BIOGENIC REEFS

An overview of dynamic 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	Circalittoral 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

Nature, importance and distribution of the biotope complex

The most important biogenic reef forming species in inshore British waters are Sabellaria alveolata, S. spinulosa, Mytilus edulis, Modiolus modiolus and Serpula vermicularis. Biogenic reefs can have a number of important effects on the physical environment: they often stabilise sands, gravels and stones; the shells or tubes of the organisms themselves provide hard substrata for attachment of sessile organisms; they may provide a diversity of crevices, surfaces and sediments for colonisation; and accumulated faeces, pseudofaeces and other sediments may be an important source of food for other organisms. For these reasons many biogenic reefs have a very rich associated fauna and flora, which at least in terms of macrofauna is often much richer and more diverse than in surrounding areas. Moreover, *Mytilus* is particularly important both as a fishery, and as a source of food for birds and for many benthic predators.

Biogenic reefs have been defined for the purposes of this report as "Solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms."

Many of these species form extremely variable community types, with obvious gradation between non-reef and reef biotopes. Furthermore, the concept of biogenic reefs has not been an important consideration in past survey work, and community/habitat descriptions by many workers, including to some extent the MNCR biotope classifications, are often inadequate to decide whether a habitat / biotope constitutes a biogenic reef. This is a major problem for many *Modiolus modiolus* and *Sabellaria spinulosa* communities, and less so for *Mytilus edulis* and intertidal *Sabellaria alveolata* (though there is little experience of categorisation of subtidal *S. alveolata*). Identification of serpulid reefs appears to pose no problem.

There is perhaps surprisingly little consistency in the biology, ecology and sensitivity within the grouping 'biogenic reefs', which is to some degree an artificial conglomerate of biotopes with differing characteristics. It is clear that management issues must be considered separately for each type.

Sabellaria alveolata reefs may take the form of extensive sheets, hummocks, or more massive and extensive reefs, consisting of honeycomb like masses of worm tubes. They reach their northerly limit of distribution in the outer Solway Firth, and rarely penetrate further east than Lyme Bay in the English Channel. They seem to be absent from many exposed peninsulas. They are well represented in candidate SACs (cSACs) though some of the best and most extensive reefs in Cumbria, which can cover hundreds of hectares, are in unprotected areas.

The existence of well developed, stable *S. spinulosa* reefs was only recently demonstrated conclusively. The only certain occurrence seems to be in the mouth of the Wash, where reefs raised up to 30 cm proud of the seabed extend for hundreds of metres, both within and outside the Wash and North Norfolk Coast cSAC. Similar communities may occur in the Bristol Channel, although this is very uncertain. Less stable, often annual 'crusts' or clumps seem to be much more widespread in turbid sublittoral areas, although a few are known from Scottish waters.

Modiolus modiolus reefs occur in two main physical forms: semi-infaunal reefs, which grade in density and thickness from continuous dense, raised reefs to scattered clumps which may not actually fit the definition of biogenic reefs; and a more unusual infaunal gravel-embedded reef community which can form wave like mounds up to 1 metre high. *Modiolus* has a predominantly northern and western distribution, with few reef areas known south of the Humber or Severn. A number of cSACs include semi-infaunal *Modiolus* reefs, but the infaunal gravel-embedded reef community has only been identified outside UK waters.

Well developed *Mytilus edulis* reefs generally take the form of hummocks or ribbons, rarely exceeding 30-50 cm in thickness but with very high densities of living and dead mussels, and are often very extensive. They accumulate large amounts of 'mussel mud' (faeces, pseudofaeces and sediments). They are widespread but the best examples are limited to large shallow inlets and bays, especially estuarine areas. Several cSACs include good examples.

The only known *Serpula vermicularis* reefs in Britain are in Loch Creran, and there are probably few equivalent examples in Europe. They were also present in part of Loch Sween during the 1980's, although more recent diving surveys found only dead colonies for unknown reasons. They are often discrete structures up to 75 cm high and 1 m across, but adjacent reefs can coalesce. They are formed by calcareous worms tubes up to around 15-20 cm in length growing sinuously upwards in a relatively open structure. They occur in sheltered, relatively shallow parts of sealochs, however, and might potentially be found in SACs in the future.

