  $2.57 \mu\text{m d}^{-1}$  respectively. These were increases in the diameter of the thalli, so represent approximately double the apical growth rate. The overall increase in the diameter of *L. corallioides* thalli over 7 months (July to January) was 0.96 mm, or approximately 1 mm tip growth per year. This figure, although very low by comparison with other algae, is nevertheless an order of magnitude higher than Adey & McKibbin's (1970) figures for Spanish maerl. The differences recorded may be related to different methodology (the Spanish thalli were tied to a line while the Irish ones were free) and highlight the difficulties of extrapolating from the results of single studies.

A comparison with the encrusting species *Lithophyllum incrustans*, for which extension of the margins was a mean of  $2.9 \text{ mm yr}^{-1}$  (Edyvean & Ford, 1987), shows that maerl growth rate appears to be of the same order as that of temperate encrusting corallines.

## C. ECOLOGICAL ROLES

### 1. *Community structure*

To date, little work has been carried out explicitly from the point of view of community structure, although a study is currently underway in Brittany as part of the BIOMAERL programme. However, considerable relevant information is available from studies of maerl species and of other organisms.

Many coralline algae produce chemicals which promote the settlement of the larvae of certain herbivorous invertebrates. The herbivores then graze off the epiphytic, and often fast-growing, algae which might otherwise overgrow the coralline algae, competing for light and nutrients. Another strategy for maintaining epiphyte-free surfaces of coralline algae has recently demonstrated in Japanese representatives of the crustose genus *Lithophyllum* (Suzuki *et al.*, 1998). The allelopathic production of chemicals by the crust directly prevents overgrowth by epiphytes.

The presence of herbivores associated with corallines can generate patchiness in the survival of dominant seaweeds. In addition to the ecological importance of live maerl beds, which is described below, dead maerl contributes in two ways. Firstly, dead maerl supports diverse communities, although these are generally reported to be less rich than those in live maerl beds (Keegan, 1974). Secondly, maerl is one of the sources of subtidal and beach-forming calcareous sediments. In Scotland, maerl can form up to 4% of calcareous sediments (Farrow *et al.*, 1978).

There are numerous features of maerl that contribute to its value as a habitat for other marine species (Nunn, 1992):

- It provides a surface to which other seaweeds e.g. *Plocamium cartilagineum* can attach. Other organisms, e.g. *Aplysia punctata* and rissoids, then feed on these seaweeds.
- It can be grazed itself by organisms such as *Tectura (Acmaea) virginea*.
- The algal film and detritus can also be grazed by e.g. *Jujubinus montagui*.
- It provides attachment sites for animals which in turn are food for others, e.g. *Antedon bifida*, hydroids, bryozoans.
- The infauna in maerl beds includes many bivalves, e.g. *Mya truncata*, *Dosinia exoleta*.
- Its loose structure provides shelter, e.g. for small gastropods.

### 2. *Trophic groups and microhabitats*

#### a. **Fauna**

Bosence (1979) carried out a community analysis of all animals associated with maerl in Mannin Bay, Galway (**Table 5**), classifying them into vagile (i.e. mobile) epifauna, sessile epifauna, burrowing infauna and boring infauna, and further indicated their trophic group (herbivore, carnivore/scavenger, deposit feeder, suspension feeder, commensal). The maerl bank community was characterized by abundant vagile epifauna. Gastropods were common in the lattice formed by the maerl, the most abundant species being the herbivores *Bittium reticulatum* and *Gibbula*

*cineraria*. Small decapod crustaceans such as *Porcellana longicornis* and *Galathea squamifera* could move within the maerl lattice, while larger species formed burrows or swam over the surface. More recently, Grall & Glémarec (1997) have examined the community structure of maerl at control and impacted (eutrophicated or harvested) sites in Brittany using multivariate analysis (see Sensitivity to human activities).

**Table 5. Most abundant fauna in maerl beds in Mannin Bay, Galway, classified by habitat and trophic group (Bosence, 1979). Includes only species found at a maximum abundance  $\geq 10$  per  $0.25 \text{ m}^2$ .**

Species name	Habitat and trophic group	Maximum abundance (per $0.25 \text{ m}^2$ )
<i>Bittium reticulatum</i>	Vagile epifauna; herbivore	270
<i>Gibbula cineraria</i>	Vagile epifauna; herbivore	93
<i>Porcellana longicornis</i>	Vagile epifauna; carnivore/scavenger	74
<i>Rissoa parva</i>	Vagile epifauna; herbivore	40
<i>Idotea</i> sp.	Vagile epifauna; scavenger	30
<i>Tricolia pullus</i>	Vagile epifauna; herbivore	
<i>Xantho</i> sp.	Vagile epifauna; carnivore/scavenger	24
<i>Musculus discors</i>	Sessile epifauna; suspension feeder	80
<i>Golfingia</i> sp.	Burrowing infauna; deposit feeder (commensal)	16
<i>Mysella bidentata</i>	Burrowing infauna; suspension feeder (commensal)	40
<i>Lucinoma borealis</i>	Burrowing infauna; suspension feeder	11
<i>Hiatella arctica</i>	Boring infauna; suspension feeder	10

## b. Algae

Both floristic and faunistic studies have focussed on biodiversity aspects of maerl communities, as discussed in the next chapter. Some of the epifloral species listed in Appendix 5 may be key to the integrity of the maerl bed, either physically binding the maerl or biologically interacting within the biotope.

Although bare maerl substratum occurs throughout the year, competition for space between crustose species is high. The chemical and growth rate interactions between crustose algae in competing for space have been investigated (Fletcher, 1975; Maggs, 1983a) and some crustose species are known to slough epithelial layers as a means of reducing epiphyte cover. These mechanisms make for continual shifts in the population of the epiflora and promote the diversity of the maerl biotope flora. Changes in the environment of the maerl biotope, particularly any which influenced the interactions of the coralline species, might affect settlement of the epiflora, changing the species mix, probably reducing the epifloral diversity and possibly resulting in the dispersion of the maerl bed. Alternatively, reduction of epiphytism by some species could enhance the growth rate of maerl due to increased penetration of light to the maerl thalli.

Several species of red and green filamentous algae are common borers into maerl (Cabioc, 1969), and may contribute to the breakup of maerl thalli. As noted above (under Reproduction), the most important maerl-forming species, *Phymatolithon calcareum*, rarely produces conceptacles. The main way maerl beds of this species build up is through fragmentation. J.

Hall-Spencer (pers. comm.) has noted that it can colonise new areas of sedimentary substrata by transport of live thalli attached to algae - particularly *Laminaria saccharina* and *Phycodrys rubens* in Scotland. These large algae can transport maerl over considerable distances after storms.

### 3. *Keystone and associated species*

The various maerl species can be regarded as keystone species within the maerl beds in which they occur because the community depends on their biological and structural characteristics. However, the integrity of some forms of maerl bank in turn requires at least some elements of the rich epiflora associated with it, and interactions with invertebrate grazers are also very important in keeping open substratum clear for settlement by algal and animal species. It should be pointed out here that some of the deeper Scottish maerl beds are floristically poor so that this does not apply to them (J. Hall-Spencer, pers. comm.).

In general, maerl beds form a fragile and easily disturbed habitat for a rich assemblage of seaweeds and invertebrates. Under some conditions, they can be relatively stable communities over long timescales. In Northern Norway, for example, although the maerl beds have fluctuated with glaciation-related changes in the relative sealevel and shore position, the oldest layers within the accumulated sediments have been  $^{14}\text{C}$  dated to about 6000 years old (Freiwald *et al.*, 1991). Individual pieces of dead maerl in the Sound of Iona, Scotland, were dated at c. 4000 years old (Farrow, 1983).

Both Jacquotte (1962) and Cabioch (1969) discussed the importance of various prostrate algae in stabilising the maerl deposits by the formation of stolons and secondary attachments (see **Table 6**). These growths apparently act as an effective means of vegetative reproduction for these prostrate species, several of which were never observed with reproductive organs. The morphology of *Gelidiella calcicola* (as *Gelidiella* sp. in Cabioch, 1969), which is largely confined to maerl, seems to have evolved in response to the maerl habitat. Unlike other gelidiacean algae, it forms no erect axes - all axes bend down at the tips and reattach to the maerl by specialised peg-like holdfasts that penetrate into the maerl.

**Table 6. Species of algae reported to stabilise maerl beds**

Species name	Maerl bed location studied	Reference
<i>Gelidium</i> sp. (Rhodophyta)	Mediterranean	Jacquotte, 1962
<i>Flabellia petiolata</i> (Chlorophyta) <i>Polysiphonia setacea</i> (Rhodophyta)	Mediterranean	BIOMAERL, in press
<i>Laminaria saccharina</i> (Phaeophyta)	Scotland	J. Hall-Spencer, pers. comm.
<i>Gelidiella calcicola</i> <i>Brongniartella byssoides</i> <i>Audouinella floridula</i> <i>Spermothamnion repens</i> (all Rhodophyta)	Brittany and Ireland	Cabioch, 1969 Maggs & Guiry, 1987a

In general, the seasonal stabilisation of maerl beds is advantageous, permitting the summer growth of many larger algae, but clearly, if the structure became permanently bound together by excessive algal turfs, this could affect the nature of the maerl bed detrimentally. It may be significant that the alien red alga *Polysiphonia setacea*, which stabilises maerl beds in the

Mediterranean, is currently increasing greatly in abundance and may soon affect the majority of Mediterranean maerl beds.

Invertebrates are also important in the structural integrity of maerl. The bivalves *Modiolus modiolus* and *Limaria hians* bind maerl together with their byssal threads. Deep burrowers and tube dwellers (e.g. *Cerianthus*, *Sabella*, *Chaetopterus* and *Upogebia*) can stabilise surface sediments. Crabs (*Cancer pagurus*) and starfish (*Asterias rubens*) dig pitfall traps to catch prey.

#### 4. *Nursery areas*

Suggestions have been made that maerl beds may be important nursery areas for commercially valuable molluscs and crustaceans. However, maerl has been little-studied as a habitat for the juvenile stages of demersal and pelagic fish species. Divers visiting maerl beds or collecting samples for maerl studies have commented on the large numbers of small individuals of many species that can be seen, and certainly the open structure of a maerl bed would provide a secure habitat for juveniles as well as a wide range of flora and fauna as food for them.

The nursery interpretation of maerl biotopes is rather controversial (e.g. in south-west Ireland no nursery activity was observed during maerl bed surveys; S. de Grave, pers. comm.) but there is some good evidence that maerl beds are nurseries for at least a few species. In Co. Clare, maerl deposits are known to act as nursery grounds for the black sea urchin *Paracentrotus lividus*. Juvenile urchins can be obtained for aquaculture purposes by dredging small quantities of maerl and removing the urchins using benzocaine (Minchin, 1997). In these maerl beds, densities of more than 1600 individuals per square metre of surface area (down through the depth of the maerl) have been counted (Keegan, 1974). In France, juvenile scallops have been collected experimentally from spat collectors placed over maerl (Thouzeau, 1991). Similarly, the presence and abundance of scallop spat in benthic samples from the west of Scotland (Sound of Raasay) was apparently correlated with the presence of maerl (D. McKay, pers. comm.).

#### 5. *Flora/fauna interactions*

##### **a. Spatial competition**

Spatial competition between flora and fauna was not generally noted as a major factor of population structure control (Hily *et al.*, 1992) in the maerl beds of the rade de Brest. However, at a few locations the abundance of large suspension feeders (e.g. the ascidian *Phallusia mamillata*) was such that they occupied more than half the available surface area. In sites such as these it was noted that opportunistic algae were best adapted to compete for space. Bosence (1979) described competition for space between encrusting algae and animals in Mannin Bay. Bryozoans and foraminiferans were overgrown by coralline algae, whereas *Halichondria*, *Anemonia sulcata* and serpulids overgrew the living maerl.

**b. Herbivory**

The presence of both generalist and specialist herbivores is essential for the health of maerl beds. Generalist herbivores graze off epiphytic algae which might otherwise shade the coralline algae. There is constant erosion of the surface of the maerl by sea urchins and specialist grazers such as the small limpet *Tectura virginea*. Around the UK, *T. virginea*, which also feeds on shell-boring algae (Farrow & Clokie, 1979), is one of the main grazers on maerl. Very large populations may be found and it is likely that these small limpets settle selectively on coralline algae, as has been shown for *Haliotis* species (abalone) by Morse & Morse (1984). The surface of the maerl is kept clear of microalgae and algal sporelings by the feeding activities of *Tectura*, so that bare substratum is always available. The radula action also wears away the surface layers of maerl thalli creating a clear and more easily penetrable surface for settlement of algal spores.

Population densities of *Sphaerechinus granularis* of 2-3 m<sup>-2</sup> were found to affect the algal cover, on small temporal and spatial scales, on maerl beds in the rade de Brest (Hily *et al.*, 1992) but on a larger scale and longer time span, it was suggested that the grazing pressure was not of an intensity to modify the species composition of the assemblage. Maggs (1983a), however, reported that the high diversity of algae on maerl in Galway Bay (50-80 species of epiphytic algae per sample depending on sample size (300 cm<sup>3</sup> or 1500 cm<sup>3</sup>)) might be due in part to the reduced grazing pressure relative to hard substrata. The microtopography of the maerl itself provides some protection from grazers in that the interlocking, branched shapes restrict access to larger grazing species.

Boring polychaetes and sponges probably affect production rates and may be involved in maerl fragmentation. The most conspicuous borer into live algae is the polychaete *Polydora*, which is thought to bore both mechanically and by chemical activity (Bosence, 1979).

**c. Changes to the substratum**

One of the principal substrata in several maerl biotopes is mollusc shells, present usually as shell gravel, but also as variable quantities of intact shells. Intact shells are favoured by large species of algae, such as young kelps. In the rade de Brest, the population dynamics, particularly the mortality rates, of the shelled molluscan species in the maerl beds had an indirect effect on the algal population (Hily *et al.*, 1992). The dead shells formed a major substratum for the algae, but as the attached biomass increased, the shell/algae assembly became more buoyant and susceptible to transport by tide and wave currents, thus moving the shell support shoreward and removing the attached species of algae from the population of the maerl bed.



## KEY POINTS

### Biological characteristics

- Two fundamentally different growth forms of *Lithothamnion corallioides*, *L. glaciale* and *Phymatolithon calcareum* occur. Plants may form crusts attached to rock, pebbles or sometimes shells, or free-living thalli, growing as nodules, rhodoliths or branched structures. In some areas, the free-living thalli originate from branches of the crustose forms, but in other areas crustose thalli are not important in the life history.
- Reproductive organs are rarely found in some maerl species and frequencies of reproductive thalli vary seasonally from site to site.
- Unattached *L. corallioides* and *P. calcareum* thalli in UK waters are probably almost entirely vegetatively propagated. This has important implications for management: if large quantities of living maerl are removed for any purpose, or killed (e.g. by scallop dredging) then the chances of biotope regeneration are greatly reduced.
- Growth rates vary for different maerl species, between seasons and between sites. Growth rates have only been measured for a few species at a few sites, but the consensus from these studies is that maerl grows very slowly in comparison to most seaweeds in UK waters (up to a few mm per year), and an order of magnitude more slowly than tropical coralline algae.
- The slowest growing maerl species is *L. corallioides*, for which tip extension rates of 0.1 and 1.0 mm per year have been measured in Spain and Ireland respectively.

### Ecological role

- The few floristic and faunistic studies undertaken to date have focussed on the biodiversity aspects of maerl biotopes, rather than on interactions and community structure, although an EC MAST programme (BIOMAERL) is currently addressing these issues.
- Changes in the environment of the maerl biotope would affect settlement of the epiflora, possibly resulting in the dispersion of the maerl bed.
- The maerl species themselves can be regarded as keystone species within the maerl bed, as can the various creeping algae which are important in stabilising the beds. However, these species, their distributions and frequency within the different biotopes are known only for a few sites.
- The potential importance of maerl as a habitat for the juvenile stages of demersal and pelagic fish species has not been specifically addressed, but maerl may be an important biotope for nurseries of some molluscs and crustacea.
- Interactions between the flora and fauna have rarely been specifically investigated. Competition for space, herbivory and changes in the biological component of the substratum have all been noted to affect the flora and fauna. Boring algae and polychaetes may be important in fragmenting, and thereby propagating, maerl.



## IV. BIODIVERSITY

### A. INTRODUCTION

The maerl beds of Brittany and of the Mediterranean have long been recognized as communities with a particularly high diversity of plant and animal species. In the British Isles, there may be somewhere in the range of 150 macroalgal species found on maerl (see Appendix 5), and 500 benthic faunal species (over 400 were found in Scotland alone; Scott & Moore, 1996; Appendix 6). Numbers and identities of microflora and microfauna and protozoan and fungal species on maerl are almost entirely unknown. Attempts have been made to document as far as possible the entire flora and fauna of maerl beds within a given area. Hall-Spencer (unpublished) has produced a preliminary species list for the flora and fauna of the Clyde, while knowledge of animals and algae living on maerl on the west coast of Ireland has been accumulating for the last three decades (Keegan, 1974; Maggs, 1983a; Maggs & Guiry, 1987; O'Connor *et al.*, 1993; O'Connor & McGrath, 1997).

Biodiversity of maerl beds has been examined in Europe and the British Isles in regard to:

- comparisons with other biotopes in the same geographical area;
- comparisons between maerl beds in different geographical areas;
- seasonal changes in biodiversity; and
- local differences (e.g. proportion of live thalli).

### B. TAXONOMIC CONSIDERATIONS

One of the most important aspects of biodiversity studies on maerl is the consideration of the serious taxonomic problems involved. The algae include a high proportion of winter-fertile crustose species, which are rarely collected with the reproductive organs essential for identification. Accurate identification of epiphytic coralline algae and boring green and red algae requires a long protocol including decalcification, staining and mounting of specimens. A further problem is posed by the occurrence of heteromorphic life histories among species common in the maerl epiflora. Problems with identification of the animals present may be exacerbated by the presence of sibling species in several genera.

The frequent use of large mesh sizes for sieving of samples is another problem. Recent studies of meiofauna have shown that there may be undescribed or very rare species present, some of which may be restricted to maerl (Davies & Hall-Spencer, 1996; O'Connor & McGrath, 1997). During the course of an extensive survey of macrobenthic communities in the greater Galway Bay area, maerl locations were sampled by different methods (O'Connor & McGrath, 1997). Sampling at South Bay, off Inisheer and at Casla Bay was carried out with a dredge and the mesh size used for washing the samples was 2 mm. The macrofauna was dominated by a number of characteristic bivalve and echinoderm species, e.g. *Venus fasciata* and *Neopentadactyla mixta*. More detailed work in Kilkieran Bay based on diver-collected samples which were relaxed with menthol crystals revealed a variety of species from a number of phyla which are either unrecorded or poorly recorded from Irish waters. Many of these organisms are <2 mm and were therefore lost in earlier surveys (O'Connor & McGrath, 1997).

### C. COMPARISONS WITH OTHER BIOTOPES

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Although maerl beds are analagous in many ways to kelp forests and seagrass beds (BIOMAERL, in press), to our knowledge there have been no overall comparisons of the diversity of maerl fauna and flora with those in equivalent samples from other biotopes. However, the algal diversity on maerl in Galway Bay (Maggs, 1983a, 1983b) can be compared with algal diversity in photophilic algal communities in the Mediterranean (Coppejans, 1980). Similar methods and sample sizes were used in both studies, showing that Galway Bay maerl flora is as diverse (average of 60 species per 300 cm<sup>3</sup> sample at 10 m depth) as these highly speciose Mediterranean communities (average of 70 species per 400 cm<sup>2</sup> sample).

The branching of the maerl thalli provides shelter for small plants and animals, and the communities in the maerl beds are much richer than those on gravel or shell bottoms of an equivalent granulometry (J. Cabioch, 1969). Biodiversity in maerl, particularly of the faunal elements, has rarely been compared with that of other sedimentary substrata and with rock. Bosence (1979) found that maerl banks had more abundant epifauna and boring infauna than other sediments in Mannin Bay, such as sand and gravel. However, the overall species richness in maerl, as judged from his tables of animals found in each substratum type, was lower than in muddy algal gravel and clean algal gravel, similar to that in fine sand, but greater than in mud communities. Earlier workers such as L. Cabioch (1968) were concerned that the maerl 'biocoenosis' (equivalent to biotope complex) might be only a form of the '*Venus fasciata* biocoenosis'. Later multivariate analysis (e.g. O'Connor *et al.*, 1993) showed that maerl faunas were a distinct assemblage that clustered with other sedimentary faunas.

There are several reports of mobile substrata (i.e. substrata that move at least occasionally, e.g. stones, shells, maerl) supporting a more diverse algal community than the adjacent solid substratum (Lieberman *et al.*, 1979; Sears & Wilce, 1975). In Galway Bay, the diversity of the algal community of maerl beds was very high compared with that of the surrounding habitat (Maggs, 1983a). The rocky outcrops adjacent to these maerl beds were subject to heavy grazing pressure by *Echinus esculentus* and these rocks supported only 24 algal species per 0.09 m<sup>2</sup>, of which 13 were epiphytic on the larger algae. Samples of a similar surface area collected on the nearby maerl beds contained a year-round average of 46 species (Maggs, 1983a).

Unstable sediments such as shell or maerl banks may act as a reservoir for weakly competitive algal species, living on the fringes of their distribution range (Waern, 1958, p. 332). Most studies have been of cobbles or shells. Waern (1958) examined algae growing on deposits of dead shells off the west coast of Sweden; Kain (1960) briefly described the algae growing on pebble and gravel bottoms off the Isle of Man; Sears & Wilce (1975) and Connor (1980) included shell bottoms in their study of algal communities in North America; Lieberman *et al.* (1979) reported on the ecology of seasonally devastated cobble substrata off Ghana.

#### D. GEOGRAPHICAL COMPARISONS BETWEEN MAERL BEDS

Maerl epiflora and fauna has been compared between and within geographical areas by several workers. For example, Jacquotte (1962) reported that the fauna of maerl beds in the Mediterranean was more diverse than the maerl beds of Brittany. However, these rough comparisons were based on very limited data. Given the paucity of detailed information concerning the biodiversity of European maerl beds, it is difficult to say which exhibit the highest diversity. As a general rule, Mediterranean biotopes have a high species diversity but low productivity due to low nutrient concentrations (Boudouresque, 1993). On Atlantic coasts,

preliminary comparisons of maerl biodiversity are possible for seaweeds and molluscs which have been relatively well studied.

For example, a total of 123 live species of mollusc were found by Nunn (1992) in maerl beds in Scotland and Ireland, while Hall-Spencer (1998) found 130 species on two very small areas of maerl in the Clyde (**Table 7**; Appendix 5). Data in Table 7 indicate that maerl biotopes can exhibit impressive levels of biodiversity. Those from Galway Bay seem to be particularly species-rich for algae compared with the west of Scotland. Although this may be related to the small number of samples examined from Scotland, maerl beds off Coll and Tiree, Hebrides, undoubtedly support a much reduced epifloral community compared with that found on the maerl beds of the more southerly Galway Bay. Factors that are probably involved include the northern distributional limits of some species lying to the south of the Hebrides, the lack of *Lithothamnion corallioides*, as this species tended to support a higher diversity of algae in Galway Bay than did *Phymatolithon calcareum* beds, and the greater wave action to which these beds are exposed. High wave-exposure is correlated with low species richness (see Local variations section below). The relatively low overall total for the Fal is a result of a single period of collecting, by contrast with the extended sampling in Galway Bay. There is no clear pattern for the molluscs.

**Table 7. Comparison of species diversity (ie richness) reported by different authors, for algae and molluscs in maerl beds of the British Isles**

Samples collected by Maggs were all equivalent (300 cm<sup>3</sup>); see Appendix 5 for more details

Reference	Location and depth range (m below chart datum, where available)	Number of species (total recorded or no. found in limited samples)
<b>Algae</b>		
Maggs, 1983a	2 sites in Galway Bay; 5 and 10 m	147 (total); mean per summer sample set, 51-58 (n = 6)
Maggs in Dipper, 1981	Coll & Tiree, Hebrides; 14-19 m.	28-35 per sample (n = 3)
Maggs in Dipper, 1981	Coll & Tiree, Hebrides; 9 m.	43 (in samples)
Hall-Spencer, 1998	Clyde Sea area; 10 m	57 (total)
Davies & Hall-Spencer, 1996	Sound of Arisaig, 2-21 m	85 (total)
Howson, 1990; Howson <i>et al.</i> , 1994	Arisaig area	42 (total)
Maggs in Rostron, 1988	St Mawes Bank, Fal; 7 m	60 (total); 44-50 per sample (n = 3)
<b>Molluscs</b>		
Keegan, 1974	Galway Bay; 0-30 m	59 (total)
Nunn, 1992	Strangford Lough; c. 8 m	78 (total)
Nunn, 1992	Galway Bay	56 (total)
Nunn, 1992	W. Scotland	42, 17, 14 (in samples)
Hall-Spencer, 1998	Clyde Sea area; 10 m	130 (total)
Davies & Hall-Spencer, 1996	Sound of Arisaig; 2-21 m	72 (total)
Howson, 1990; Howson <i>et al.</i> , 1994	Arisaig area	32 (total)

Comparisons can also be made in terms of species composition, rather than simply species richness. Farnham & Jephson (1977) reported that the maerl beds at Falmouth supported a

seaweed flora similar to that found across the Channel in Brittany. Blunden *et al.* (1981) gave more details of the maerl epiflora, and described the algae from three maerl bed sites near Galway (at Finavarra, near Carna and in Kilkieran Bay). These also showed similarities with the epiflora in Brittany, including some of the most characteristic species of the Brittany maerl beds.

## E. SEASONAL AND OTHER TEMPORAL CHANGES IN BIODIVERSITY

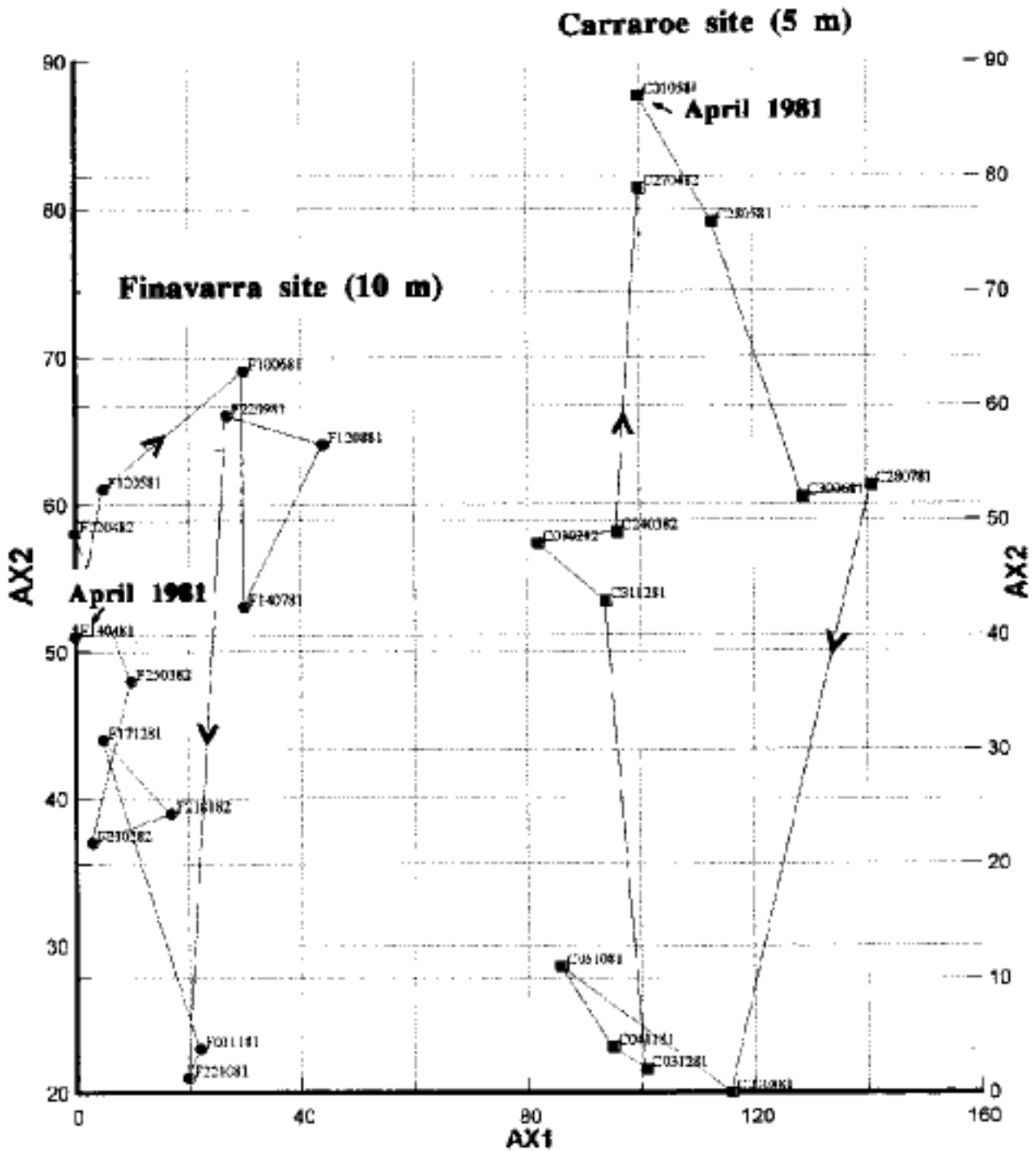
### 1. *Quantitative changes*

There is a very marked seasonality within European maerl communities. Both Jacquotte (1962) and J. Cabioch (1969) investigated the seasonal changes on the maerl and reported that of the “constant association” of characteristic epifloral species about half were found throughout the year, while most of the others were collected only in summer. Jacquotte found *Halopitys incurvus* to be more frequent in winter, and Cabioch reported that a few crustose species were more abundant during the winter months. Jacquotte attributed the seasonal changes in the epiflora of the maerl beds in the Mediterranean to seasonal changes in illumination, as the temperature at depth remained more or less constant throughout the year.

A study in Galway Bay focussed on seasonality of two subtidal maerl beds during 1980 and 1981 (Maggs, 1983a, 1983b). The two maerl beds chosen differ considerably: the Carraroe site at 5 m depth is exposed to wave action and strong currents, and the principal maerl species is *Phymatolithon calcareum*, while the Finavarra bed at 10 m is more sheltered, and is composed largely of *Lithothamnium corallioides*. The cover of macroalgae and the number of species were counted monthly. The algal diversity increased in the summer, probably due to the greater stability of the beds as a result of the calmer weather. Although nutrient levels in seawater are very low in summer, macroalgae can generally utilise stored nitrogen, e.g. by metabolising pigments (so that red algae become yellow), to continue growth and reproduction.

All cover and presence data were analysed by cluster analysis (CLUSTAN) and DECORANA. Seasonal changes in both total algal abundance and diversity were apparent on both maerl beds, but were more marked at 5 m which was dominated in summer by almost 100% cover of *Dictyota dichotoma*, while at 10 m the maximum cover was 60%. DECORANA (**Figure 4**) showed clearly that the composition of samples followed an annual cycle, which was more marked at Carraroe than at Finavarra. Likely causes of this were the greater seasonal changes in the shallow depths at Carraroe in environmental variables such as temperature, photon irradiance, amount of blue light, and wave perturbation. The maerl community had several features in common with other communities on mobile substrata, including a high proportion of ephemeral species. The majority of the perennial species are crustose.

Preliminary studies of faunal seasonality on maerl in the BIOMAERL programme have also found dramatic seasonal variations, such as massive juvenile recruitments and mortality, and the switching of feeding mode depending on food availability (J. Hall-Spencer, pers. comm.). An example is the seasonal pattern of population densities of the infaunal holothurian *Neopentadactyla mixta* at Bute, where this species was recorded only in March and April, and was apparently absent during the rest of the year (BIOMAERL, unpublished data).



**Figure 4.** DECORANA (DEtrended COrrrespondence ANALysis) of maerl flora at two sites in Galway Bay, at 10 m (circles) and 5 m (squares) depths. Presence and abundance data for all algae in 5 replicate samples in 13 consecutive months was used. The start date (April 1981) is indicated and arrows show time progression between samples. Cyclic change is apparent at both sites, but it is more pronounced at 5 m due to the great seasonal changes at shallow depth in environmental parameters e.g. irradiance.

2. *Qualitative changes*

One important aspect of seasonal changes in biodiversity is that of **heteromorphic life histories** of algae, in which an erect phase (usually the haploid gametophyte) alternates with a cryptic crustose, boring or filamentous phase (typically the diploid sporophyte). The maerl epiflora can be divided into three main groups of species:

- Present as mature thalli all year, probably mostly quite long-lived.
- Present as the erect form for only part of the year, then as cryptic crustose or perennating fragments for the rest of the year.
- Absent from the community for part of the year and depending on input from reproducing populations for their presence.

Examples of maerl epiphytes with heteromorphic phases are given in **Table 8**. The different phases in the heteromorphic life histories of these species which are of survival value on mobile substrata must be related to the environmental conditions which obtain during each season. In general, the erect phases of the life history are found only during the summer months. Each species must respond appropriately to the main environmental conditions of temperature, light, and daylength. A combination of field studies and laboratory culture experiments can provide some understanding of the nature of the complex interactions of the environmental stimuli governing the life histories of some of the maerl epiphytes, and thus may be used to explain - and possibly predict - some of the seasonally related changes in the maerl epiflora.

**Table 8. Species having heteromorphic life histories and found as epiflora on maerl beds**

Conspicuous phase	Cryptic phase
<i>Halarachnion ligulatum</i>	<i>Cruoria rosea</i>
<i>Derbesia marina</i>	<i>Halicystis ovalis</i>
<i>Bonnemaisonia asparagoides</i>	<i>Hymenoclonium serpens</i>
<i>Asparagopsis armata</i>	<i>Falkenbergia rufolanosa</i>
<i>Atractophora hypnoides</i>	<i>Rhododiscus pulcherrimus</i>
<i>Naccaria wiggii</i>	un-named filamentous phase
<i>Bonnemaisonia hamifera</i>	<i>Trailliella intricata</i>
<i>Scinaia turgida</i>	un-named boring phase

Over the course of a medium-term investigation, species can both appear and disappear in a non-seasonal pattern. Maggs (1983a) reported that during a 2-year-long sampling programme 9 conspicuous species disappeared from the maerl beds under investigation while a further 3 species appeared in the biotope. This highlights the problems that may be encountered in trying to interpret data from monitoring the epifloral component of maerl beds.



## F. LOCAL VARIATIONS IN MAERL BIOTOPE BIODIVERSITY

Two maerl beds in the same area may differ markedly from each other, not only in the most common live maerl species forming the bed, but also in the flora and fauna associated with the bed. This can be illustrated for epifloral species by a comparison of the data obtained for two maerl beds in Galway Bay (see Appendix 5). The variation in both floral and faunal composition of maerl beds is dramatic and can be seen by comparing species lists from different sites. The species composition of the biotopes is also known to change over periods of years. Furthermore, the number of individuals of a species and the biomass density of a species and the reproductive habits of individual species will also vary from site to site.

J. Cabioch (1969) noted that, in addition to the seasonal changes within a maerl bed, there were local variations in maerl epiflora in the Baie de Morlaix. These variations were associated with the prevailing environmental conditions and the principal maerl species of which the beds were composed. In maerl beds composed of finely branching *L. corallioides* (var. *minima*) *Audouinella floridula* dominated, together with *Aglaozonia parvula* and *Plocamium cartilagineum*. The more open maerl beds formed by more coarsely branched *L. corallioides* (var. *corallioides*) and *P. calcareum* supported a wider variety of abundant species, some of which were only found in the absence of sand mixed in with the maerl.

Fazakerley & Guiry (1998) related the algal species diversity of maerl beds at five sites in Co. Galway to wave exposure. Diversity, measured as the the number of epiphytic species per maerl thallus (n=50 for each site), was very significantly higher at the two wave-sheltered sites compared with two paired wave-exposed sites in the same bays.

Keegan (1974) compared the fauna associated with a series of maerl beds in Galway Bay. The maerl species was identified as *Lithothamnion corallioides* var. *corallioides*. Samples of the fauna associated with the maerl were collected using a suction dredge. Maerl beds were divided into the following categories:

**1. Intertidal maerl bank.** The areas of the bank composed of maerl debris were relatively compacted and strikingly barren of animal life. In contrast, the living maerl was loosely accumulated and supported a large sub-surface community. Local aggregations of *Paracentrotus lividus* were reported, reaching densities within the layers of the deposit of over 1600 m<sup>-2</sup> surface area.

**2. Subtidal maerl bank.** A thick blanket of living maerl on a wave-exposed sloping bottom (Kilkieran Bay), with stong tidal flows. An open lattice formation of the maerl permitted a great depth of habitat available to the infaunal species. The water depth was variable.

**3. Maerl on soft ground,** the thin covering of maerl being swept into wide, shallow ridges by the strong tidal currents. There was no maerl cover in the troughs. Water depth 16 m. Most of the animals were living in the top 25 cm of the sediment although some, particularly large individuals, extended to a depth of more than 50 cm (e.g. *Mya arenaria*).

**4. Maerl on hard ground,** transient deposits of maerl debris in high current areas, and less tide-swept areas with stable banks of maerl and gravel. Water depth 17 m. Dominated by *Antedon bifida* and *Ophiocomina nigra*, with dense aggregations of crinoids (1200 m<sup>-2</sup>).

**5. Unstable maerl debris,** mixed with some sediment.

**5 a. Formed into ripples** by wave action reflecting the most recent storm activity. The storm ripples become flattened by the tidal currents, filling in the troughs. Water depth 17 m. A relatively poor faunal diversity with heavy settlement of flora and faunal species on any stable objects.

**5 b. Transitory accumulation of maerl** within a channel subject to very strong tidal flows which render the maerl mobile. Formed from the erosion of material from mobile dunes of live and dead maerl, piled up to 5 m in height. Water depth 19 m. A restricted faunal diversity.

**6. Mixed maerl and muddy sand.** A patchwork of deposits and rocky outcrops, the latter causing interruptions to the current flow and so giving rise to a range of sheltered, depositional sub-systems.

There is only a limited amount of correlation possible between Keegan's classification and that of the MNCR biotopes classification (Connor *et al.*, 1997), because the Galway Bay maerl was predominantly *L. corallioides* whereas most of the MNCR biotopes were found in Scotland or characterised by the rarer Irish maerl species *Lithophyllum fasciculatum* and *L. dentatum*. Nevertheless, both schemes recognise the importance of general habitat features (e.g depth, wave exposure) for maerl bed classification.