Environmental requirements

Sabellaria alveolata occurs mainly in the low intertidal, or shallow subtidal zone. It is limited to areas of moderate to considerable water movement where there is a good supply of suspended sand, and does not penetrate into very low salinity areas. It requires some degree of hard substratum (stable rocks and boulders or boulder/ cobble scars) on which to form. Areas dominated by *S. alveolata* can cover hundreds of hectares. It is markedly affected by cold winters in the UK, with death of large areas of reef reported, particularly at higher shore levels. Reefs are moderately fragile, particularly the cup-shaped 'porches' at the outward end, which can be damaged by light trampling.

S. spinulosa forms crusts and occasionally well developed, raised reefs sublittorally in turbid waters from a few metres to at least 40 m or so. The best reefs probably form on sandy sediments with some hard substrata. *S. spinulosa* does not seem to penetrate into low salinity areas. Thin crusts seem to be moderately fragile and are quite easily broken up by storms or physical impacts. Substantial reefs are probably stronger than those of *S. alveolata*.

M. modiolus occurs in a wide variety of biotopes. Infaunal reefs have been reported in strong tidal waters of moderate depths (15-40 m). Semi-infaunal reefs and beds occur in a variety of situations on mixed or muddy sediments and in a variety of current regimes, mainly between the shallow infralittoral and around 50 m. *Modiolus* reef communities are often patchy but may nevertheless be extensive, covering many hectares. They are not found in low salinity areas. The fragility of reefs probably varies with the degree to which they are infaunal.

Mytilus edulis is tolerant of a wide range of environmental variables such as temperature, food supply, and water turbidity, but forms large reefs mainly on mixed firm sediments in relatively wave sheltered bays and estuaries where there are strong currents. Reefs form mainly in the mid and low intertidal zone but can occur down to 10 m in places. Resistance of many reefs to wave and current action seems to deteriorate as the reefs get thicker and accumulate more

mussel mud. Beds of only a single year class are often particularly poorly attached to the substratum.

Serpula vermicularis reefs form initially on a variety of hard substrata such as stones and shells, but can subsequently spread over wider areas. The main environmental requirements seem to be an enclosed body of water with limited water exchange, allowing for retention of larvae, and probably a lack of competition for space. Siltation and anoxic bottom water seem to limit downward distribution. The reefs seems to have a moderate tolerance to reductions in salinity. They are very fragile.

Biology and ecological functioning

S. alveolata spawn in July. Larval life seems to be long, with settlement occurring mainly over autumn and winter. Settlement is strongly stimulated by the presence of *Sabellaria* tubes. The worms themselves probably have a typical life cycle of 4 or 5 years (up to 9 or 10). *S. alveolata* reefs undergo cycles of development and decay over a few years, with rapid growth and development of reefs in the first year Recruitment is sporadic. In the long term there appears to be a moderate stability, with reefs being found largely in the same areas, but there are examples of more transient reefs. The associated community is unremarkable, being very species poor on dense, young reefs and somewhat higher, with up to 38 species reported on older reefs. There is some evidence of differences in community structure between the different reef forms. Reefs can lead to increased heterogeneity of mobile sediments and stones, exposed barnacle dominated shores and sand scoured rocks, and sheets may impede drainage to form pools. There is little information on predators, which do not seem to have important effects. There is also little information on any aspect of subtidal communities.

S. spinulosa seems in many cases to be annual, but on more stable reefs the animals seem to be able to live for a few years. Spawning probably occurs largely over winter and settlement in early spring. Settlement is stimulated by the presence of *S. spinulosa* tubes, but not as strongly as in *S. alveolata*. The commercially valuable pink shrimp *Pandalus montagui* seems to have a strong association with *S. spinulosa* reefs. Recruitment is probably variable and can be greatly reduced by dense brittle stars *Ophiothrix fragilis*. Associated communities on reef areas are noticeably richer than surrounding areas but there is presently a lack of detailed information on this subject.

M. modiolus is a very long-lived species and animals in reef communities are frequently 25 years old or more. Spawning seasons are variable. The larvae spend a long time in the plankton and recruitment is slow and sometimes very sporadic. Although reefs in enclosed sea lochs are probably self recruiting, those from more open areas may not be. Predation rates, especially by crabs and starfish, are high in the early years. *Modiolus* does not mature sexually until it is 3-6 years old, allowing all of its efforts to be directed into rapid growth in the early years after which it is less vulnerable to predation. *Modiolus* has a very strong structuring influence on the sediments in which reef areas usually occur, and extremely rich associated faunas containing hundreds of species have been found.