In a desk study, Scott & Moore (1996) drew attention to the fact that, contrary to previous suggestions, the diversity of species found in a maerl bed is not necessarily correlated with the proportion of live maerl within that bed. This conflicts to some degree with Keegan's findings that the degradation of granulometry detrimentally affected diversity, making the maerl less different from gravel substrata. It is likely that the lack of direct correlation in Scott & Moore's analysis was due to the variability of other important factors, which were not compared, and a multivariate analysis of their data would be a better indication of the importance of live versus dead maerl.

## G. RARE SPECIES AND SPECIES CONFINED TO MAERL BIOTOPES

### 1. *Species rarity*

Although no work has been compiled specifically on the rarity of species in maerl biotopes, the importance of rarity in the marine environment has recently been considered by Sanderson (1997). Some species may be deemed rare because they are sparsely distributed, others may be rare simply because they remain unrecognised by all but the most skilled observers. For the algae, in particular, if the cryptic phase only of a conspicuous species is present, giving rise occasionally to the conspicuous phase, the species may appear rare when it is actually common. In an area towards the edges of its habitat range a species generally becomes less common. In theory, therefore, if a site is known to be on the margins for a particular species, then monitoring the population of that species might be a suitable method of indicating that changes are occurring in the area.

## 2. Algae

There are algal species which are characteristically found growing in maerl beds, but these species are not, as a general rule, restricted to maerl beds as their sole habitat. Some of the species found (such as *Halymenia latifolia* and *Scinaia turgida*) are apparently restricted to calcareous habitats by their requirement for a substratum in which the shell-boring microthallus can grow. Crustose *Peyssonnelia* species also show a preference for settlement on calcareous surfaces. Other species found on maerl beds may be present because they are restricted to mobile substrata rather than to those with a calcareous composition. *Halarachnion ligulatum* and *Atractophora hypnoides* are probably largely confined to mobile substrata by the poor competitive ability of the crustose tetrasporophytic phase of their life cycle. However, on mobile substrata the heteromorphic life history of some species is probably a distinct advantage in that the algae can survive periods of physical disturbance as the cryptic, boring or crustose phase (Maggs & Guiry, 1987b). These phases also assist the species in withstanding grazing pressure (Lubchenco & Cubit, 1980). Crusts or boring filaments can be severely grazed without the destruction of the entire plant, which can regenerate from remaining fragments.

There are a few algae that are almost entirely confined to maerl biotopes. For example of 23 stations around the UK, Ireland and N. France from which the new species *Gelidiella calcicola* was described, all but 4 were on maerl (Maggs & Guiry, 1987a). Recently, a morphologically similar species, *Gelidium maggsiae* Rico & Guiry (1997), has been described from maerl and coralline algal pebbles in Ireland. Similarly, of 11 sites where the crustose species *Cruoria cruoriaeformis* was found, only one was not a maerl bed (Maggs & Guiry, 1989).

## 3. Molluscs

As already mentioned, large numbers of molluscan species are found on maerl (Nunn, 1992; Hall-Spencer, 1998), but the majority of these species probably reflect the nature of the substratum on which the maerl lies, rather than the maerl as a habitat in its own right. Only four species were present at most of Nunn's sites (*Tectura virginea*, *Gibbula cineraria*, *Rissoa interrupta*, *Modiolarca tumida*), and of these, only *Tectura virginea* can be considered to be associated with maerl, the others being ubiquitous in lower shore and sublittoral environments. *T. virginea* is found most commonly on encrusting *Lithothamnion* spp. on the lower shore in semi-exposed sites or areas of current. Other species frequently found with maerl were *Hinia incrassata*, *Rissoa parva*, *Tricolia pullus*, *Hiatella arctica*, *Lepidochitona cinereus*, *Onoba semicostata* and *Heteranomia squamula*, but all of these are common in other habitats not associated with maerl.

## 4. Other invertebrates

In Ireland, two new species of amphipod crustaceans in the genera *Stenothoe* and *Listriella* were recently described from maerl (Myers & McGrath, 1980, 1983; Costello, 1987) and Costello *et al.* (1997) consider that it is likely that several more rare species will be found to be restricted to maerl habitats. Davies & Hall-Spencer (1996) reported that most of the maerl polychaetes were characteristic of coarse sediments, and included some probable new species in the genera *Sphaerosyllis* and *Opisthodonta*. Material from Loch Ailort maerl beds included several epifaunal species also found on Irish maerl, such as *Stomatopora incurvata* and an undescribed species of *Monocrepidium*, both of which were considered by G. Konnecker to be exclusively associated with maerl.

KEY POINTS

- There are taxonomic problems involved in determining the biodiversity of the maerl biotopes, such as the existence of sibling species of invertebrates, and the high proportion of crustose or otherwise cryptic algae. For example, accurate identification of epiphytic coralline algae and boring green and red algae requires a long protocol including decalcification, staining and mounting of specimens.
- Maerl biotopes often include a highly diverse community, analagous in structure to kelp forests or eelgrass beds. To our knowledge there have been no overall comparisons of the diversity of maerl fauna and flora with those in equivalent samples from other biotopes, but the algal diversity on maerl in Galway Bay is similar to that in photophilic algal communities in the Mediterranean.
- Species richness of maerl beds shows geographical patterns for the algae but not for the best-known animal group, the molluscs. Floristically, the richest beds are in western Ireland and the Fal while Scottish maerl beds are relatively depauperate. Although the differences may to some extent be due to sampling density, most Scottish maerl beds are undoubtedly less rich in algal species than are most Irish beds.
- There are marked seasonal changes in both species abundance and species diversity within maerl communities. For the algae, at least, these are greater in shallow beds due to the greater seasonal changes in environmental variables such as temperature, photon irradiance and wave action.
- Although most studies have concluded that the larger particle sizes of live maerl support a more diverse community than that found in dead maerl, the diversity of species found in a maerl bed may not be directly related to the proportion of live maerl within that bed.
- Two maerl beds in the same area may differ markedly from each other. Attempted classifications of maerl beds include those of Keegan in 1974 and the recent MNCR biotopes classification. Both schemes recognize the importance of the general habitat features (e.g depth, wave exposure) for maerl bed classification. Algal diversity decreases with increasing wave exposure.
- Relatively few of the species found in maerl biotopes are confined to those biotopes; it is the total assemblage of species within the maerl biotope that makes it unique.

## V. SENSITIVITY TO NATURAL EVENTS

### A. INTRODUCTION

All marine benthic communities are subject to natural events which may or may not prove to be catastrophic to the biotopes present. These events may present on a geological time scale (volcanic activity, tectonic movements, accumulation of sediments, all of which are likely to be chronic stresses) or on a seasonal basis (severe storms, river flooding) or may be single catastrophic changes to biotopes or their components as a result of a wide variety of local events (such as exposure of the upper subtidal zone to bright sunlight during a series of unexpectedly low tides: Hruby, 1975), which can be regarded as acute stresses.

Because of their extreme longevity and very slow rates of accumulation, maerl beds will be exposed to potential perturbations over a very long period. Maerl thalli (and hence maerl biotopes) can be classed as sensitive according to most of the criteria listed by Hiscock (1997) because they

- are fragile (brittle)
- are long-lived (thalli of *Lithophyllum dentatum* have been estimated by H. Fazakerley, unpublished data, to be 20-100 years old)
- recruit poorly
- have poor larval (= spore) dispersal or no spore stage
- are unable to move away.

For maerl beds the most significant natural events affecting the biotopes on an ongoing basis are storms. Resulting water movement has been found to be very important in determining the loss rates of thalli from the beds, and the turbidity that follows storms almost certainly reduces photosynthesis and thus growth rates. A distinction should perhaps be made between the type of storms that occur on a regular basis, to which maerl beds must be adapted and perhaps depend on to prevent excessive stabilisation by algae and animals, and occasional hurricane-like storms that could cause long-term damage. Sedimentation of phytoplankton blooms is also an important seasonal event.

### B. EFFECTS OF NATURAL EVENTS

#### 1. Storm damage

In areas that are exposed to the prevailing wind and the open ocean, both local as well as distant storms may affect the swell conditions. Large swells can produce oscillatory currents at proportional depths and where maerl beds are found in exposed shallow areas the stability of the surface layers may be completely disrupted as a result. Maerl beds can form underwater dune systems (Keegan, 1974), and are widely reported to exhibit ripples and various-sized megaripples, which have been specifically related to storm conditions of various intensities (Hall-Spencer, 1995a). The onset of calmer periods of weather may re-stabilise the surface, but a preponderance of perennial, opportunistic algal species would be expected. In such an area the species composition would be unpredictable over both temporal and spatial scales, especially in the short term (Hily *et al.*, 1992).

Storm-related damage as a result of increased river discharges and increased turbidity of the coastal waters may affect maerl biotopes, but these effects have not been studied. Salinity reduction could affect species with narrow salinity tolerances.

#### a. Case studies UK and elsewhere

Hall-Spencer (1995a) has studied the effects of storm damage on maerl in Scotland and work is continuing in Alicante, Galicia and Brittany under the BIOMAERL programme. Despite the occurrence of several winter storms that extensively affected the maerl at 10 m depth, the survival of permanently marked megafaunal burrows showed that only the coarse upper layer of maerl was moved while the underlying layers, including the burrows, were stable (BIOMAERL, in press). Following the storms, infaunal organisms renewed their burrow linings within a week. At 38 m off Alicante, maerl was not obviously affected by a major storm, with the exception of additional silt deposition.

As part of an experiment to measure growth rates of maerl species in the Ria de Vigo, Spain (Adey & McKibbin, 1970) some indication was obtained of the movement of maerl thalli within the study area. At a depth of 5-6 m in a part of the ria exposed to heavy swell during periods of south-westerly winds (winter months) the following loss rates for individually tagged rhodoliths on the surface of the maerl bed were found:

February	March	April	June	July	August
70%	47%	25%	13%	11%	10%
Data abstracted from Adey & McKibbin, 1970.					

H. Fazakerley (unpublished data) likewise observed a loss of 100% of marked thalli from monitored areas during strong winter storms in Mannin Bay, Connemara. The thalli, although not necessarily destroyed, were moved outside the study area.

Severe disturbance of the maerl epifloral community was reported for maerl beds in Galway Bay (Maggs, 1983a), with the deeper beds showing a less marked drop in total algal abundance during the winter months than the shallower beds. Doty (1971) found that in Hawaii storms were the principal factor governing total algal biomass, and the structure of the community studied by Lieberman *et al.* (1979) was also controlled by seasonal abundance resulting from storm mobilisation of the substratum.

#### 2. Weather

Annual weather cycles cause the seasonal pattern of species abundances and species richness in maerl communities referred to in the Biodiversity chapter. Although macroalgae and maerl fauna are not directly affected by nutrient availability, winter remineralisation of sea water causes increases in dissolved nutrients that result in spring phytoplankton blooms. In the Clyde Sea, the spring diatom bloom eventually settles out on the maerl leading to high BOD and anoxic conditions so that large infauna such as the urchin *Spatangus purpureus* come out of the sediment to obtain oxygen (BIOMAERL, in press).

#### 3. Climate changes

It is only in recent years that the potential effects of climate change (whether natural or accelerated by anthropogenic influences) on the natural environment have been considered in depth, because of the enormous amounts of computing power required for modelling studies. Most research effort has been directed towards the effects of anthropogenic climate change, as natural changes in climate are thought to proceed on a geological time scale so are unlikely to influence biotopes from one generation of scientists to the next.

Even in the relatively short term, global warming of the anticipated 1-3°C within the next century could have an effect on the composition of maerl beds in the UK, in that the cold-intolerant species *Lithothamnion corallioides* might be able to extend its distribution northwards, and *L. glaciale* might retreat northwards. Associated effects of global warming have been predicted to include changed rainfall patterns and storm systems, both of which would affect maerl by increased water turbidity and sediment deposition, as discussed above. Changes in sea level could affect these slow-growing algae, some beds of which are estimated to be about 8000 years old.

Maerl biotopes in some parts of the EU and possibly in parts of the UK are thought to be very long-lived and as such the maerl beds may be stratified. It should be possible to determine marine palaeoclimatic information from such maerl beds in the same way that terrestrial palaeoclimatic information is obtained from peat accumulations and stratified lakebed sediments. The occurrence of relict dead maerl beds off the Fal estuary and nearby Cornish coast and in the rade de Brest suggests that natural changes, perhaps in currents and sedimentation load, have killed the maerl (J. Hall-Spencer, pers. comm.). The dead bed near the Fal represents many centuries of maerl growth, being 17 km long, 2 km wide and c. 30 cm deep (Anon., 1993).

The geological literature available on palaeoclimate assessment based on the study of coralline algae is considerable. Hall-Spencer (pers. comm.) has found, at depths of 1 m in the maerl bed, shells of molluscs that are now extinct in Scotland but still occur further north. This suggests that the maerl bed dates back to the last ice age. Attempts at assessing the palaeoclimatic conditions present during the formation of fossil and semi-fossil maerl deposits have been made in several parts of the world. Foster *et al.* (1997) investigated the rhodolith beds in the Gulf of California, looking at the morphology of the rhodoliths in both modern and fossil deposits, attempting to correlate the branching density of the live rhodoliths to wave motion. Freiwald *et al.* (1991) used maerl deposits to reconstruct holocene climatic changes.

### C. PATHOGENS

Although no diseases of European maerl or other coralline algal species are known, Littler & Littler (1995) recently discovered a potentially serious threat to coralline algae in the Pacific. A bacterial pathogen of coralline algae was initially observed during June 1993 and by 1995 occurred in South Pacific reefs that span a geographical range of at least 6000 km. The occurrence of the coralline algal pathogen at Great Astrolabe Reef sites (Fiji) increased from 0% in 1992 to 100% in 1993, which indicates that the pathogen may be in an early stage of virulence and dispersal. Because of the important role played by coralline algae in reef building, this pathogen, designated coralline lethal orange disease (CLOD), has the potential to greatly influence coral reef ecology and reef-building processes. If such a disease were to occur in temperate maerl beds, the effects could be devastating. We suggest that the possibility of disease should be borne in mind during monitoring programmes. Increased stress levels due, for example, to elevated sea temperatures, might increase the susceptibility of corallines to disease.

## KEY POINTS

### *Fragility*

- Maerl thalli and biotopes can be classed as sensitive because maerl thalli are fragile (brittle), long-lived, recruit poorly, have poor spore dispersal, and are unable to move away.

### *Storm damage*

- Maerl beds, like other mobile marine substrata, are susceptible to disturbance caused by the passage of storm waves. High proportions of thalli can be lost from beds during storms. 'Normal storms' are likely to have beneficial results in preventing overgrowth by perennial species, but 'freak' storms of the strength that occurs once per century or so could cause serious damage.

### *Weather effects*

- Although seasonal changes in the weather mainly affect the annual cycling of diversity and abundance of species in maerl communities, the winter remineralisation and subsequent spring plankton bloom can have detrimental effects on maerl beds. Settlement of large quantities of flocc causes anoxia, resulting in severe disturbance to infauna.

### *Climate changes*

- Palaeoclimatological data may be obtainable from present-day maerl beds as well as fossil and sub-fossil maerl deposits.
- Dead maerl beds in some parts of the UK appear to be relicts and may indicate the effects of past climate change.
- Anthropogenic global warming could affect maerl distribution, due to different temperature requirements for each species. Changed weather patterns and storms, and changes in sea level, could have serious consequences for the survival of the finely balanced maerl biotopes.

### *Pathogens*

- A disease such as the coralline lethal orange disease recently discovered in the Pacific could have devastating consequences for maerl beds although no such diseases are known to affect European Corallinaceae at present.



## VI. SENSITIVITY TO HUMAN ACTIVITIES

### A. DIRECT AND INDIRECT EFFECTS

Maerl beds in subtidal waters have been utilised over a long period. An early reference to maerl beds in Britain was made by Ray (1690, cited by Irvine & Chamberlain, 1994) “*Corallium album pumilum nostras*. Small white coral. .... It is found plentifully in the ouze dredged out of Falmouth Haven to manure their lands in Cornwall”. In France also, maerl has been used as a soil fertilizer for several centuries (Cabioch, 1969).

Maerl is extracted in large amounts for use in animal food additives, water filtration systems, etc, but mostly to replace lime as an agricultural soil conditioner. It is occasionally used for miscellaneous other purposes such as hardcore for filling roads, and surfacing garden paths. Maerl can also be used for soil improvement in horticulture. Maerl extraction forms a major part of the French seaweed industry, both in terms of tonnage and value of harvest (Briand, 1991). There are conflicting reports on the benefits of maerl use as opposed to the use of dolomite or calcium carbonate limestone (Blunden *et al.*, 1997). As a result of the commercial interest in maerl beds, most research work has been based on the three main areas of commercial exploitation, namely Brittany, Cornwall and the west of Ireland.

In addition to the obvious direct effects on maerl of harvesting, other direct and indirect effects on maerl beds have also been noted. Damage to the surface of the beds is caused by heavy demersal fishing gear. Permanent moorings for pleasure boats can have similar, more localized, effects, due to the effects of mooring chains being dragged in circles on the maerl, particular at low tide. The changes in farming practices this century have resulted in increased turbidity in coastal waters both from silt loads and from nutrient run-off. However, there is very little evidence supporting claims that these factors are damaging to maerl beds.

There is little doubt that many human activities can and will result in damage to maerl biotopes but there is an urgent need for continued and rigorous scientific study to better link human activities and impacts on these biotopes, especially beyond localised areas, looking at communities and beds as a whole. In addition, in cases where an alternative resource can be found, e.g. using lime as a soil condition instead of maerl, use of the alternative material should be required, and justified by the real economic costs of large-scale habitat loss.

Several types of human impact on maerl beds are being studied by the BIOMAERL programme. Anthropogenically impacted maerl beds are paired with relatively pristine control grounds. The impacts are from the use of towed demersal fishing gears; culture of the edible mussel; eutrophication; and maerl extraction.

### B. DIRECT IMPACTS

#### 1. *Extraction of maerl*

Extraction of maerl, either from beds where live thalli are present or where the maerl is dead or semi-fossilised, has been carried out in Europe for hundreds of years. Initially, the quantities extracted were small, being dug by hand from intertidal banks, but in the 1970s c. 600,000 tonnes of maerl was extracted per annum in France alone (Briand, 1991). Amounts have declined to c. 500,000 tonnes p.a. since then. Live maerl extraction is obviously very problematic with regard to growth rates for replacement. Dead maerl extraction is liable to lead to muddy plumes and excessive sediment load in water that later settles out and smothers surrounding

communities. 'Commercial dredging of maerl deposits is particularly destructive since this removes the productive surface layer and dumps sediment on any plants which escape dredging, inhibiting habitat recovery' (Hall-Spencer, 1994).

#### **a. Case studies UK**

In the Fal the Cornish Calcified Seaweed Co. has extracted dead maerl since 1975. Only the dead maerl is taken, and the most serious danger to the important St Mawes bank has therefore been thought to be the settling out of the dredge plume (Anon., 1993). The company has attempted to minimise damage by dredging only on the ebb tide so that the plume was taken out to sea. Reports on the maerl beds made over the last 15 years (e.g. Farnham & Bishop, 1985) have indicated that the flora and fauna are very diverse. However, direct comparisons of the flora with that of maerl in Galway Bay (Rostron, 1988; see Appendix 6) show that the Fal beds are less species-rich than those in Galway Bay. It is not known whether this is related specifically to effects of dredging. Perrins *et al.* (1995) reported that between 1982 and 1992 the proportion of dead maerl on the St Mawes bank increased significantly, from 12% to 23%.

Hardiman *et al.* (1976) attempted to assess the effects of maerl dredging in the Fal by taking core samples. They found black anaerobic mud under the living maerl, the amount of mud increasing towards the main river channel. They apparently advocated the removal of maerl as it provided a poor settlement ground for oysters!

#### **b. Case studies elsewhere**

A report prepared for IFREMER on the maerl beds at Brest, Brittany (Augris & Berthou, 1990), suggested that due to the very slow rate of growth, maerl beds develop very slowly. The biological equilibrium is precarious - effectively, maerl extraction is the exploitation of a non-renewable resource as the slow rate of growth implies a slow rate of accumulation. Grall & Glémarec (1997) compared various indices of biological health for exploited and control maerl beds at the isles of Glénan, and found few significant differences except for a reduction in the number of individuals of each species counted in samples.

### **2. Fish farms**

The positioning of cages over a maerl biotope is likely to lead to fish faeces and partly consumed food pellets contaminating the maerl bed and resulting in anaerobiosis due to the oxygen demand of the decomposing material. The detrital rain from the cages could act in a similar way to terrigenous silt, reducing light penetration through the water column and smothering the maerl surface so that the stabilizing epiphytic algae could no longer establish themselves. As a minimum impact the increase in nutrient levels might produce local eutrophication effects.

#### **a. Case studies UK**

SNH reported in *Marine Scene* (Autumn 1996) that part of Loch Ailort was surveyed to establish a location where the development of a mussel farm would not affect the maerl beds present in the area. Monitoring of a salmon farm anchored over a maerl bed in Shetland has shown a buildup over a 10-year period of *Beggiotoa* and anoxic conditions (J. Hall-Spencer, pers. comm.).

**b. Case studies elsewhere**

In Ardmore Bay, Kilkieran Bay, Co. Galway, fish cages are anchored over maerl beds in one area. Current speed seems to be sufficient to clear detrital material and the maerl has not suffered obvious damage (B. O'Connor, pers. comm.). However, at a sheltered site at Mweenish Island, also in Co. Galway, Maggs & Guiry (1987a) noted that maerl under fish cages was covered with *Beggiotoa* and fungi.

In the Galician rias, Spain, mussel rafts have affected maerl beds (J. Hall-Spencer, pers. comm.). Mussel faeces and pseudofaeces rain down onto the maerl surface, altering sediment structure and compromising the ability of maerl thalli to photosynthesise and grow - work is ongoing under the BIOMAERL programme to evaluate this damage.

3. *Scallop dredging*

The removal of the living maerl thalli from the biotope surface, the loss of the stabilising algae and the disruption of the structure of both the physical habitat and the community structure occur. These major changes have been reported from areas where scallops are dredged from maerl beds (Hily *et al.*, 1992; Hall-Spencer, 1995a, 1998).

**a. Case studies UK**

The effects of scallop (*Pecten maximus*) dredging in the upper Firth of Clyde, where maerl beds are rare, has been evaluated by Hall-Spencer (1995a, 1998), using video and direct observation. Passage of the dredges destroyed large animals and algae and raised particulate sediments into the water, which later settled over a large area, stressing filter feeders and reducing photosynthesis. Dredge teeth penetrated 10 cm into the maerl, crushing maerl fragments and killing them by burial. Four months after dredging there were less than half as many live maerl thalli as in control undredged areas. There was evidence that the community structure was altered in favour of opportunistic species such as scavengers. Overall, the effect of scallop dredging on maerl beds was very serious, with the effects on living maerl compromising habitat integrity and future recovery.

**b. Case studies elsewhere**

In the rade de Brest the maerl beds support populations of the black scallop *Chlamys varia*, which are locally abundant and are intensively fished during the winter months. The dredging activity has been reported to result in severe disruption to the maerl bed and associated flora and fauna (Hily & Le Fol, 1990).

4. *Suction dredging of bivalves*

One of the biggest threats to live and dead maerl beds is suction dredging for large burrowing bivalves such as *Ensis* and *Venerupis* species, which are marketed in Spain (D. McKay, pers. comm.). Suction dredging not only has major impacts on the target species, but causes structural damage to the community from which they are being extracted. The detrimental effects on maerl beds are expected to include impacts of resuspended sediment settling out over the maerl and reducing photosynthesis.

## Case studies UK and elsewhere

Along the west coast of Scotland, sublittoral harvesting of *Venerupis* has occurred in the North Sound, Arisaig, and *Ensis* has been harvested at various locations including Shetland and Orkney (D. McKay, pers. comm.). Suction dredging for these species causes disruption of the substratum to considerable depths, creating holes up to 2 m across and 1 m deep in sandy substrata. Comparable studies have not been made in maerl habitats, however.

### 5. *Channel dredging*

In order to renew or enlarge navigational channels, extensive dredging may take place. This involves removing the seabed, which results in the suspension of the fine silt and clay fractions of the sediment. This fine sediment may be deposited by the inshore currents either locally or at a considerable distance from the dredging operation. The additional sediment load will increase local turbidity and may also settle on maerl beds, burying the calcareous thalli, smothering other algae and animals, possibly destroying the physical stability of the habitat as well as the ecology of the biotope. Seabed removal where a maerl bed is present will of course result in the removal of the maerl itself. If the underlying substratum is altered, it is unlikely that maerl will be able to re-establish itself at that site, given the probable method of reproduction of the species involved.

No case studies are known.

### 6. *Coastal construction and land fill*

The results of these activities would be similar to those mentioned above, such as removal of the seabed, redistribution of mud, and destroying the biotope stability and viability.

No case studies are known.

## C. INDIRECT EFFECTS

### 1. *Coastal alteration*

The addition of breakwaters, promenades and sea defences to EU coasts is becoming commonplace. These constructions inevitably result in changes in the depositional and erosional patterns of the local coastal area. These changes may be gradual and continuous or may be catastrophic (storm related) but intermittent. Gradual but continuous changes are the norm on mobile depositional shorelines such as much of the east coast of England. Where an area of shore is protected with solid defences, erosional scouring increases adjacent to the ends of the protected area. If constructions result in the formation of tide driven or wind and wave driven eddies, the scouring may take place at a considerable distance from the structure. Previous comments on the effects of sediment loading and turbidity apply to coastal alterations.

No case studies are known.

### 2. *Increases in agricultural and sewage discharges*

Eutrophication, the increase in the levels of macronutrients (particularly nitrogen and phosphorus), is due in European coastal waters principally to the use of artificial fertilisers and also to the discharge of untreated sewage or sewage with only primary treatment. It can result

in the excessive growth of ephemeral species of macroalgae (commonly referred to as green tides where the effects are visible on the shore). Eutrophication also causes increased turbidity of the coastal water due to more prolific growth of phytoplankton. Both these effects could result in damage to maerl biotopes. Heavy overgrowth of epiphytic algae would reduce light levels available to the maerl, presumably reducing growth rates, as would increased turbidity from planktonic blooms. In addition, the macroalgal overgrowths and phytoplankton might compete with the maerl for selected nutrients.

There are reports that the effects of deep ploughing, field boundary removal, irrigation and the canalising of rivers is resulting in the increased silt loading of river-waters disgorged into the sea. The activities of the US Army Corps of Engineers on the major river systems of the USA are now recognised to be deleterious to the riverine ecosystems themselves but more recently are suspected to be causing increased sediment deposition in coastal areas (Tibbetts, 1997).

#### **a. Case studies UK and elsewhere**

Hily *et al.* (1992) reported for Brittany that increased terrigenous material in river effluents, as a result of unspecified changes in agricultural activities, is responsible for the increase in turbidity in the rade de Brest. Where high turbidity and eutrophication occurred, these prevented the establishment of many algal species, causing the ubiquitous ones to dominate (*Ulva* sp., *Ceramium rubrum*).

Grall & Glémarec (1997) investigated the effects of eutrophication in the rade de Brest, by comparing impacted and control sites. Overall, there was an increase in algal cover, shown as greatly increased biomass at the impacted site. Species richness of animals in most of the trophic groups (e.g. carnivores, detritivores and scavengers) was slightly reduced, although diversity of surface deposit feeders was enhanced. The numbers of individuals per sample was slightly increased for the most abundant trophic group, detritivores.

### *3. Fishing for ecological critical species*

The harvesting of one or more species from a biotope may result in an ecological imbalance within the maerl bed. If this is not ameliorated by the influx of replacement individuals of the harvested species, then long-term shifts in the composition of the biotope may occur. Information available on the relationships between species in maerl biotopes suggests some possible effects of predator removal.

#### **a. Case studies UK and elsewhere**

In the rade de Brest, the presence of the echinoderm *Sphaerechinus granularis* at local densities of 2 or 3 m<sup>-2</sup> can affect algal cover over small spatial and temporal scales (Hily *et al.*, 1992). Predation by decapods and *Asterias rubens* maintained the densities of most molluscan and echinoderm herbivores below the presumed capacity of the environment, and at normal herbivore densities, the growth of algae restricted the ability of the herbivores to eat the young plants. It could be postulated that removal of selected decapod species would enable the development of a larger herbivore population, grazing out the algal species stabilising the surface of the maerl bed.

#### 4. *Leisure activities*

Leisure activities, particularly marine ones, are part of an important growth industry at present. Several activities connected with yachting, e.g. anchoring either by temporary anchors or by permanent moorings, can damage maerl. In the Fal, the action of the mooring chain as vessels swing in the tide has been observed to crush maerl and other organisms. It is likely, however, that yachtsmen would be open to suggestions of less damaging types of moorings.

#### D. OSPAR CLASSIFICATION

Sensitivity of maerl biotopes has been categorised by OSPAR (IMPACT, 1998) under the headings “habitat sensitivity” (scale of increasing sensitivity from 0 to 5) and “recovery potential” (scale of decreasing recoverability from 0 to 5).

In terms of **habitat sensitivity**, maerl biotopes are classed for different types of impacts as:

- 2. Force of impact would have to be ‘crushing or prolonged/concentration high and long-term/variation from normal would be required to cause habitat and/or community to be lost.

**Impact types:** Temperature change, sewage discharge, deoxygenation from aquaculture, predator removal.

- 3. Considerable force/concentration/variation from normal or prolonged or several events required to cause habitat and/or community to be lost.

**Impact types:** Scallop dredging, sediment loading, channel dredging.

- 4. Minor impact/concentration/variation from normal in a prolonged or multiple event would cause habitat and/or community to be lost.

**Impact type:** Maerl extraction.

**Recovery potential** in relation to a single event causing mortality has been classed as

- 4. Poor, partial recovery likely within 10 years, full recovery like to take up to 25 years.

## KEY POINTS

### *Introduction*

- Information on the sensitivity of maerl biotopes to human activities is scarce but informed speculations can be made about the relative seriousness of potential impacts. Both direct and indirect impacts can be assessed.

### *Extraction of maerl*

- Commercial dredging of maerl deposits is particularly destructive since this removes the productive surface layer and dumps sediment on any plants which escape dredging, inhibiting habitat recovery.

### *Fish farms*

- Finfish and shellfish aquaculture activities can be detrimental to maerl biotopes.

### *Mollusc dredging*

- Scallop dredging results in the removal of the living maerl thalli from the biotope surface, the loss of the stabilising algae and the disruption of the structure of the maerl bed, and could potentially change the trophic structure of maerl communities.
- One of the biggest threats to live and dead maerl beds is suction dredging for large burrowing bivalves such as *Ensis* and *Venerupis* species.

### *Construction*

- Coastal construction, landfill and channel dredging are all likely to result in increased sediment load, resulting in the smothering of maerl biotopes, but specific information is lacking.
- Coastal alterations such as the construction of sea defences may alter the depositional patterns with the same consequences to maerl biotopes as dredging.
- If the underlying substratum is altered, it is unlikely that maerl will be able to re-establish itself at that site.

### *Increases in agricultural and sewage discharges*

- As a result of changes in agricultural practices, increased sediment is carried into the coastal waters by rivers.
- Eutrophication of coastal waters from agriculture and sewage discharges can result in the excessive growth of ephemeral species of macroalgae.

### *Harvesting of predator species*

- There is insufficient information available on the relationships between species in maerl biotopes to attempt any more than a broad speculation as to the effects of predator removal by fisheries, but these could be serious.

### *OSPAR classification*

- Maerl beds have been classified as moderately (2) to highly (4) sensitive to different threats, the most serious being that of commercial maerl extraction.





## VII. MONITORING AND SURVEILLANCE OPTIONS

### A. INTRODUCTION

Monitoring is defined by Hiscock (1998) as "a procedure by which a series of surveys is conducted in a sufficiently rigorous manner for changes in the attributes of a site (or species) to be detected over a period of time". Surveillance or surveillance monitoring is "an attempt to detect unanticipated impacts, particularly ones that may be wide ranging, subtle or that only slowly become large and obvious". Hiscock (1998) notes that in a marine protected area, there is likely to be a background of surveillance of the features important for the designation of the site with monitoring being undertaken in relation to features which may be or are being affected by human activities. Initial survey will be followed by surveillance which gives a broad idea of the scale of the changes taking place, followed by monitoring which uses the results of surveillance to set limits outside which management action is likely to be taken. The process involves the identification of natural variability in order to determine the normal level of change in an unimpacted habitat. The purpose of site monitoring is essentially to

- Determine whether the desired condition of the feature of interest for which the site was designated is being achieved. This can enable judgements to be made about whether the management of the site is appropriate, or whether changes are necessary.
- To enable managers and policy makers to determine whether the site series as a whole is achieving the required condition, and the degree to which current legal, administrative and incentive measures are proving effective.

Methods for monitoring and surveillance of marine conservation areas in the UK are at a relatively early stage of development; there are considerable gaps in our basic understanding of the ecology of coastal habitats and for maerl biotopes in particular (see Chapter VIII). However, although no European maerl beds could be described as either having been under surveillance or as having been monitored, there are nevertheless a number of maerl beds in Europe where research work has taken place at intervals over a number of years, perhaps sufficiently to begin to identify natural variation, for example.

In this introductory section we first highlight the challenges involved in monitoring maerl biotopes, then suggest some of the opportunities available, detail the methodology appropriate to different conservation objectives, and offer some guidance as to how progress may be made. The UK Marine SACs Project is conducting and publishing the proceedings of a series of workshops devoted to the development of monitoring and management programmes for marine SACs (Hiscock, 1998).

#### *1. Challenges*

- Maerl biotopes are underwater, often offshore in areas with dangerous currents and exposed to storm action, and can be found to depths in excess of 25 m.
- Most of the species of plants and animals found in the maerl biotopes are small and difficult to identify.
- There are no short cuts or high technology solutions available for the derivation of detailed, accurate, reliable biological data.

- Sample collecting and sorting is extremely time-consuming, sorting alone requiring ‘... at least two full days per sample prior to the identification of maerl and the associated organisms ...’ (Hall-Spencer, 1995c).

## 2. *Opportunities*

In any monitoring programme, these factors, among others, will need to be accepted and budgeted for. However, some conservation objectives, such as determining the extent and gross topography of the maerl beds, can be surveyed relatively cheaply. Remote sensing techniques are one of the most cost-effective methods of resource mapping: sonar is the optimal method of remote sensing the seabed in turbid, temperate marine waters. Inventory of biotopes, including amount of living maerl, can also benefit from remote techniques.

With regard to the determination of species richness and quantification of species present, studies in other biotopes are increasingly showing that identification of organisms to higher categories, rather than to the species level, can be ecologically informative (Warwick *et al.*, 1990). This type of information is currently lacking for maerl, but it should be obtained to determine whether equally useful data could be obtained at lower cost.

## 3. *Monitoring considerations*

There are methods of studying the biology and ecology of maerl beds which have been used successfully in the past, and these are described below. However, given the present limited knowledge and understanding of the maerl biotopes, suitable methods of monitoring the status of these biotopes need ongoing evaluation and updating. In particular, methods for monitoring the chemical and physical parameters of maerl biotopes will need to be developed, probably by modifying present oceanographic techniques.

Five conservation objectives (Hiscock, 1998) appear to be relevant to maerl as a feature of SACs:

- Ensure that major habitat types supporting maerl beds retain their area. This includes mapping the extent of major substratum features and the maerl biotope complex.
- Ensure that the range and types of maerl biotopes or biotope complex present in an area is maintained. This involves the inventory of maerl biotopes present in a defined area.
- Maintain or increase the species richness in the maerl biotope and/or abundance of key (rare, fragile, declining, representative) species in maerl biotopes. Survey objectives are to quantify the species present in maerl biotopes and their density or percentage cover, with statistical evaluation of the data.
- Maintain or increase the quantity of particular species of conservation importance (those for which the site is ‘special’), which involves the recording of numbers or cover of named species.
- Establish degree of likely sensitivity of a population through gaining an understanding of longevity and growth rate of the species.

Relevant methodology for each of these conservation objectives is described below.

## B. DETERMINING THE EXTENT OF THE BIOTOPE COMPLEX

### 1. *Acoustic ground discrimination survey*

At Newcastle University, the BioMar project (Davies *et al.*, 1997) has developed a survey protocol for mapping the sea floor using acoustic techniques, validated by biological sampling, with the data stored and analysed using geographic information systems (GIS). A *RoxAnn*<sup>TM</sup> processor was used for acoustic mapping. Based on the video samples, grab samples, diver surveys and previous detailed records of biological surveys in the Sound of Arisaig study area (Howson, 1990; Howson *et al.*, 1994), a map of the sea-bed showing the predicted distribution of a total of 23 biotopes was constructed. Acoustic mapping using a *RoxAnn*<sup>TM</sup> system provided data on the physical nature of the sea-bed (depth, smooth/rough, soft/hard), and biological information was then added to the acoustic data. It was not found practicable to relate each biologically based biotope classification to a particular acoustic pattern. Instead, the biotopes determined from a biological approach had to be grouped into 15 much broader categories in which the species component was generally lost. The acoustic signatures for maerl, maerl-derived life forms, gravel and coarse sand were all very similar. *RoxAnn*<sup>TM</sup> methodology has also been used in the Fal.

Although no statistical estimates of the probable accuracy of the group of biotopes predicted from a set of *RoxAnn*<sup>TM</sup> data have been presented, it is probable that the development of the *RoxAnn*<sup>TM</sup> method will allow mapping of maerl beds in areas where they are known to be present. An important consideration is the density of the ship tracking, which will affect the accuracy of the resulting maps.

Large-scale features such as plains, ripples and megaripples can be monitored by remote devices, such as side-scan sonar or by direct observation (Hall-Spencer, 1995a). Methods of seabed survey at present in use for geological and archaeological survey work can be adapted to monitor the topology of maerl biotopes.

### 2. *Admiralty charts*

The notation “Crl” as used on the hydrographic charts produced by European nations generally designates deposits of coralline algae (Minchin, 1997). These details were recorded around the coasts of the British Isles during the 19th century as invaluable information to the shipping trade for navigating, beaching and anchoring of sailing vessels. The nature of the bottom was determined by “swinging the lead”, where a hollowed lead cylinder was plugged with tallow and dropped to the bottom. The depth of water was noted and the tallow trapped evidence of the nature of the bottom. This is a minimal technology method and a rapid and extremely accurate way of determining the nature of (especially) soft bottoms. Detailed historical charts of European waters are readily available from which could be derived possible locations of maerl beds in the past. Modern hydrographic mapping techniques do not generally provide this detailed information on the nature of the benthos.