Mytilus edulis, in contrast to *Modiolus*, spawns in its first year. There may be a number of spawnings in spring and summer, and settlement occurs usually within a month or so. In some populations there is a primary settlement on filamentous substrata followed by detachment, and subsequent reattachment on adult beds. Recruitment is highly variable from year to year in most places. *Mytilus* can be very long-lived but reef populations are usually only up to two or three years old, with rapid growth and high rates of production. Predation is usually very high; fish and invertebrates are important on the lower shore and often prevent the extension of *Mytilus* beds subtidally. Intertidal bird predation, especially by eiders and oystercatchers, can

be responsible for up to 72% of the annual mussel production, and mussels form an important part of the diet of these birds. The communities associated with large mussel reefs in bays and estuaries are much less rich and diverse than the older, more stable beds on moderately exposed rocky shores, or than subtidal biogenic reef communities (*Modiolus, S. spinulosa* and *Serpula*), and contain no remarkable species, but may represent the only hard substrate communities over wide areas. They can also provide nutrition in the form of organically enriched biodeposits for wide ranges of deposit feeding invertebrates over wide areas of tidal flats as well as within the reefs. Mussels reefs may have the ability to locally deplete the phytoplankton and may compete with cockle beds in this way.

Serpula vermicularis probably spawns in the summer of its first year, and settlement would be expected to be maximal in late summer and early autumn. Growth rates seem to be fast, but the rate of accumulation of reefs is presumably very slow, requiring many years to reach the maximum sizes observed in Loch Creran. Little is known about feeding ecology. The reefs, being relatively long-lived and stable, and with a relatively open structure affording much crevice habitat, seem to have a very rich associated fauna, but only limited video and diver recording studies have been done. The tunicate *Pyura microcosmus* is reportedly limited largely to this habitat. There is limited information on the effects of predators.

Sensitivity to natural events

S. alveolata often suffers from burial as a result of large movements of sand, which it can tolerate for periods of days or even weeks, although this severely hampers its growth. Longer term burial kills it. Colonies can die back for many years as a result of cold winters. In many parts of its range it seems to compete for space with mussels *Mytilus edulis*, interactions with which are not fully understood.

There is little knowledge of sensitivity to natural events of *S. spinulosa* reefs. Interactions with brittle stars *Ophiothrix fragilis*, which can reduce recruitment, growth and probably fecundity of *S. spinulosa*, may be important.

In general *Modiolus* beds seem to be persistent features over decadal time spans, and there is little documented evidence of sensitivity to particular natural events. It can be speculated, therefore, that density and age structure within reefs might vary considerably over periods of years or decades, although no studies have been carried out which might prove or disprove this. It can also be speculated that infaunal beds might be more subject to predation than semi-infaunal reefs due to the greater inaccessibility of the byssus threads, which are thought to be very important in providing shelter to young *Modiolus*. It is also possible that increased densities of *Ophiothrix fragilis*, known to have highly variable population densities in some areas, might be detrimental to *Modiolus*.

Mytilus has been much more extensively studied than other biogenic reef species, and as is often the case the factors affecting it appear to be more complex, probably simply because more is known. In less sheltered areas *Mytilus* reefs are subject to removal by storms. In places massive predation by *Asterias* has been reported to eradicate large beds. Bird predation is also extremely important and changes in bird populations appear to have the potential to alter mussel communities, although this is probably a less important factor than storms. Recruitment is thought to be favoured by cold preceding winters as a result of decreased predation on the spatfall, although loss of entire beds due to ice scour has been reported in the Wash. Phytoplankton blooms have been reported to cause mortalities in *Mytilus* but are probably less important than storms, predation and winter temperatures. Overall, however, mussel beds are resilient, with a strong ability to regenerate after losses.

There is little information upon which to base an assessment of the sensitivity of serpulid reefs to natural events.