However, caution must be used in interpreting the information on charts, as other calcareous sediments not obviously made up of mollusc shells were also sometimes called Crl. Hall-Spencer (1995a) noted that in the Clyde some reports were based on true coral (*Lophelia*), *Sabellaria alveolata* reefs, or piles of bryozoan/hydroid tests.

3. *Aerial surveys*

Minchin (1997) has found that maerl beds, even when subtidal down to several metres depth, can be identified from aerial photographs. This method can be used to make a very broad-scale, rapid assessment of the extent of maerl deposits where there is no excessive water turbidity. This applies to most of western Ireland, the Western Isles of Scotland and other island groups.

C. INVENTORY OF MAERL BIOTOPES PRESENT

1. *Video survey*

The towing of a remote camera or the use of divers on sledges to record video images enables a large area to be examined. It is an excellent method for providing basic information on the extent of a maerl bed and gross features such as patchiness. The disadvantages are the inability to record any information about the biotope below the surface of the maerl bed; few species can be identified using this method.

2. *Grab and dredge samples*

These are useful methods to employ if large but non-quantitative samples are sought. Much of the early work on the extent and species diversity of maerl beds was based on benthic samples using these methods. The major disadvantage, other than the sampling of an uncertain surface area, is that the depth to which the devices penetrate the substratum cannot be controlled. Dredge sampling has been employed in the most extensive recent survey of sediment fauna, which covered 849 stations (O'Connor *et al.*, 1993). Smaller grab samples were also taken for quantitative analysis.

More recently, the BIOMAERL project has found that grabs sample very effectively in the top 10 cm. However, Keegan & Könnecker (1973) have shown that many large animals can penetrate to depths of 40-60 cm into maerl or maerl debris.

3. *Photographic monitoring of fixed quadrats*

For determining change in biotopes at a particular spot, for example with regard to a localised impact, a fixed locating point can be established by drilling a positioning pole through the maerl and underlying sediments to a depth at which it remains stable, without disturbing the surface of the maerl bed. The mobile habitat that is the maerl bed can then move past the fixed point and photographs be used to record any changes. This method requires skilled divers to locate sites and take the photographs and has the disadvantage of recording only the surface species. Few species within a maerl biotope can be identified by this method, but it can record broad changes in biotopes.

D. QUANTITATIVE SAMPLING OF MAERL BIOTOPES

1. *Problems concerning quantification of maerl biota*

Much of the early work on the fauna of maerl beds was based on benthic grab samples. More recently, faunal recording has used divers extensively but this is only suited to a few of the species present as many are difficult to see. For the flora, there are similar problems with some

additional ones. The development of an adequate quantitative sampling technique for maerl epiflora presents several problems (Maggs, 1983a), as follows.

- Fixed quadrats cannot be used due to the mobility of the substratum. (However, fixed rods may be helpful as they can withstand substratum mobility.)
- The same sample cannot be examined twice.
- Maerl branches in three dimensions, so the sampling is not planar. This means that the total surface area sampled using a quadrat based system will vary depending on the size and shape of the maerl thalli.
- Possible methods of assessment of abundance of maerl epiflora species are severely limited by the size and form of the substratum and the epiflora species themselves.
- Abundance scales would be almost meaningless due to the complex configuration of the substratum and the size and growth habit of many of the algae, which do allow reasonable estimates of relative cover.
- Biomass of individual species could not be used for the maerl community with its high proportion of crustose, shell-boring and minute species. For erect species, some estimates of biomass could be made, however.
- Most of the species do not grow as individuals, and thus counts of numbers per sample cannot be made.

In addition, as with all benthic habitats, there is the issue of the patchy nature inherent to the distribution of flora and fauna. This raises the additional questions of

- how large a surface area should form each sample?
- how deep a sample should be collected?
- how many samples are needed in order to obtain an adequate representation of the species diversity and biomass of the site?

The **minimal sample size** is one in which the species composition of the community must be “adequately represented” (Mueller-Dombois & Ellenberg, 1974). There is no exact definition of minimal area, and in some studies the sample size has been chosen to be practical and manageable despite containing only a fraction of the species present within the biotope. Maggs (1983a, b) suggests the minimal subsample size to be taken from a maerl sample should be one where a 10% increase in the number of species in the subsample is derived from a 10% increase in the area. Sears & Wilce (1975) used individual shells of *Crepidula* as a sample unit, recording presence, absence and frequency of species occurrence. Lieberman *et al.* (1979) treated each cobble as a separate sample with a known surface area while investigating a seasonally devastated cobble based community in Ghana, recording the algal flora by the weight of each species per unit area.

2. *Methodology for quantification of maerl biota*

**a. Algal diversity and cover**

Conspicuous species can be recorded semi-quantitatively using divers and abundance scales as for hard substrata. Species richness can be determined only by removal of samples of known size and subsequent laboratory examination. Maggs (1983a) used 300 cm<sup>3</sup> maerl samples, each of which took several hours to work through, recorded the presence of all species. The only practicable approach to the assessment of abundances of small maerl epifloral species is to use a point quadrat method.

**b. Core sampling**

Divers can use hand-held circular cores which are driven into the maerl bed, sealed top and bottom and returned to the surface. Box corers can be remotely operated from the ship. Samples are taken to a depth of about 20 cm of sediment. The sediment sample is then washed through a sieve (e.g. 0.5 mm mesh) and the sample treated with Rose Bengal to stain living material before being preserved. The sample is then later picked through to remove any visible plants and animals which can then be identified and counted or weighed as needed (Hall-Spencer, 1995a).

**c. Diver-sampled quadrat**

A pair of divers positions a quadrat boundary of known size and either collects all the material within the quadrat to a specified depth, records all visible species without disturbing the surface, or collects all living material from the quadrat as a sample for detailed analysis in the laboratory. Only the larger species would be collected by this method.

**d. Suction dredge**

Suction dredges can be either diver-operated or can be used from the surface. They are not accurately quantitative. The samples of algae and soft-body invertebrate fauna are frequently severely damaged by this collection method. Large quantities of waste sediment and silt may be produced which could prove deleterious to the maerl bed being sampled. The range of species collected and the population structure of the collection are dependent on the mesh size used for sieving. Keegan & Könnecker (1973) designed a suction sampler for use on substrata including maerl beds. Hall-Spencer (1998) provides data on the mollusc species most suitably sampled by suction sampling, as opposed to diver-recorded quadrat or diver-operated corer.

**E. RECORDING NUMBERS OR COVER OF NAMED SPECIES**

Methodology for recording the numbers or cover of named species is similar to that for general quantitative sampling. For large and conspicuous epifaunal species, divers with quadrats or towed video surveys are probably the most efficient methods. Determining numbers, cover or biomass of small species requires sampling and laboratory sorting. However, sample sorting can be greatly speeded up if only one or a few species are being quantified. The relative amounts of different maerl species, particularly of the large *Lithophyllum* species, could be determined to some extent by video survey.

## F. DETERMINING LONGEVITY AND GROWTH RATES

The species in maerl biotopes for which these measurements are most urgently required are the maerl species themselves. Growth rate determination requires some way of repeatedly retrieving and identifying individual thalli in the natural habitat. Various workers have used tagged thalli placed in marked areas; tagged thalli tied to fixed lines; and maerl thalli placed in baskets. Two main methods have been used to measure growth rates of maerl. Growth of bulk samples can be determined by buoyant weight measurements. Baskets of maerl are suspended from a balance in a medium of known density. Accuracy is low due to the weight of epiphytic animals and algae and attached sediment. Growth of individual thalli can be obtained by repeated photographic or caliper measurements of tagged thalli. Accuracy is high but problems arise due to fragmentation of thalli between measurements, for example. A further potential difficulty has been identified: growth rates may decrease due to effect of making the measurements, i.e. the desiccation involved is detrimental to the thalli.

Maerl thalli are thought to be very long-lived. Determination of longevity can be made by extrapolating from growth rates or by aging of individual thalli. It is not currently known whether thalli can be aged by  $^{14}\text{C}$  methods but these would appear to have considerable potential.

## G. CHEMICAL AND PHYSICAL PROPERTIES OF MAERL BIOTOPES

Equipment and protocols for monitoring water quality and water movement have been developed for oceanographic use and for use by water companies and river authorities. This equipment requires skilled personnel in order to operate and maintain the equipment as well as for interpretation of the results. Devices such as fixed *in situ* current meters and pressure sensors can be used to measure wave height, tide height and water movement near the seabed. Irradiance and water turbidity can both be recorded using *in situ* remote devices. Devices for measuring water quality are being improved continually. Suitable devices can be placed *in situ* and data recorded for collection or for transmission to a base station.

## H. RECOMMENDATIONS

Different types of methodology are required for the monitoring of different target groups. The key to biological monitoring is the identification of indicators, indicator species or indicator communities. However, at present we have very little information on maerl bed species that may function as “sentinel organisms”, i.e. those indicator species which, for example, accumulate pollutants in their tissues and can therefore be used as bioindicators (Phillips & Rainbow, 1993). The first potential sentinel species has been identified by the BIOMAERL team (P.G. Moore, pers. comm.). The diversity of the polychaete *Hesione pantherina* is much reduced at eutrophicated sites in Brittany compared to non-impacted sites; this species may be especially sensitive to eutrophication. Until sentinel species are identified, all species and their abundances should be monitored regularly, as far as possible, using appropriate methodology for each life-form.

The BIOMAERL team, while developing a comprehensive inventory of the biota at the study sites, have likewise concluded that it is necessary: a) to utilize as many methods of sampling as possible; and b) for sampling to take place over all seasons of the year. Not every organism present on the ground is captured in any one type of gear, and there are strong seasonal influences at work both in terms of species occurrences (migrations), and/or population fluctuations. The methodology they have used for biological sampling of the maerl biota, to

obtain detailed data on population structure, biomass and population density for the commonest and/or structurally most important key species from each ground, is a combination of:

- sampling directly by divers using quadrats and/or cores *in situ*,
- deployment of a variety of indirect sampling gears from ships (grabs, box corers).
- Infaunal samples being sieved through a 1 mm screen as standard; comparison of megafauna and macrofauna.
- The use of towed dredges and trawls and direct diver observation to obtain additional, semi-quantitative and qualitative faunistic/ floristic data.



## KEY POINTS

- There are challenges involved in monitoring maerl biotopes. Numerous methods of sampling maerl biotopes have been used in the past, each of which has advantages for particular organismal groups in particular situations.

### *Determining the extent of the biotope complex*

- Although there are many gaps in our knowledge of maerl biotopes (see Chapter VIII) there are several types of surveillance that can realistically be carried out. In particular, the demonstration that maerl can be mapped remotely using *RoxAnn*<sup>TM</sup> processors shows that basic information on the distribution of maerl beds could be obtained relatively cheaply. A combination of Admiralty charts and remote sensing could provide rough estimates of extent of maerl biotopes

### *Inventory of maerl biotopes present*

Appropriate sampling methods include the use of towed dredges and trawls and direct diver observation to identify biotopes.

### *Quantitative sampling of maerl biotopes*

- The numbers and sizes of samples and the frequency of sampling the biotope for monitoring purposes all need to be established. Suggestions can be made, however, based on statistical evaluation of the numerical variability of the organisms being studied in each maerl bed.
- Different sampling methods will have to be used for different objectives. For example, infauna cannot be assessed either qualitatively or quantitatively by non-destructive techniques. Appropriate sampling methods for different types of organisms are:
  - sampling directly by divers using quadrats and/or cores *in situ*.
  - deployment of a variety of indirect sampling gears from ships (grabs, box corers).

### *Future developments*

- Methods of monitoring various different aspects of the maerl biotopes are under continual review and development. The search for sentinel species that are particularly sensitive to particular impacts is continuing as part of the BIOMAERL research programme.
- Extrapolation from data obtained over the last few years on other marine biotopes suggests that evaluation of samples using a lower level of taxonomic expertise, e.g. to genus level only, may provide sufficient information to determine the health of the biotope.



## VIII. GAPS AND REQUIREMENTS FOR FURTHER RESEARCH

### A. INTRODUCTION

In this section is included a preliminary assessment of gaps in our present knowledge of the biology and ecology of maerl biotopes. These gaps will need to be addressed in order that management questions can be answered and monitoring programmes established. Some of the topics are already being addressed within the EU, if not specifically within UK waters. It is possible that other topics may be at least partially answered based on published and unpublished work from the rest of the world.

Management questions may be specific to maerl biotopes within UK waters but might be best addressed, at least initially, by consultation with national, regional and local conservation bodies elsewhere in the world. The problems that are presently encountered, and are expected to be encountered in the future, in marine biotope conservation in the UK are by no means unique and may have often been addressed (at least in part) by nations with a longer history of development and management of nature conservation. Many of the natural and anthropogenic events that affect maerl biotopes also affect coral reef biotopes. Much information on the legislative requirements, monitoring implementation and problems encountered in the protection of coral reef biotopes could be equally applicable to UK and EU maerl biotopes.

Much of the basic biological and ecological information pertaining specifically to UK maerl biotopes remains unknown and extensive research will be required in order to answer management questions. The demands which may in future be presented to the management of UK SACs are unknown. In principle, when there is commercial pressure on direct extraction of biotopes that have high conservation value, such as maerl beds, protection will need strong scientific justification that can withstand legal assessment and counter short-term economic arguments.

The paucity of ecological studies on the flora and fauna of mobile substrata such as maerl have presumably been due mainly to the difficulties involved in the identification of many of the species concerned. These include the meiofaunal species (which have been sampled only recently). Maerl biotopes do not seem to have been sampled for examination of the bacterial, fungal, microalgal or protozoan components of the biotope.

The most significant gaps in our information to date are (1) the location and extent of maerl beds, which are still not fully known even within candidate SACs; (2) growth rates of maerl species, which are still very poorly known; and (3) ecological relationships between species in maerl beds, a knowledge of which would enable predictions to be made from monitoring of selected species.

### B. SPECIFIC INFORMATION GAPS WITH RESPECT TO UK WATERS

#### 1. *Where are all the maerl beds?*

##### a. **Challenges**

At present, known maerl beds show a distribution pattern that suggests that coastal searches around the UK are incomplete. Small maerl beds may be just as biologically significant as the larger beds or may be representative of developing maerl beds or relict beds, investigations of which could provide valuable information for the management of maerl biotopes in conservation areas. The proposed marine SACs do not contain representatives of all the MNCR maerl

biotopes described to date. Knowledge of all other maerl sites in the UK is important to provide comparative data. This information could also be used to promote less formal conservation areas, based on the interest and goodwill of the local population.

**b. Solutions**

A detailed survey of all coastal waters. Initially this might be conducted using an acoustic survey system, combined with detailed charts and interviews with local boatmen and historical groups. Validation of the remote sensing survey might be accomplished using divers or a simple surface sediment sampling device.

2. *What are the dimensions of the maerl beds?*

**a. Challenges**

In many locations where maerl has been reported, the dimensions of the beds and the extent of the biotopes within the beds are not known. It is possible that the maerl beds in a conservation area are in fact dependent on the well being of living maerl or epilithic source plants from outside the conservation area in order to maintain the biotope integrity. The precise locations and dimensions of the beds within the proposed SACs are also required. This information needs to include the depth of accumulated maerl as well as the area covered.

**b. Solutions**

Having located an area of the seabed on which maerl is found, a detailed survey will be needed. This could be done using a slow tow of a video camera linked into a geographical plotting device, or by using a team of divers who could be given additional tasks, attempting to resolve other questions.

3. *What species of maerl are present in each maerl bed?*

**a. Challenges**

There are numerous species of maerl-forming coralline algae in the coastal waters of the UK. Coralline algae, in particular the epilithic and maerl-forming species, are not easy to identify. Determining which species of maerl form the maerl beds around the UK is necessary in order to evaluate the geographical and ecological habitat ranges for each species.

**b. Solutions**

Determine centres where there is the expertise and time required to identify samples accurately, to which all maerl samples can be sent for identification. Given the slow growth rates of maerl, any maerl species changes which might occur within monitored areas will probably be detectable only over a long period. This would necessitate the establishment of a high degree of continuity in the team of experts and the necessity to train incoming personnel carefully.

4. *Where are the distribution boundaries for each maerl species?*

**a. Challenges**

It is probable that, as the UK coast includes the ranges of boreal and lusitanian species, changes in the species composition of the maerl beds and of maerl species distribution could be a powerful tool in identification of long-term changes in the marine conditions around the UK. As maerl is a very slow-growing life form, it is possible that in some locations the species may be represented by relict populations, or even relict individuals which became established during previous climatic regimes.

**b. Solutions**

Detailed mapping of the maerl beds around the UK and the species of maerl found in the beds is required. Species composition and relative proportions of those species for both the live and dead components of the maerl populations are required.

5. *What are the growth rates of maerl species and what affects them?*

**a. Challenges**

There are nine species of maerl found around the UK. We have only very limited information on how fast some of these species grow. If the growth rate of maerl thalli is a sensitive indicator of the conservation status of the biotope, measurements of growth would form a powerful monitoring tool. Different maerl beds are subjected to different regimes of light, temperature, nutrient availability, salinity and water movement. These parameters can be measured as part of a monitoring programme and so could be used to give warning of environmental changes significant to maerl species. At present, the sensitivity of maerl species to nutrient levels is unknown. Growth rate responses to light are almost unknown; little is known of the temperature tolerances of some species.

Growth rates of maerl species and the maerl epiflora are probably light-dependent. If the irradiance reaching the seabed is reduced or the spectral quality of the irradiance changed, the growth rates of the various species may change. This might mean that some species would continue to grow at the expense of others. If the creeping species which stabilize the maerl beds were lost, the entire biotope could be lost as the maerl was dispersed.

**b. Solutions**

Develop a method or methods for measuring growth rates and, using large numbers of marked plants at locations throughout the UK, establish the expected growth rates of the different species within their present habitat ranges. Growth rates have previously been estimated using branch tip extension and buoyant mass increases. Experiments need to be conducted, both in the laboratory and under field conditions. It would be necessary to establish the tolerance range for each maerl species with each parameter individually and in combination with each other.

Determining the effect of different environmental parameters requires long-term experiments (several years' duration) preferably in mesocosms although the possibility of field experiments could be investigated. Growth rates of maerl and selected other species could be measured under different conditions of irradiance and turbidity (such as those on light quality in Mannin Bay: Fazakerley & Guiry, 1998).

6. *How old are living maerl thalli and maerl beds?*

**a. Challenges**

At present, we know that maerl thalli grow slowly and are long-lived, but do not know if we are looking at plants that are young, mature or senile. It is possible that all the plants we see in some maerl beds are senile, that for some reason no new recruits are entering the population. It is equally possible that some maerl beds consist of only very young plants, as mortality of older individuals is very high for some reason. Thalli may vary in their sensitivity to external events at different times in their lives.

It is possible that the maerl beds around the coasts of the UK are effectively only remnants of biotopes that were once more extensive. Where stable beds are present, how long have they been present in that location? Many maerl beds might effectively consist of a living skin over a semi-fossil base, having persisted *in situ* for millenia. Therefore, any changes in the bed which are noticeable in the short term (5-10 years?) may represent a disastrous rate of change for the biotope.

**b. Solutions**

Multiple samples of all maerl-forming species would be collected from a wide range of habitats and depths. A method of determining the age of each thallus will need to be developed. Geological methods of sectioning might be used for the tissue and growth rings counted; core tissue from the thallus can be dated using  $^{14}\text{C}$  or  $^{13}\text{C}$  methods. It may be possible to use geological sampling and dating methods at selected locations where large maerl beds have persisted from historical times. A stratigraphy for each bed could be established and the biological history of different biotopes compared.

7. *How is the biodiversity of maerl biotopes affected by various environmental and biogeographical factors?*

**a. Challenges**

Complete species lists for maerl biotopes do not yet exist, because of the large numbers of small species in taxonomically poorly known groups. It is already known that different maerl species have different distributions. The species of animals and plants associated with the maerl also have differential distributions.

- What are the faunistic and floristic differences between maerl biotopes in the northern parts of the UK and the southern parts?
- What differences in the flora and fauna can be distinguished between mobile and stable forms of each of the maerl biotopes?
- What are the faunistic and floristic differences between maerl where fine sediments accumulate and where the maerl is swept free of sediments?
- What are the differences in the flora and faunal species in maerl biotopes where the thalli are mostly live and biotopes where the thalli are mostly dead?

**b. Solutions**

Widespread and large scale intensive surveys of maerl beds - both in proposed SACs and elsewhere. All the different maerl biotopes would need to be included with numerous, well-separated locations of each in order to achieve representative results. This information would enable subsequent drifts in species composition to be linked to fluctuations between biotope classifications and geographical areas. If northern sites were, for example, to show a slow increase in southern species, this might be evidence of water temperature changes - although the physical measurements might still not be showing statistically significant results.

Sentinel species that are particularly sensitive to particular impacts should be sought for.

8. *What are the key species in a healthy maerl bed and what happens if a predator species is removed from the biotope?*

**a. Challenges**

If the key species are known, monitoring of the population structures of these species would form a useful indication of the status of the maerl biotope at a particular site. What would happen if a previously non-commercial species were collected for a new market, or if a disease destroyed a particular species, or if events elsewhere prevented the replenishment of a species that did not complete its life cycle within the maerl biotope? This could result in a severe and rapid imbalance in the ecology of the maerl bed.

**b. Solutions**

Identification of species that are key to a specific biotope is a long term project. In terrestrial habitats, experiments are conducted in which certain species are concentrated or excluded and the responses of other species within the study area are recorded. It may be possible to set up mesocosm experiments in aquaria to investigate this question. Although complex and time-consuming, similar methods have been used in order to determine the complex relationships of coral reef biotopes.

9. *What species make use of the maerl habitat as a nursery area?*

**a. Challenges**

It might be possible to gain increased local support for stringent conservation measures with regard to maerl biotopes if it could be demonstrated that the maerl beds form an important habitat for juveniles of commercially valuable species, such as scallops.

**b. Solutions**

Detailed survey and sampling of selected maerl biotopes that have previously been associated with juvenile stages of commercial species.

#### KEY POINTS

- There are many gaps in our present knowledge of maerl beds, ranging from simple questions such as where the maerl beds occur, to complex problems such as the effect of environmental change on the structure of maerl communities. There are three particularly significant gaps:

##### *Distribution of maerl*

- Although some gaps in knowledge require long-term or detailed research programmes, the demonstration that maerl can be mapped acoustically by remote sensing shows that basic information on the distribution of maerl beds could be obtained relatively cheaply.

##### *Growth rates and longevity*

- One of the most serious questions with regard to management of maerl as a resource as well as a biotope concerns growth rates of maerl species and longevity of maerl beds. Research into both the growth rates of different maerl-forming coralline algae under different conditions and the age of existing maerl beds and maerl thalli should be regarded as a priority. Suggested methods include field and laboratory studies of growth under different conditions, and the dating of existing beds and individual large thalli by  $^{14}\text{C}$  or  $^{13}\text{C}$  methods.

##### *Maerl ecology*

- There are many challenges facing any attempts to increase our understanding of maerl bed ecology. There is, for example, almost nothing known about other species necessary for maintenance of maerl bed integrity. More specific information on the use of maerl beds as nursery areas for commercially harvested species might be very useful in gaining support from the public and other users of SACs for maerl conservation. Identification of sentinel species that are especially sensitive to particular impacts would be an important advance in maerl bed monitoring.



## **IX. SYNTHESIS AND APPLICATION OF INFORMATION FOR CONSERVATION MANAGEMENT RELEVANT TO MARINE SACs**

### **A. INTRODUCTION**

The purpose of the present document is to draw together information on maerl biotopes relevant to conservation management of SACs. This chapter is intended to be a synthesis of the most important key points of the review. In addition, we present here the early conclusions of the BIOMAERL programme (see below also).

### **B. BASIC MANAGEMENT GUIDANCE**

#### *1. Time scales*

The time scale over which a management plan for a maerl bed is to operate has to be decided. It should be noted that political and biological time spans are irreconcilable. There is at present too little known about the long term effects on the maerl biotopes of many present-day human activities. Maerl is one of the world's slowest growing plants and, although any identifiable threat may appear to have only limited consequences in the short term (20-50 years), in the life-span of the habitat (6 000 years and more) even apparently small, insignificant present-day perturbations may have a devastating effect on the habitat.

#### *2. Maintenance and restoration*

Maerl beds should be managed in order to contribute to the maintenance or restoration of the favourable conservation status of the natural habitat and species composition of the biotope. Each maerl bed, and in some cases each area within a maerl bed, has a different biological composition, which, given the mobile nature of the habitat, is more than likely to be variable over time. Amongst many detailed gaps in our knowledge, are the time scales of the natural variability of the maerl habitat and the extent of temporal variation in species composition.

One important consideration is that scientific investigation and the monitoring process itself do not damage maerl beds. Extensive use of towed vehicles, for example, might have an impact of maerl beds, as might the extensive use of suction samplers which create silt plumes.

#### *3. Integrity of sites of maerl beds*

The conservation status of the maerl beds must be considered before any activity, plan or project is undertaken that is likely to have a significant effect on the maerl biotope.

#### *4. Monitoring requirements*

Monitoring the marine environment is a time-consuming and very expensive task, requiring high levels of expertise in a wide range of techniques. The maerl biotopes are extraordinary for their species richness and diversity and as such present a challenge with regard to monitoring their status. Monitoring of selected maerl biotopes must be conducted in such a manner that biologically and statistically significant changes can be linked to changes in local conditions, management practices or human activities. Other maerl biotopes could be monitored at a lower level.

#### *5. Avoidance of habitat deterioration*

This requirement of the Habitats Directive implies that whatever monitoring programme is implemented must be adequate to enable the present status, the optimum status and any changes in the status of the maerl biotopes to be detected. Physical parameters should be checked regularly, such as

- the dimensions of the maerl bed.
- the density of the epiphytic cover.
- the silt content of the background sediment within the bed.
- Water quality, salinity and temperature need to be monitored on a time scale and to a degree of accuracy that is probably (as a statistical statement) able to identify any natural or anthropogenic events which might be detrimental to the maerl biotopes.
- The percentage of living maerl thalli in the surface layer of the biotope should be monitored.
- Species diversity within the maerl biotopes should be monitored; this will include the epiflora and epifauna as well as the endofauna. Meiofauna will be an important category to include.

#### 6. *Local human needs*

Despite all the strictures within the Habitats Directive with regard to the conservation of the environment and the species therein, the economic, cultural, social and recreational needs of the local people are to be taken into account.

- International experience demonstrates that local co-operation and voluntary systems *alone* are, in practice, inadequate to protect habitats and the species that they sustain.
- Any management scheme will be reliant on the quality of the monitoring programmes to provide adequate *scientifically robust data* to support any legal cases which may be required in order to defend the maerl biotopes against “local needs” prejudicial to the conservation of the biotopes.

## C. PARALLEL CONSERVATION MANAGEMENT ACTIVITIES

### 1. *UK biodiversity action plan for maerl*

A biodiversity action plan for maerl as a habitat is being prepared by S. Scott, and is currently in draft stage. The action plan notes that three of the statutory Marine Nature Reserves in Britain, Skomer in Wales, Lundy in England and Strangford Lough in Northern Ireland, contain maerl (although none have particularly well-developed beds). It also notes the potential value of SSSI legislation in protecting maerl. Although most maerl beds cannot normally be included within SSSI designations in England and Wales where the lower limit of SSSI designation is usually mean low water, in Scotland, the planning boundary is normally the mean low water of spring tides, which could include maerl where it occurs in the subtidal fringe. This happens at a few sites, for instance at Taynish on the shores of Loch Sween, Argyll, where the SSSI boundary (but not the NNR boundary) extends to mean low water of spring tides and includes the high marine interest in the rapids. However at best SSSI designation can only afford limited protection to a very small proportion of total maerl populations. Proposed actions include

- Listing maerl beds under Annex 1 of the Habitats Directive, both in their own right and as a specific component of sealoch systems.
- Pressing for the addition of *Lithothamnion glaciale* to Annex V of the Habitats Directive.
- Ensuring that planning applications for structures such as roads and aquaculture installations are compatible with the conservation requirements of maerl beds.
- Completing surveys of the extent, quality and composition of UK maerl bed communities.
- Listing further sites for eventual classification as SACs to ensure the full range of maerl bed and associated community types and ecological conditions is represented in the network of protected sites.
- Including provision for the maintenance of the extent and health of maerl bed communities in management plans for SACs where these include maerl beds.
- Taking account of the conservation requirements for maerl bed communities in the development and implementation of coastal zone management plans and ensuring that they are not managed in isolation from other habitats and communities in these areas.

### 2. *BIOMAERL programme*

The EU MAST-funding BIOMAERL programme, co-ordinated by Prof. P.G. Moore, Millport, is a 3-year collaborative programme between laboratories in UK, Spain, France and Malta, and began in February 1996. Pairs of maerl grounds have been identified for study by participants in the Clyde Sea area (Scotland), Galicia (Spain), Brittany (France), Alicante (Spain) and Malta. Each pair represents a ground that has been impacted anthropogenically and a relatively pristine control ground. In Scotland, Alicante and Malta, impacts to maerl habitats derive mainly from the use of towed demersal fishing gears. In the Ria de Vigo (Galicia), the major impacts derive from organic matter falling from moored rafts used in the culture of the edible mussel. In the Bay of Brest (Brittany), maerl beds are also affected by high nutrient and sediment loadings due to

eutrophication. Another pair of sites in Brittany (in the Glenan archipelago) are being compared to assess the impact of maerl extraction practices.

The BIOMAERL programme, when complete, will provide the first biogeographical inventory of macrofaunal and floral species in European seas, including identification of key species, their population structure and an analysis of their functional significance in this ecosystem. Assessment of the different anthropogenic threats to this biodiversity experienced over the range of sites considered will generate recommendations as to the most effective management strategies for this sensitive habitat.

The BIOMAERL team propose that one way to advance maerl conservation is the establishment of an Environmental Quality Standard for European maerl grounds which is capable of containing, and integrating, all the pertinent structural and functional aspects of the habitat revealed by their studies. They suggest that this might be achievable by allocating a point score to each of the following indicators: edaphic complexity (sediment stratification), basic energy resources (% organic matter, % epifauna/infauna, % macrodetritivores), complex trophic interactions (% predators, % microdetritivores). A summated score would then represent the overall biodiversity status of a particular maerl bed. Such an index would be capable of being monitored over time to provide a check on environmental change, especially any deterioration. It would also supply a mappable, objectively-derived descriptor that, by virtue of being independent of species composition, would be capable of direct comparison at a pan-European scale.

#### KEY POINTS

- A pan-European approach to maerl bed conservation is advocated by the BIOMAERL programme. An index based on various biotic and abiotic measures would represent the overall biodiversity status of a particular maerl bed. Such an index would be capable of being monitored over time to provide a check on environmental change, especially any deterioration. It would also supply a mappable, objectively-derived descriptor that, by virtue of being independent of species composition, would be capable of direct comparison at a pan-European scale.
- As maerl is one of the slowest-growing plant life forms, at least some monitoring should be designed to be very long-term. Short periods of monitoring, of growth rates for example, might give misleading results.
- Cheap options, such as acoustic surveys, are appropriate for some conservation objectives.
- To achieve some conservation objectives, quantitative studies of maerl biotope species diversity and abundances, requiring intensive and time-consuming research, are necessary.
- Selected maerl beds or maerl biotopes, particularly those in SACs, should be monitored at a higher resolution, in order to permit efficient management plans and monitoring programmes to be refined. This would include faunal and flora surveys, with population monitoring of species selected for their likely importance to community structure.

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**APPENDIX 1. NOTES (BY J. HALL-SPENCER) ON THE DISTRIBUTION OF MAERL SPECIES, SUPPLEMENTARY TO TABLE 1**

Numerous encrusting species of non-geniculate Corallinaceae can continue to grow from pieces that break off the attached part of the thallus. I have done this in aquaria with *Mesophyllum lichenoides*, which is a southern species in the UK but is common as part of Mediterranean maerl beds. It is likely that the number of species that contribute to maerl deposits around the UK is greater than that listed in Table 1.

Free-living *Lithophyllum* spp. form a minor component of many maerl beds on Atlantic coasts of Europe and can be common in the Mediterranean. The taxonomic status of *Lithophyllum* specimens is confused and hampered by a lack of fertile material. Old names refer to the overall shape of specimens which can be as much a product of the environment in which they grew as a reflection of their taxonomic status. For example, Lemoine (1913) and Irvine & Chamberlain (1994) suggest that *L. dentatum* could be a free-living form of *L. incrustans* Phillippi which is a common encrusting species reported from the Mediterranean to Trondheimsfjord in Norway. Basso *et al.* (1996) found that *Lithophyllum duckeri* Woelkerling (listed as part of the British flora in Irvine & Chamberlain, 1994) should be considered conspecific with *Lithophyllum racemus* which has nomenclatural priority. Irvine & Chamberlain (1994) recorded one UK specimen that was similar to descriptions of *Lithophyllum duckeri* Woelkerling but suggested that it could also be a free-living form of *L. incrustans* based on the internal structure of its conceptacles. Thus the European range of *Lithophyllum racemus* (= *duckeri* in Irvine & Chamberlain, 1994) is uncertain, and Basso *et al.* (1996) consider it to be a Mediterranean endemic. The validity of '*Lithophyllum hibernicum*' is also uncertain as it is only known from three records of sterile specimens made in Galway in the 19th century.





**APPENDIX 2. FEATURES CONTRASTING AND COMPARING  
LITHOTHAMNION CORALLIOIDES, L. GLACIALE AND  
PHYMATOLITHON CALCAREUM**  
(Derived from Irvine & Chamberlain, 1994)

Character	<i>L. corallioides</i>	<i>L. glaciale</i>	<i>P. calcareum</i>
Colour tendency (fresh)	Brownish pink	Reddish to deep pink with violet tinge	Mauvish brown
Thallus surface	Covered with low mounds	Mainly smooth, some scattered low mounds	Some lowish mounds, frequently flaky areas
Thallus texture	Slightly glossy	Matt	Somewhat chalky
Branch hardness	Brittle	Hard	Quite hard
Branch size	Mainly < 1 mm diameter	Variable	Mainly >1 mm diameter
<b>Crustose plants in vertical section</b>			
Epithallial cells	Mainly flared	Mainly flared	Mainly domed
Cortical cells l x d	Fusiform 5-35 x 5-10 $\mu\text{m}$	Elliptical 8-12 x 4-8 $\mu\text{m}$	Elliptical 5-10 x 3.5 $\mu\text{m}$
Cortical fusions	Very extensive	More localised	More localised
Groups of fused cells	Star-like	Bead-like	Bead-like
Primary pits	Occupying entire end wall	Occupying only centre of end wall	Occupying only centre of end wall
Medullary filaments	5-6-layers	To 17 layers	5-6 layers
Medullary cells (length x diameter)	10-30 x 5-12 $\mu\text{m}$	7-26 x 3-8 $\mu\text{m}$	8-18 x 7-10 $\mu\text{m}$
<b>Branch anatomy in longitudinal section</b>			
Medullary cell distribution	Tiered	Tiered	Not tiered
Medullary cells lxd	Rectangular 20-35 x 8-12 $\mu\text{m}$	Elliptical to rectangular 3-18 x 3-11 $\mu\text{m}$	Elliptical 5-18 x 3-10 $\mu\text{m}$
Medullary cells pits	Bilenticular primary pits	Not known	Not bilenticular primary pits
Cortical cells lxd	5-35 x 5-10 $\mu\text{m}$	8-12 x 4-8 $\mu\text{m}$	8-18 x 7-10 $\mu\text{m}$
<b>Tetrasporangial/bisporangial conceptacles</b>			
Shape	Without rim; pore plate convex	With narrow, non-raised rim; pore plate level	Either with rim and prominent, or without rim and immersed; pore plate level
External diameter	To c. 350 $\mu\text{m}$	To c. 380 $\mu\text{m}$	To c. 450 $\mu\text{m}$
Pores SEM	Ringed by 5 cells SEM	Ringed by 6 cells SEM	Ringed by 6 cells SEM
Chamber VS diam.	234-380 $\mu\text{m}$	150-360 $\mu\text{m}$	230-350 $\mu\text{m}$
height	83-117 $\mu\text{m}$	110-180 $\mu\text{m}$	117-130 $\mu\text{m}$
Roof thickness	29-39 $\mu\text{m}$	5-40 $\mu\text{m}$	30-40 $\mu\text{m}$
<b>Tetra/bisporangia</b>			
Shape	Long and thin	Elliptical	Plump
Length	78-86 $\mu\text{m}$	65-96 $\mu\text{m}$	90-125 $\mu\text{m}$
Diameter	21-26 $\mu\text{m}$	23-47 $\mu\text{m}$	49-73 $\mu\text{m}$
Old conceptacles	Not known	Usually becoming buried	Becoming buried



**APPENDIX 3. SUBSTRATA ON WHICH MAERL BEDS OCCUR IN THE  
BRITISH ISLES**

Location	Substratum	Depth; main Maerl species	Author
Greatman's Bay, Galway	calcareous sand; quartz pebbles	3-6 m <i>P. calcareum</i>	Maggs, 1983
Finavarra peninsula, Galway	limestone outcrops & pebbles; sand & silt	10-18 m <i>L. corallioides</i>	Maggs, 1983
Loch Ewe	sandy mud	5-6 m <i>L. glaciale</i> ?	Maggs, in Howson, 1991
Falmouth	sandy mud	to 6 m <i>L. corallioides</i> 6-10 m <i>P. calcareum</i>	Blunden <i>et al.</i> , 1981.