Sensitivity to human activities

Fishing activities:

By their nature biogenic reefs are likely to be sensitive to strong physical disturbance. Fishing is the most widespread and damaging activity in a variety of biogenic reef types. *Mytilus* is the only one which itself is an important fishery (although *Modiolus* is edible and taken on a local scale in places, and more commercially in Norway). Natural mussel reefs harvested by hand seem to retain their biodiversity, but are vulnerable to over-exploitation, particularly when combined with recruitment failure. They generally seem to recover well when managed correctly, but there is a strong suspicion that over-exploitation on a very wide scale can greatly hinder recovery. The habit of relaying mussel seed may have increased areas of dense mussel bed in many areas, but these are not allowed to develop into true reef areas. In many cases the 'seed' mussels taken for relaying would be unlikely to persist if left alone.

Modiolus and *Sabellaria spinulosa* reef areas have both almost certainly suffered widespread and long lasting damage due to the activities of bottom fishing. Reports of *S. spinulosa* reef losses are more widespread than *Modiolus* reefs, probably because of the link between the *Sabellaria* reefs and the pink shrimp, *Pandalus montagui*, which seems to be associated with it. In both these cases recovery is impossible while the fishery activities persist in the area. The likelihood of recovery in the absence of the fishery is rather an unknown quantity in both cases; recent surveys suggest recovery of *S. spinulosa* has not occurred in Morecambe Bay despite the cessation of fishing many years ago, and this seems most likely to be due either to lack of larval supply, or to permanent or ongoing alterations to the habitat. Recovery of *Modiolus* reefs would undoubtedly be very slow at best. Infaunal *Modiolus* reefs are likely to be both less sensitive and less vulnerable to fishing by towed bottom gear than more epifaunal reefs. Most of the serpulid reefs in Loch Creran are probably protected from bottom fishing by virtue of the topography of the areas in which they live; if areas are identified where this is not so, steps would need to be taken to prevent fishing for queen scallops which would potentially be very damaging.

Other activities:

Sabellaria alveolata is potentially vulnerable to changes in sediment regime as a result of shoreline development plans; both large scale increases and decreases in sand could be potentially damaging, although it is likely that in most cases this would be on a local scale only. *S. alveolata* is also moderately susceptible to trampling damage in recreational areas, and on a very small scale perhaps to collection of worms for bait. *S. alveolata* appears to be favoured by elevated winter temperatures (8-10°C) associated with cooling water discharges. Sensitivities of subtidal reef areas can only be guessed at at present, but are likely to be similar to those of *S. spinulosa*.

S. spinulosa occurs in the type of area which is often of value for marine gravel extraction. Direct damage would clearly be heavy, and there is presently little knowledge of recovery. It seems likely that damage to adjacent populations of *Sabellaria* by resulting sediment plumes would not be particularly high, but nevertheless this has yet to be demonstrated conclusively. Moreover damage to associated fauna and flora on particularly rich reefs may be more significant. *S. spinulosa* itself seems generally quite tolerant to changes in water quality. Similar arguments would apply to other physical activities such pipelaying and cable trenching.

Modiolus reefs are likely to be susceptible to any physical activity such as pipelaying, trenchlaying and use of jack up oil rigs. Recovery times would be expected to be long. Limited short term surveys in connection with drilling of a single oil well using water based muds detected barium contamination up to at least 250 m from the well but no obvious damage to gravel-embedded reefs. Sensitivity to many impacts may depend on the nature of the reefs concerned, including the current regime. In sheltered sealochs there may be some sensitivity to organic enrichment from aquaculture, particularly salmon farming.

Mytilus has been shown to be sensitive to some pollutants, including TBT, diesel and sunflower oil. It is known to bioaccumulate a wide variety of contaminants, often with sublethal effects, although whether it is any more sensitive than other marine organisms in this respect is unclear. Greatly increased sediment levels as a result of dredging activities have been shown to result in enhanced infestation by the shell weakening parasite *Polydora ciliata*, with an associated loss of condition and increased predation by crabs.

Serpulid reefs are physically fragile and therefore easily damaged by moorings, as has been observed in Loch Creran. Physical removal by divers occurs, although at present levels this seems unlikely to be a problem. Large scale disposal of de-alginated seaweed residue has caused widespread loses but these have recently ceased.

Monitoring suggestions for each biogenic reef type have been given. It seems likely that aerial photographs backed up by groundtruthing would provide a useful way of monitoring changes in the extent and integrity of intertidal reef areas, as has been well demonstrated for *Mytilus* reefs. It is as yet unproven for *S. alveolata* reef areas, although it seems likely to be successful. There are a variety of standard techniques available for monitoring changes in community structure, including the richness and diversity of associated fauna.