**APPENDIX 4. GROWTH RATES OF MAERL**  
(from Adey & McKibbin, 1970)

Mean growth rates recorded from field measurements in the Ria de Vigo ( $\mu\text{m d}^{-1}$ )		
	<i>Phymatolithon calcareum</i>	<i>Lithothamnion corallioides</i>
February	0.2	shrinkage
March	1.0	shrinkage
April	1.5	0.0
June	2.9	1.2
July	5.1	1.5
August	3.2	0.4
October-January	no date presented - zero growth rate assumed	

Mean growth rates recorded from laboratory experiments ( $\mu\text{m d}^{-1}$ )				
	<i>Phymatolithon calcareum</i>		<i>Lithothamnion corallioides</i>	
light:dark (h)	14 : 10 @ 4-4.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ "summer"	8 : 16 @ 2-2.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ "winter"	14 : 10 @ 4-4.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ "summer"	8 : 16 @ 2-2.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ "winter"
°C				
0.2	-	died	-	died
0.4	died	-	died	-
2.1	-	no growth	-	died
5.0	no growth	-	no growth	-
6.0	-	no growth	-	no growth
10.0	3.3	0.7 @ 1.03 $\mu\text{mol m}^{-2} \text{s}^{-1}$	3.9	0.5 @ 1.03 $\mu\text{mol m}^{-2} \text{s}^{-1}$
15.1	4.2	0.7	1.9	-
17.0	3.2	-	1.1	-
19.0	2.3	-	0.2	-
			<i>Lithothamnion glaciale</i>	
13.5			13.0	



**APPENDIX 5. COMPARISON OF EPIFLORA SPECIES ON MAERL BEDS IN THE FAL ESTUARY (ROSTRON, 1985), MILFORD HAVEN, SCOTLAND (MAGGS, UNPUBLISHED) AND 2 SITES IN GALWAY BAY (MAGGS, 1983)**

- \* found
- \*\* found about half the year
- \*\*\* found most of the year
- \*\*\*\* frequent
- \*\*\*\*\* very frequent

Epiphytic species	Fal Estuary	Milford Haven	Scotland	Carraroe (Galway)	Finavarra (Galway)
<i>Aglaozonia parvula</i>	+			**	**
<i>Ahnfeltia plicata</i>				**	*
<i>Pterothamnion crispum</i>					***
<i>Antithamnion cruciatum</i>		+		***	*****
<i>Pterothamnion plumula</i>	+	+	+	**	****
<i>Antithamnionella spirographidis</i>	+	+		**	****
<i>Apoglossum ruscifolium</i>		+		**	**
<i>Arthrocladia villosa</i>		+			
<i>Asperococcus fistulosus</i>				*	
<i>Atractophora hypnoides</i>					*
<i>Audouinella floridula</i>	+	+	+	***	*****
<i>Audouinella spp.</i>	+	+	+	*****	*****
<i>Bangia atropurpurea</i>				*	*
<i>Berkeleya sp.</i>		+	+	**	*
<i>Bonnemaisonia asparagoides</i>					**
<i>Bonnemaisonia hamifera</i>					*
<i>Brongiartella byssoides</i>	+	+		*****	*****
<i>Bryopsis plumosa</i>	+	+	+	**	****
<i>Calliblepharis ciliata</i>				***	***
<i>Aglaothamnion bipinnatum</i>				**	***
<i>Aglaothamnion byssoides</i>		+		**	***
<i>Callithamnion corymbosum</i>				*	
<i>Aglaothamnion hookeri</i>		+			*
<i>Callophyllis laciniata</i>				*	
<i>Ceramium ciliatum</i>	+			**	**
<i>Ceramium deslongchampsii</i>				*	**
<i>Ceramium echionotum</i>	+			**	**
<i>Ceramium nodulosum</i>	+	+	+	***	***
<i>Ceramium cimbricum</i>	+	+		***	***
<i>Chaetomorpha capillaris</i>		+		**	**
<i>Chaetomorpha linum</i>	+	+	+	**	****



Epiphytic species	Fal Estuary	Milford Haven	Scotland	Carraroe (Galway)	Finavarra (Galway)
<i>Champia parvula</i>					*
<i>Chondria dasyphylla</i>		+		*****	*****
<i>Chondria tenuissima</i>					*
<i>Chondrus crispus</i>			+	*	
<i>Chylocladia verticillata</i>	+			**	***
<i>Cladophora albida</i>				***	***
<i>Cladophora battersia</i>				***	*
<i>Cladophora hutchinsiae</i>		+	+	***	*
<i>Cladophora pellucida</i>				*	**
<i>Cladophora pygmaea</i>		+	+	**	*
<i>Cladophora retroflexa</i>				*	
<i>Cladophora rupestris</i>	+	+	+	***	***
<i>Cladostephus spongiosus</i>				*	
<i>Codiolum phase</i>					*
<i>Compsothamnion thuyoides</i>				**	*****
<i>Corallina officinalis</i>				***	**
<i>Cordylecladia erecta</i>		+	+	*	***
<i>Cruoria cruoriaeformis</i>	+	+		***	*****
<i>Cruoria pellita</i>				*	
<i>Cruoria rosea</i>	+	+		*****	*****
<i>Cryptopleura ramosa</i>		+		*****	***
<i>Cystoclonium purpureum</i>			+		
<i>Cystoseira sp.</i>				*	
<i>Dasya sp.</i>					*
<i>Derbesia marina</i>	+			***	***
<i>Dermatolithon pustulatum</i>				*	
<i>Dermocarpa sp.</i>	+				***
<i>Dermocarpa sphaerica</i>				***	*****
<i>Dermocorynus montagnei</i>			+		*
<i>Dictyota dichotoma</i>	+	+	+	*****	*****
<i>Dudresnaya verticillata</i>	+			**	*****
<i>Ectochaete wittrockii</i>			+		
<i>Enteromorpha ramulosa</i>	+	+	+	**	**
<i>Erythrotrichia carnea</i>	+	+		*	*
<i>Erythroglossum laciniatum</i>				*	
<i>Falkenbergia rufolanosa</i>				***	*****
<i>Feldmannia sp.</i>				*	**
<i>Fosliella sp.</i>			+		

Epiphytic species	Fal Estuary	Milford Haven	Scotland	Carraroe (Galway)	Finavarra (Galway)
<i>Furcellaria lumbricalis</i>			+	***	*****
<i>Gastroclonium reflexum</i>				*	*
<i>Gelidiella calcicola</i>	+	+	+	*****	*****
<i>Gelidium latifolium</i>				*	
<i>Giffordia ? secunda</i>	+			*	**
<i>Gigartina acicularis</i>				*	*
<i>Gonimophyllum buffhamii</i>				**	***
<i>Goniotrichum alsidii</i>		+		*	**
<i>Gracilaria verrucosa</i>	+	+	+	***	***
<i>Griffithsia corallinoides</i>	+	+		**	***
<i>Halurus flosculosus</i>				***	***
<i>Halarachnion ligulatum</i>	+	+		*****	*****
<i>Halicystis ovalis</i>				**	
<i>Halopteris filicina</i>				*	*
<i>Halymenia latifolia</i>					****
<i>Heterogonium salinum ?</i>				*	
<i>Heterosiphonia plumosa</i>				***	***
<i>Hildenbrandia rubra</i>				*	*
<i>Holmesella pachyderma</i>	+	+	+	**	***
<i>Hymenoclonium serpens</i>				*	*
<i>Hypoglossum hypoglossoides</i>	+	+		***	*****
<i>Jania rubens</i>				*	**
<i>Laminaria saccharina</i>				**	*
<i>Laurencia pinnatifida</i>				***	**
<i>Lomentaria articulata</i>				***	**
<i>Lomentaria clavellosa</i>	+	+	+	***	**
<i>Melobesia membranacea</i>	+			*****	***
<i>Membranoptera alata</i>				**	*
<i>Mesogloia vermiculata</i>	+			*	
<i>Monosporus pedicellatus</i>				**	***
<i>Monostroma sp.</i>			+		
<i>Naccaria wiggii</i>					*
<i>Nitophyllum punctatum</i>	+	+	+	***	***
<i>Palmaria palmata</i>			+	**	*
<i>Peyssonmelia dubyi</i>	+	+	+	***	*****
<i>Peyssonmelia harveyana</i>				***	*****
<i>Peyssonmelia immersa</i>				****	***
<i>Phaeophila sp.</i>				***	***

Epiphytic species	Fal Estuary	Milford Haven	Scotland	Carraroe (Galway)	Finavarra (Galway)
<i>Phycodrys rubens</i>				***	***
<i>Phyllophora pseudoceranoides</i>					*
<i>Phyllophora crispa</i>				**	***
<i>Pleonosporium borneri</i>				**	***
<i>Plocamium cartilagineum</i>		+	+	*****	*****
<i>Plumaria plumosa</i>				***	**
<i>Polyides rotundus</i>	+	+	+	***	***
<i>Polyneura bonnemaisonii</i>				*	*
<i>Polysiphonia elongata</i>	+	+	+	***	***
<i>Polysiphonia fruticulosa</i>				**	***
<i>Polysiphonia furcellata</i>				**	
<i>Polysiphonia nigra</i>	+	+	+	***	*****
<i>Polysiphonia fucoides</i>		+		***	***
<i>Polysiphonia subulifera</i>				**	*
<i>Polysiphonia stricta</i>	+			***	*****
<i>Polysiphonia fibrillosa</i>	+			**	*
<i>Porphyra sp.</i>		+		***	***
<i>Porphyrodiscus simulans</i>			+	*	
<i>Pringsheimiella scutata</i>				***	***
<i>Pseudolithoderma sp.</i>	+	+	+	***	*****
<i>Pterocladia capillacea</i>				**	*
<i>Pterosiphonia parasitica</i>				**	***
<i>Pterosiphonia pennata</i>				*****	*****
<i>Radicilingua thysanorhizans</i>	+			*	**
<i>Ralfsia clavata</i>				**	
<i>Rhododiscus pulcherrimus</i>				***	*****
<i>Rhodomela confervoides</i>	+	+	+	*	***
<i>Rhodophyllis divaricata</i>	+	+		***	***
<i>Rhodophysema elegans</i>	+	+		*****	***
<i>Rhodymenia delicatula</i>			+	*	***
<i>Sciania turgida</i>		+		***	***
<i>Scytosiphon lomentaria</i>	+	+			
<i>Seirospora seirosperma</i>					*
<i>Spermothamnion repens</i>		+	+	*****	*****
<i>Spermothamnion sp.</i>	+			***	***
<i>Sphacelaria caespitula</i>			+	*	***
<i>Sphacelaria cirrosa</i>				*****	*****
<i>Sphacelaria plumula</i>				**	***

<b>Epiphytic species</b>	<b>Fal Estuary</b>	<b>Milford Haven</b>	<b>Scotland</b>	<b>Carraroe (Galway)</b>	<b>Finavarra (Galway)</b>
<i>Sphacelaria rigidula</i>	+				
<i>Sphondylothamnion multifidum</i>				*	*
<i>Sporochnus pedunculatus</i>		+		*	
<i>Spyridia filamentosa</i>				***	***
<i>Stenogramme interrupta</i>	+	+		***	***
<i>Striaria sp.</i>	+				
<i>Symphyocarpus strangulans</i>				*	
<i>Tilopteris mertensii</i>	+				
<i>Trailliella intricata</i>	+		+	***	*****
<i>Ulothrix sp.</i>	+				
<i>Ulva sp.</i>	+	+		***	***
<i>Uronema marina ?</i>				*	*



**APPENDIX 6. MOLLUSCAN SPECIES (LIVE) RECORDED FROM  
8 MAERL BEDS IN SCOTLAND (3 LOCATIONS) AND IRELAND  
(3 LOCATIONS, NUNN, 1992)**

<i>Abra alba</i>	<i>Lasaea adansonii</i>	<i>Trivia monacha</i>
<i>Acanthochiton crinitus</i>	<i>Lepidochiton cinereus</i>	<i>Turbonilla rufescens</i>
<i>Aeolidia papillosa</i>	<i>Leptochiton asellus</i>	<i>Turtonia minuta</i>
<i>Aequipecten opercularis</i>	<i>Limaria hians</i>	<i>Venerupis senegalensis</i>
<i>Alvania beanii</i>	<i>Littorina fabalis (L. mariaae)</i>	<i>Vitreolina philippi</i>
<i>Alvania punctura</i>	<i>Littorina littorea</i>	
<i>Ammonicerina rota</i>	<i>Littorina saxatilis</i>	
<i>Anomia ephippium</i>	<i>Lomanotus marmoratus</i>	
<i>Aplysia punctata</i>	<i>Lucinoma borealis</i>	
<i>Arca tetragona</i>	<i>Mangelia coarctata</i>	
<i>Archidoris pseudoargus</i>	<i>Margarites helicinus</i>	
<i>Berthella plumula</i>	<i>Marshallora adversa</i>	
<i>Bittium reticulatum</i>	<i>Modiolarca tumida</i>	
<i>Buccinum undatum</i>	<i>Modiolula phaseolina</i>	
<i>Caecum glabrum</i>	<i>Modiolus barbatus</i>	
<i>Calliostoma zizphium</i>	<i>Musculus discors</i>	
<i>Callochiton septemvalvis</i>	<i>Mya truncata</i>	
<i>Cerithiopsis tubercularis</i>	<i>Mysella bidentata</i>	
<i>Chlamys varia</i>	<i>Mytilus edulis</i>	
<i>Chrysallida decussata</i>	<i>Nucella lapillus</i>	
<i>Chrysallids obtusa</i>	<i>Nucula nucleus</i>	
<i>Cingula trifasciata</i>	<i>Ocenebra erinacea</i>	
<i>Circomphalus casina</i>	<i>Odostomia turrata</i>	
<i>Clausinella fasciata</i>	<i>Odostomia unidentata</i>	
<i>Corbula gibba</i>	<i>Omalogyra atomus</i>	
<i>Coryphella lineata</i>	<i>Onchidoris muricata</i>	
<i>Coryphella pedata</i>	<i>Onoba semicostata</i>	
<i>Crenella decussata</i>	<i>Ousillina inconspicua</i>	
<i>Cuthona concinna</i>	<i>Palliolum tigrinum</i>	
<i>Dendronotus frondosus</i>	<i>Parvicardium exiguum</i>	
<i>Diodora graeca</i>	<i>Parvicardium ovale</i>	
<i>Discodoris planata</i>	<i>Parvicardium scabrum</i>	
<i>Dosinia exoleta</i>	<i>Patella vulgata</i>	
<i>Doto fragilis</i>	<i>Pecten maximus</i>	
<i>Eatonina fulgida</i>	<i>Pododesmus patelliformis</i>	
<i>Elysia viridis</i>	<i>Pododesmus squamula</i>	
<i>Emarginula fissura</i>	<i>Polinices montagui</i>	
<i>Embletonia pulchra</i>	<i>Polinices policanus</i>	
<i>Ensis arcuatus</i>	<i>Polycera quadrilineata</i>	
<i>Epitonium clathratulum</i>	<i>Pusillina sarsi</i>	
<i>Eubranchus farrani</i>	<i>Raphituma linearis</i>	
<i>Gari tellinella</i>	<i>Retusa truncatula</i>	
<i>Gibbula cineraria</i>	<i>Rissoa interrupta</i>	
<i>Gibbula magus</i>	<i>Rissoa lilacina</i>	
	<i>Rissoa parva</i>	
<i>Gibbula tumida</i>	<i>Rissoella diaphana</i>	
<i>Gibbula umbilicalis</i>	<i>Rissoella opalina</i>	
<i>Gouldia minima</i>	<i>Skeneopsis planorbis</i>	
<i>Helcion pellucidum</i>	<i>Spisula elliptica</i>	
<i>Hiatella arctica</i>	<i>Spisula solida</i>	
<i>Hinia incrassata</i>	<i>Tapes rhomboides</i>	
<i>Hinia reticulata</i>	<i>Tectura testudinalis</i>	
<i>Ischnochiton albus</i>	<i>Tectura virginea</i>	
<i>Janolus cristatus</i>	<i>Thracia villosiuscula</i>	
<i>Jujubinus montagui</i>	<i>Timoclea ovata</i>	
<i>Kellia suborbicularis</i>	<i>Tonicella marmorea</i>	
<i>Lacuna pallidula</i>	<i>Tonicella rubra</i>	
<i>Lacunda parva</i>	<i>Tricolia pullus</i>	
<i>Lacunda vineta</i>	<i>Trivia arctica</i>	



**APPENDIX 7. MAERL BED SPECIES LIST, RECORDED FROM  
SCOTTISH SITES DESIGNATED AS MAERL BEDS**  
(from Scott & Moore, 1996)

Species code	taxa
<b>PORIFERA:</b>	<b>CALCAREA</b>
C0000	PORIFERA
C0025	<i>Leucosolenia botryoides</i>
C0035	<i>Scypha ciliata</i>
C0070	<i>Grantia compressa</i>
	<b>DEMOSPONGIA</b>
C0220	<i>Suberites carnosus</i>
C0221	<i>Suberites domuncula</i>
C0258	<i>Polymastia boletiformis</i>
C0300	<i>Cliona</i>
C0302	<i>Cliona celata</i>
C0479	<i>Halichondria</i>
C0481	<i>Halichondria bowerbanki</i>
C0484	<i>Halichondria panicea</i>
C0523	<i>Hymeniacidon perleve</i>
C0596	<i>Esperiopsis fucorum</i>
C0645	<i>Myxilla incrustans</i>
C0854	<i>Haliclona</i>
C0865	<i>Haliclona viscosa</i>
C0920	Porifera indet. (crusts)
<b>CNIDARIA:</b>	<b>SCYPHOZOA</b>
D0076	<i>Cyanea capillata</i>
D0083	<i>Aurelia aurita</i> (scyphistomae)
	<b>HYDROZOA</b>
D0121	<i>Corymorpha nutans</i>
D0237	<i>Eudendrium rameum</i>
D0306	<i>Bougainvillia ramosa</i>
D0335	<i>Hydractinia echinata</i>
D0358	<i>Clava multicornis</i>
D0525	<i>Halecium beanii</i>
D0526	<i>Halecium halecium</i>
D0578	<i>Halopteris catharina</i>
D0585	<i>Kirchenpaueria pinnata</i>
D0597	<i>Nemertesia antennina</i>
D0599	<i>Nemertesia ramosa</i>
D0605	<i>Plumularia setacea</i>
D0626	<i>Abietinaria abietina</i>
D0627	<i>Abietinaria filicula</i>
D0648	<i>Dynamena pumila</i>
D0653	<i>Hydrallmania falcata</i>
D0676	<i>Sertularia argentea</i>
D0703	<i>Clytia hemisphaerica</i>
D0728	<i>Obelia</i>
D0730	<i>Obelia dichotoma</i>
D0731	<i>Obelia geniculata</i> hydroids indet.
	<b>ANTHOZOA</b>
D1024	<i>Alcyonium digitatum</i>
D1056	<i>Virgularia mirabilis</i>
D1075	<i>Cerianthus lloydii</i>
D1158	<i>Anemonia viridis</i>
D1163	<i>Bolocera tuediae</i>
D1168	<i>Urticina felina</i>
D1169	<i>Urticina eques</i>
D1192	<i>Stomphia coccinea</i>
D1225	<i>Metridium senile</i>
D1231	<i>Sagartia elegans</i>
D1232	<i>Sagartia troglodytes</i>
D1292	<i>Adamsia carciniopados</i>
D1303	<i>Halacampoides elongatus</i>
D1319	<i>Peachia cylindrica</i>
D1325	<i>Halocampa chrysanthellum</i>
D1341	<i>Edwardsia claparedii</i>
F0000	<b>PLATYHELMINTHES</b>
G0000	<b>NEMERTEA</b>
G0040	<i>Tubulanus annulatus</i>
G0047	<i>Tubulanus superbus</i>
G0078	<i>Lineus longissimus</i>
N0011	<i>Golfingia vulgaris</i>
<b>ANNELIDA:</b>	<b>POLYCHAETA</b>
P0001	<b>POLYCHEATA</b>
P0020	<i>Pisione remota</i>
P0027	<i>Aphrodita aculeata</i>
P0042	Polynoidae
P0060	<i>Alentia gelatinosa</i>
P0097	<i>Harmothoe</i>
P0103	<i>Harmothoe fragilis</i>
P0104	<i>Harmothoe fraserthomsoni</i>
P0108	<i>Harmothoe ljunmani</i>
P0110	<i>Harmothoe mcintoshii</i>
P0120	<i>Harmothoe lunulata</i>
P0169	<i>Pholoe inornata</i>
P0171	<i>Pholoe synophthalmica</i>
P0230	<i>Mystides limbata</i>



P0285	<i>Eumida sanguinea</i>
P0476	<i>Glycera lapidum</i>
P0500	<i>Goniadella bobretzkii</i>
P0539	<i>Gyptis</i>
P0635	Syllidae
P0648	<i>Langerhansia comuta</i>
P0661	<i>Trypanosyllis coeliaca</i>
P0674	<i>Typosyllis vittata</i>
P0733	<i>Exogoninae</i>
P0750	<i>Sphaerosyllis</i>
P0751	<i>Sphaerosyllis bulbosa</i>
P0752	<i>Sphaerosyllis magnidentata</i>
P0780	<i>Myrianida pinnigera</i>
P0936	<i>Aponuphis bilineata</i>
P0991	<i>Nematonereis unicornis</i>
P1011	<i>Lumbrineris latreilli</i>
P1104	<i>Prododorvillea kefersteini</i>
P1114	<i>Schistomeringos neglecta</i>
P1115	<i>Schistomeringos rudolphi</i>
P1155	<i>Paraonidae</i>
P1179	<i>Levinsenia gracilis</i>
P1228	<i>Aonides paucibranchiata</i>
P1250	<i>Laonice bahusiensis</i>
P1269	<i>Minuspio cirrifera</i>
p1344	<i>Spiophanes kroeyeri</i>
P1375	<i>Chaetopterus variopedatus</i>
P1403	<i>Chaetozone setosa</i>
P1484	<i>Flabelligera fragilis</i>
P1491	<i>Pherusa plumosa</i>
P1501	<i>Macrochaeta sp.</i>
P1558	<i>Mediomastus fragilis</i>
P1563	<i>Notomastus latericeus</i>
P1576	<i>Arenicola marina</i>
P1668	<i>Ophelia</i>
P1689	<i>Ophelia bicornis</i>
P1743	<i>Scalibregma inflatum</i>
P1798	<i>Polygordius</i>
P1854	<i>Lagis koreni</i>
P1876	<i>Sabellaria spinulosa</i>
P1907	<i>Ampharete finmarchia</i>
P1990	<i>Terebellides stroemi</i>
P2000	<i>Terebellidae</i>
P2019	<i>Eupolymnia nebulosa</i>
P2020	<i>Eupolymnia nesidensis</i>
P2031	<i>Lanice conchilega</i>
P2061	<i>Nicolea zostericola</i>
P2076	<i>Pista cristata</i>
P2150	<i>Sabellidae</i>
P2171	<i>Chone filicaudata</i>
P2172	<i>Chone infundibuliformis</i>

P2193	<i>Fabricia sabella</i>
P2221	<i>Megalomma vesiculosum</i>
P2227	<i>Myxicola infundibulum</i>
P2263	<i>Eualus pusiolus</i>
P2261	<i>Sabella pavonina</i>
P2302	<i>Pomatoceros</i>
P2304	<i>Pomatoceros triqueter</i>
P2309	<i>Serpula vermicularis</i>
P2326	<i>Filograna implexa</i>
P2346	<i>Protula tubularia</i>
P2355	Spirorbidae
P2401	<i>Spirorbis</i>
P2417	OLIGOCHAETA
<b>CHELICERATA</b>	
Q0080	Acaridae indet.
<b>CRUSTACEA: CIRRIPEDIA</b>	
R0109	<i>Balanus balanus</i>
R0110	<i>Balanus crenatus</i>
<b>MYSIDAE</b>	
S0046	Mysidae
<b>AMPHIPODA</b>	
S0166	AMPHIPODA
S0193	<i>Eusirus longipes</i>
S0392	<i>Hyale nilssoni</i>
S0447	<i>Metaphoxus fultoni</i>
S0509	<i>Lysianassa ceratina</i>
S0511	<i>Lysianassa plumosa</i>
S0556	<i>Socarnes erythrophthalmus</i>
S0624	<i>Iphimedia</i>
S0690	<i>Dexamine spinosa</i>
S0696	<i>Guerna coalita</i>
S0824	<i>Cheirocratus intermedius</i>
S0899	<i>Gammaropsis nitida</i>
S0944	<i>Eriethonius punctatus</i>
S0998	<i>Leptocheirus hirsutimanus</i>
S1018	<i>Corophium acherusicum</i>
S1070	Caprellidae
S1451	<i>Sphaeroma rugicauda</i>
S1474	<i>Jaera albifrons</i>
S1484	<i>Janira maculosa</i>
S1592	<i>Astacilla longicornis</i>
<b>TANAIDACEA</b>	
S1868	TANAIDACEA
S1931	<i>Tanaopsis graciloides</i>
S1994	<i>Vauntomsonia cristata</i>
S2022	<i>Eudorella truncatula</i>

S2055	<i>Nannastacus unguiculatus</i>
<b>DECAPODA</b>	
S2210	<i>Palaemon serratus</i>
S2263	<i>Eualus pusiolus</i>
S2269	<i>Hippolyte inermis</i>
S2316	<i>Pandalina brevisrostris</i>
S2331	<i>Crangon crangon</i>
S2444	Paguridae
S2446	<i>Anapagurus chiroacanthus</i>
S2447	<i>Anapagurus hyndmanni</i>
S2462	<i>Pagurus</i>
S2465	<i>Pagurus bernhardus</i>
S2468	<i>Pagurus cuanensis</i>
S2470	<i>Pagurus prideaux</i>
S2471	<i>Pagurus pubescens</i>
S2484	<i>Galathea</i>
S2486	<i>Galathea intermedia</i>
S2488	<i>Galathea nexa</i>
S2489	<i>Galathea squamifera</i>
S2495	<i>Munida rugosa</i>
S2502	<i>Pisidia longicornis</i>
S2507	<i>Porcellana playtcheles</i>
S2543	<i>Ebalia tuberosa</i>
S2559	<i>Hyas araneus</i>
S2560	<i>Hyas coarctatus</i>
S2576	<i>Inachus dorsettensis</i>
S2578	<i>Inachus phalangium</i>
S2582	<i>Macropodia</i>
S2585	<i>Macropodia rostrata</i>
S2593	<i>Eurynome spinosa</i>
S2620	<i>Corystes cassivelaunus</i>
S2626	<i>Atelecyclus rotundatus</i>
S2646	<i>Cancer pagurus</i>
S2666	<i>Liocarcinus</i>
S2668	<i>Liocarcinus corrugatus</i>
S2669	<i>Liocarcinus depurator</i>
S2670	<i>Liocarcinus holsatus</i>
S2672	<i>Liocarcinus puber</i>
S2673	<i>Liocarcinus pusillus</i>
S2690	<i>Carcinus maenas</i>
S2746	<i>Xantho pilipes</i>
<b>MOLLUSCA      POLYPLACOPHORA</b>	
W0050	POLYPLACOPHORA
W0055	<i>Leptochiton asellus</i>
W0074	<i>Lepidochitona cinereus</i>
W0078	<i>Tonicella marmorea</i>
W0079	<i>Tonicella rubra</i>

<b>GASROPODA</b>	
W0111	<i>Emarginula fissura</i>
W0124	<i>Tectura</i>
W0125	<i>Tectura testudinalis</i>
W0126	<i>Tectura virginea</i>
W0139	<i>Helcion pellucidum</i>
W0161	<i>Margarites helicinus</i>
W0183	<i>Jujubinus montagui</i>
W0189	<i>Gibbula magus</i>
W0191	<i>Gibbula tumida</i>
W0193	<i>Gibbula cineraria</i>
W0195	<i>Gibbula umbilicalis</i>
W0200	<i>Calliostoma zizyphinum</i>
W0231	<i>Tricolia pullus</i>
W0244	<i>Lacuna vineta</i>
W0250	<i>Littorina littorea</i>
W0255	<i>Littorina obtusata</i>
W0435	<i>Caecum glabrum</i>
W0442	<i>Turritella communis</i>
W0664	<i>Melanella alba</i>
W0689	<i>Vitreolina phillipi</i>
W0700	<i>Aporrhais pespelecani</i>
W0737	<i>Trivia arctica</i>
W0748	<i>Lamellaria latens</i>
W0754	<i>Velutina velutina</i>
W0773	<i>Polineces catena</i>
W0777	<i>Polinices poliana</i>
W0844	<i>Buccinum undatum</i>
W0860	<i>Neptunea antiqua</i>
W0887	<i>Hinia incrassata</i>
W0889	<i>Hinia reticulata</i>
W0916	<i>Mangelia</i>
W0977	<i>Philine</i>
W0979	<i>Philine aperta</i>
W0983	<i>Philine pruinosa</i>
<b>OPISTHBRANCHIA</b>	
W1062	<i>Elysia viridis</i>
W1067	<i>Hermæa bifida</i>
W1102	<i>Aplysia punctata</i>
W1277	<i>Doto dunnei</i>
W1279	<i>Doto fragilis</i>
W1324	<i>Adalaria proxima</i>
W1355	<i>Onchidoris muricata</i>
W1358	<i>Limacia clavigera</i>
W1403	<i>Archidoris pseudoargus</i>
W1418	<i>Jorunna tomentosa</i>
W1452	<i>Coryphella lineata</i>
W1460	<i>Flabellina pedata</i>
W1526	<i>Facelina bostoniensis</i>

W1542	<i>Favorinus branchialis</i>
<b>PELECYPODA</b>	
W1648	Mytilidae
W1650	<i>Mytilus edulis</i>
W1662	<i>Musculus</i>
W1675	<i>Modiolus modiolus</i>
W1717	<i>Glycymeris glycymeris</i>
W1739	<i>Limaria hians</i>
W1769	<i>Ostrea edulis</i>
W1778	<i>Palliolum tigrinum</i>
W1795	<i>Chlamys</i>
W1800	<i>Chlamys varia</i>
W1801	<i>Chlamys varia nivea</i>
W1805	<i>Aequipecten opercularis</i>
W1809	<i>Pecten maximus</i>
W1813	Anomiidae
W1820	<i>Pododesmus patelliformis</i>
W1822	<i>Pododesmus squamula</i>
W1905	<i>Mysella bidentata</i>
W1945	<i>Astarte sulcata</i>
W1977	<i>Parvicardium ovale</i>
W1987	<i>Laevicardium crassum</i>
W2011	<i>Lutraria lutraria</i>
W2022	<i>Ensis</i>
W2023	<i>Ensis arcuatus</i>
W2025	<i>Ensis ensis</i>
W2027	<i>Ensis siliqua</i>
W2051	<i>Arcopagia crassa</i>
W2061	<i>Moerella donacina</i>
W2090	<i>Gari tellinella</i>
W2111	<i>Solecurtus scopula</i>
W2125	<i>Arctica isslandica</i>
W2147	<i>Venus verrucosa</i>
W2151	<i>Circomphalus casina</i>
W2155	<i>Gouldia minima</i>
W2166	<i>Dosinia exoleta</i>
W2181	<i>Paphia rhomboides</i>
W2189	<i>Chamelea gallina</i>
W2193	<i>Clausinella fasciata</i>
W2201	<i>Timoclea ovata</i>
W2227	<i>Mya truncata</i>
W2551	<i>Hiatella arctica</i>
W2348	<i>Thracia</i>
W2351	<i>Thracia phaseolina</i>
W2361	<i>Cochlodesma praetenuae</i>
<b>CEPHALOPODA</b>	
W2408	<i>Sepiola atlantica</i>
W2522	<i>Eledone cirrhosa</i>

<b>BRACHIOPODA</b>	
X007	<i>Neocrania anomala</i>
<b>BRYOZOA</b>	
Y0027	<i>Crisia denticulata</i>
Y0030	<i>Crisia ramosa</i>
Y0137	<i>Alcyonidium diaphanum</i>
Y0139	<i>Alcyonidium hirsutum</i>
Y0141	<i>Alcyonidium mytili</i>
Y0377	<i>Parasmittina trispinosa</i>
Y0448	<i>Schizomavella linearis</i>
Y0606	<i>Cellepora pumicosa</i>
Y0658	<i>Eucratea loricata</i>
Y0664	<i>Membranipora membranacea</i>
Y0678	<i>Electra pilosa</i>
Y0694	<i>Flustra foliacea</i>
Y0836	<i>Scrupocellaria</i>
Y0838	<i>Scrupocellaria reptans</i>
Y0841	<i>Scrupocellaria scruposa</i>
Y0879	<i>Bugula turbinata</i>
Y0888	Bryozoa indet. crusts
ZA0003	<i>Phoronis</i>

<b>ECHINODERMATA: CRINOIDEA</b>	
ZB0011	<i>Antedon bifida</i>
ZB0012	<i>Antedon petasus</i>
<b>ASTEROIDEA</b>	
ZB0041	<i>Asteropecten irregularis</i>
ZB0067	<i>Luidia ciliaris</i>
ZB0101	<i>Porania pulvillus</i>
ZB0113	<i>Asterina gibbosa</i>
ZB0143	<i>Solaster endeca</i>
ZB0149	<i>Crossaster papposus</i>
ZB0164	<i>Henrica</i>
ZB0165	<i>Henricia oculata</i>
ZB0166	<i>Henricia sanguinolenta</i>
ZB0190	<i>Asterias rubens</i>
ZB0195	<i>Leptasterias muelleri</i>
ZB0200	<i>Marthasterias glacialis</i>
<b>OPHIUROIDEA</b>	
ZB0235	<i>Ophiothrix fragilis</i>
ZB0242	<i>Ophiocomina nigra</i>
ZB0278	<i>Ophiopholis aculeata</i>
ZB0283	<i>Amphiura</i>
ZB0286	<i>Amphiura chiajei</i>
ZB0292	<i>Amphiura chiajei/filiformis</i>
ZB0300	<i>Amphipholis squamata</i>
ZB0312	<i>Ophiura affinis</i>
ZB0313	<i>Ophiura albida</i>
ZB0315	<i>Ophiura ophiura</i>
ZB0316	<i>Ophiura robusta</i>
<b>ECHINOIDEA</b>	
ZB0355	<i>Psammechinus miliaris</i>
ZB0362	<i>Echinus esculentus</i>
ZB0381	<i>Stronglyocentrotus droebachiensis</i>
ZB0388	<i>Echinocyamus pusillus</i>
ZB0401	<i>Spatangus purpureus</i>
ZB0408	<i>Echinocardium flavescens</i>
<b>HOLOTHUROIDEA</b>	
ZB0452	<i>Holothuria forskali</i>
ZB0458	<i>Cucumaria</i>
ZB0459	<i>Cucumaria frondosa</i>
ZB0495	<i>Thyone fusus</i>
ZB0498	<i>Thyone roscovita</i>
ZB0503	<i>Neopentadactyla mixta</i>
<b>TUNICATA</b>	
ZD0006	<i>Clavelina lepadiformis</i>

ZD0052	<i>Sidnyum turbinatum</i>
ZD0057	<i>Aplidium</i>
ZD0064	<i>Aplidium punctum</i>
ZD0068	Didemnidae
ZD0097	<i>Diplosoma listerianum</i>
ZD0117	<i>Ciona intestinalis</i>
ZD0135	<i>Corella parallelogramma</i>
ZD0141	<i>Ascidella aspersa</i>
ZD0143	<i>Ascidella scabra</i>
ZD0149	<i>Ascidia conchilega</i>
ZD0150	<i>Ascidia mentula</i>
ZD0153	<i>Ascidia virginea</i>
ZD0194	<i>Dendrodoa grossularia</i>
ZD0209	<i>Botryllus schlosseri</i>
ZD0214	<i>Botrylloides leachi</i>
ZD0240	<i>Pyura microcosmus</i>
ZD0241	<i>Pyura squamulosa</i>
ZD0258	<i>Molgula oculata</i>
ZD0314	<i>Salpa</i>
<b>CHONDROCHTHYES</b>	
ZF0040	<i>Scyliorhinus canicula</i>
ZF0055	<i>Mustelus mustelus</i>
<b>OSTEICHTHYES</b>	
ZG0022	<i>Conger conger</i>
ZG0124	<i>Diplecogaster bimaculata</i>
ZG0127	<i>Lepadogaster</i>
ZG0118	Gobiesocidae
ZG0136	<i>Lophius piscatorius</i>
ZG0150	Gadidae
ZG0173	<i>Gadus morhua</i>
ZG0208	<i>Pollachius pollachius</i>
ZG0209	<i>Pollachius virens</i>
ZG0351	<i>Spinachia spinachia</i>
ZG0434	<i>Myoxocephalus scorpius</i>
ZG0438	<i>Taurulus bubalis</i>
ZG0448	<i>Agonus cataphractus</i>
ZG0457	<i>Liparis liparis</i>
ZG0632	<i>Lipophrys pholis</i>
ZG0680	<i>Pholis gunnellus</i>
ZG0799	<i>Callionymus</i>
ZG0700	<i>Callionymus lyra</i>
ZG0702	<i>Callionymus reticulatus</i>
ZG0705	Gobiidae
ZG0728	<i>Gobiusculus flavescens</i>
ZG0740	<i>Pomatoschistus</i>
ZG0742	<i>Pomatoschistus minutus</i>
ZG0744	<i>Pomatoschistus pictus</i>
ZG0867	<i>Zeugopterus punctatus</i>

ZG0887	Pleuronectidae
ZG0891	<i>Limanda limanda</i>
ZG0903	<i>Pleuronectes platessa</i>
ZL0000	CYANOPHYCOTA
<b>RHODOPHYCOTA: BANGIALES</b>	
ZM0072	<i>Porphyropsis coccinea</i>
ZM0083	<i>Porphyra</i>
ZM0088	<i>Porphyra miniata</i>
<b>NEMALIALES</b>	
ZM0097	<i>Audouinella</i>
ZM0182	<i>Sciania</i>
ZM0185	<i>Scinaia turgida</i>
ZM0202	<i>Asparagopsis armata</i>
ZM0208	<i>Bonnemaisonia asparagoides</i>
ZM0211	<i>Bonnemaisonia hamifera</i>
ZM0215	<i>Gelidium</i>
<b>PALMARIALES</b>	
ZM0242	<i>Palmaria palmata</i>
<b>CRYPTONEMIALES</b>	
ZM0256	<i>Dilsea carnosa</i>
ZM0261	<i>Dudresnaya verticillata</i>
ZM0266	<i>Dumontia contorta</i>
ZM0299	<i>Dermocorynus montagnei</i>
ZM0306	<i>Grateloupia filicina</i>
ZM0322	<i>Callophyllis cristata</i>
ZM0323	<i>Callophyllis laciniata</i>
ZM0328	<i>Kallymenia reniformis</i>
ZM0344	<i>Gloiosiphonia capillaris</i>
ZM0367	<i>Peyssonelia dubyi</i>
ZM0369	<i>Peyssonelia immersa</i>
ZM0376	<i>Hildenbrandia</i>
<b>CORALLINALES</b>	
ZM0384	Corallinaceae
ZM0404	<i>Corallina officinalis</i>
ZM0459	<i>Lithothamnion</i>
ZM0460	<i>Lithothamnion corallioides</i>
ZM0461	<i>Lithothamnion glaciale</i>
ZM0491	<i>Phymatolithon calcareum</i>
ZM0530	maerl indet.
<b>ANGIOSPERMA</b>	
ZX0002	<i>Zostera marina</i>