Monitoring of changes in the extent of sublittoral biogenic reef communities will require acoustic methods in many cases, particularly where they are deep and extensive. Acoustic methods always require some groundtruthing, whether by towed video/ROV, and in some circumstances perhaps diver surveys. Present experience of both is limited but very promising.

Techniques for monitoring the richness and diversity of associated communities subtidally are more problematical than intertidally and likely in many cases to be limited to surveys of large epifauna by video/ROV in deeper areas, or diver recording surveys and fixed photographic surveys in shallow areas. These methods have limitations but are likely to be of use in detecting gross changes

Recruitment processes are important in all biogenic reef communities and it is suggested that efforts are made to monitor settlement patterns both spatially and temporally (preferably annually) in all these communities. Such monitoring would be essential to identify the cause of any change in status of the reefs.

Gaps in knowledge

The following are thought to be of high priority:

Serpulid reefs are of national importance and are not found in any presently proposed cSACs. It would be extremely useful to know the true status in Loch Sween. This probably requires the preparation of as detailed a report as possible on the recent diving surveys (not presently available) followed if necessary by further surveys.

Information on potential for recovery of reefs of *Sabellaria spinulosa* and *Modiolus modiolus* damaged by physical impacts and especially by fishing is of high importance but at present, given the political sensitivities of closure of fishing grounds, it is not likely that a realistic programme could be devised to investigate recovery from fishing impacts. In the absence of such, studies on recruitment processes aimed at improving our knowledge of the major influences on them should take a high priority.

Further information on distribution of *S. spinulosa* reefs and certain types of *Modiolus* communities is of high importance. Allied to this is the need for development of better, and standardised, survey and monitoring methods for subtidal biogenic reefs.

Recruitment range and sources for S. alveolata, S. spinulosa, Mytilus edulis and Modiolus modiolus reefs need to be identified.

A better understanding of the 'Added Value' of the biodiversity of reef areas versus adjacent areas, and in particular a better understanding of the role of reef builders as ecosystem engineers, would help in promoting the conservation of biogenic reefs.

A better knowledge of the natural variation in extent, density and population structure of reefs, especially serpulid and *Sabellaria spinulosa* reefs, is required.

Conservation and management issues

All five biogenic reef types are regarded as of high conservation importance. This may not be apparent to many coastal users, particularly those involved in fishing, since many of these species are common and widespread. Conservation importance of biogenic reefs may need to be the subject of educational campaigns in order to secure support for their conservation.

Limits of acceptable change for monitoring and management purposes are going to be very difficult to determine, except for *Modiolus* reefs which appear to be relatively stable communities in which any detectable changes over periods of a few years are likely to be regarded as unacceptable. Intertidal *Sabellaria alveolata* populations are generally highly variable and it seems likely that large scale losses over wide areas can be attributable to natural causes such as cold winters or lack of recruitment. Even in areas where *S. alveolata* is always found, there may be very large scale fluctuations in populations over periods of years due to variations in recruitment. There is some evidence that recruitment cells are moderately localised, as with *Mytilus*, but considerably more information on the geographical scale over which recruitment occurs is essential with all species to be able to decide whether local or more widespread action would be required to prevent, or mitigate, loss of communities in an SAC.

Some impacts are too widespread for local management decisions to be effective, but need to be recognised so that changes resulting from them may be distinguished from those where local action may be effective. These include general eutrophication, global warming, and diffuse pollutants.

The experience gained during the designation of Strangford Lough as a result of its designation in 1993 will be invaluable. Fisheries regulations preventing the use of mobile fishing gear in areas which include some relatively undisturbed beds of *Modiolus* were introduced in 1993. This was prior to designation but as a direct consequence of the MNR consultation procedure. There was some conflict with fishermen during this process and lessons may be learned from the experience. The opportunity now exists to study the recovery process in damaged areas.

In the case of a *Modiolus modiolus*, *Sabellaria spinulosa* and *Serpula vermicularis* where important reefs occur within cSACs in areas where trawling or dredging can occur they can only be protected from damage by prohibiting such bottom fishing.

Serpulid reefs are susceptible to physical damage and it seems likely that they would also be damaged by potting, and are known to be susceptible to damage by mooring systems for salmons cages. Likewise, *Modiolus* reefs and *Sabellaria spinulosa* reefs would doubtless be badly impacted by physical activities such as cable trenching and pipelaying. The latter is particularly likely to be directly affected by sand and gravel extraction since it tends to inhabit areas that are suitable for commercial exploitation of aggregates. Such activities should be prevented over areas of good quality reefs both within and, preferably, outside cSACs.

Mytilus alone of the biogenic reef species is of importance as a fishery. This may lead to conflict with fishermen and re-layers and those, such as SFCs, charged with managing the fishery. It must be taken into account that legislation frequently requires that the fishery is managed so as to actively develop the fishery. However, Mytilus is a resilient species, even in reef communities, which tends to regenerate quickly from natural losses except where these are on the scale of entire large embayments such as the Wash, when recruitment failure can occur. In the most productive and exploitable biogenic reef communities the associated fauna and flora is relatively unremarkable, and ecologically speaking its importance as a food source for birds (particularly oystercatchers and eiders, but also others) is likely to be of overriding importance in many areas. It should therefore be possible to find compromises which allow active developments of fisheries without detriment to bird populations, which are likely mainly when mussels have been overexploited. Guidance should be sought from those responsible for management of SPAs, who will have a greater knowledge of the requirements of birds in such instances. There should be opportunities for sharing resources between conservation managers and fisheries scientists or managers in monitoring certain important aspects of biogenic reef communities such as recruitment, growth rates and size/age structure of populations, and this may in some cases include access to detailed unpublished historical data.

Where more stable *Mytilus* reefs exist within cSACs, greater importance should be attached to the associated fauna and flora (which are likely to be richer and more diverse) by carefully limiting, and if necessary preventing, exploitation.

There are a number of localised factors in enclosed sea lochs which could potentially be a problem for biogenic reefs found there, such as organic enrichment from salmon farms. There is no evidence of any special sensitivity to such enrichment and sensible location of farms should be able to prevent widespread damage.

I INTRODUCTION

A. PROJECT CONTEXT AND STUDY AIMS

This report focuses on 'Biogenic Reefs' as part of the UK Marine SAC Project task 1.1 which is reviewing the sensitivity of selected benthic biotope complexes. There are a number of organisms in British coastal areas which can form substantial and often quite solid aggregations ('Biogenic Reefs') in areas which would otherwise be composed predominantly of sediments, or on boulders and rocks in sandy areas. The most important of these in inshore areas are Sabellaria alveolata, S. spinulosa, Mytilus edulis, Modiolus modiolus and Serpula vermicularis.

Biogenic reefs were chosen as a target group for study because collectively they encompass a wide range of attributes and environmental requirements, and have a number of significant ecological, economic and scientific values. Biogenic reefs can have a number of important effects on the physical (and probably chemical) environment: they often stabilise sands, gravels and stones; the shells or tubes of the organisms themselves provide hard substrata for attachment of sessile organisms; they may provide a diversity of crevices, surfaces and sediments for colonisation; and accumulated faeces, pseudofaeces and other sediments may be an important source of food for other organisms. For these reasons many biogenic reefs have a very rich associated fauna and flora, which at least in terms of macrofauna is often much richer and more diverse than in surrounding areas. Moreover, *Mytilus* is particularly important both as a fishery and as a source of food for birds.

The audience for this report is typically marine resource managers working at site level. Therefore, this report summarises existing knowledge of biogenic reefs with particular emphasis on achieving a greater understanding of the ecological dynamics and sensitivity of this biotope complex, through the following:

- a) examining the fundamental environmental, physical, biological and ecological features of biogenic reefs;
- b) assessing the sensitivity of biogenic reefs to natural phenomena and anthropogenic impacts;
- c) exploring options for monitoring and research into information gaps that are relevant to the management of biogenic reef communities in marine SAC areas.

B. DEFINITION OF BIOGENIC REEFS

1. Definition of 'Biogenic Reefs' for this Report

The JNCC report on selection of Special Areas of Conservation in the UK (Brown et al., 1997), discussed the background to selection on the basis of the presence of reefs, and stated:

"Reefs are rocky marine habitats or biological concretions that rise from the sea bed. They are generally subtidal but may extend as an unbroken transition to the intertidal zone, where they are exposed to the air at low tide. Two main types of reef can be recognised; those where structure is created by the animals themselves (biogenic reefs) and those where animal and plant communities grow on raised or protruding rock. Only a few invertebrate species are able to develop biogenic reefs, which are therefore restricted in distribution and extent." This is a definition with which most marine scientists would agree, but not surprisingly there are difficulties in interpretation. There are obviously in many cases continuous gradations between communities which are clearly not reefs (e.g. scattered *Modiolus* within a gravel bed; a discontinuous bed of *Mytilus*; scattered patches of *Sabellaria spinulosa* or *S. alveolata* crust; moderate aggregations of serpulids upon rocks) and those which clearly are (e.g. continuous, dense, raised *Modiolus*, *Mytilus* or *S. spinulosa* on mixed substrata; massive aggregations of S. *alveolata* on more solid substrata; large, discrete aggregations of *Serpula vermicularis* on muddy substrata). In this report we have used the following criteria in defining biogenic reefs;

- the unit should be substantial in size (generally of the order of a metre or two across as a minimum, and somewhat raised, mainly in order to disqualify nodule like aggregations such as may be formed by *S. spinulosa* and scattered small aggregations such as occurs with many of the species under consideration);
- and should create a substratum which is reasonably discrete and substantially different to the underlying or surrounding substratum, usually with much more available hard surfaces and crevices on and in which other flora and fauna can grow.

More importance has been attached to reefs which are reasonably stable than to those which are more transient (e.g. *Sabellaria spinulosa* crusts which may just about fit the above criteria but act as an annual feature, being destroyed by winter storms and re-establishing each spring) but all have been discussed.

There are many cases where a community meets the two criteria we have suggested above, except that it is not 'somewhat raised' (i.e. it does not 'rise from the seabed' as in the JNCC definition). Although in many cases it is probably more realistic to refer to these as beds, the ecology, biology, and sensitivity of these areas are nevertheless likely to be very similar to those of protruding reefs, and they are discussed here alongside true biogenic reef communities. There are also cases, particularly with *Mytilus*, where widespread, dense aggregations are formed on hard substrata and although they undoubtedly form 'a substratum which is reasonably discrete and substantially different to the underlying or surrounding substratum' they are probably better regarded as part of the normal rocky shore biota. In many such cases these aggregations are not substantially raised above the surrounding area. Similar arguments may apply to some subtidal *Modiolus*, *Sabellaria alveolata*, and *S. spinulosa* communities.

The definition of biogenic reefs as used in this report is therefore as follows:

"Solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms."

For the purposes of this report, biogenic reefs created by the following species have been discussed in detail: *Sabellaria alveolata, S. spinulosa, Modiolus modiolus, Mytilus edulis* and *Serpula vermicularis*.

2. Species Not Considered in Detail in this Report

There are other potential candidates for the title 'biogenic reefs' which are not considered in detail in this report; these are listed below with brief reasons:

Lophelia pertusa has not been included because it is probably limited to very deep waters and there is little likelihood of reefs occurring in areas which may be designated as SACs.

Oysters: on sheltered shores and estuaries in southern Europe dense beds of oysters (*Crassostrea gigas*) occur. These tend to form sheets on rocky shores and on artificial substrata such as piles or quaysides. This species is found in southern parts of Britain but is restricted to occasional spatfalls rather than established populations. Beds of European oysters (*Ostrea edulis*) used to occur widely in the subtidal of northern Europe. To what extent these were natural is unknown, as in some locations relaying of oyster beds is thought to date back to Roman times. Many of these beds have been dredged out, or have been heavily impacted by disease. In many locations they were almost certainly the remnants of culture activities, and it is doubtful if natural beds would qualify as reefs in any case.

Limaria hians beds; although capable of binding sediment with their byssus threads, these are probably best regarded as semi-infaunal bivalve beds.

Musculus discors; this is a small mussel which forms beds on moderately exposed circalittoral rocks. However, these are not usually more than one animal thick and do not form any significant raised reef area.

Ficopomatus enigmaticus (formerly *Mercierella enigmatica*); this is an alien serpulid polychaete which can form extensive, well developed reefs in scattered low salinity habitats within Britain. Due to the low salinity in which these reefs occur few other species are found with them. It undoubtedly forms biogenic reefs, but is not considered further here because of its alien status.

Lanice conchilega; During preparation of this report, the following pers. comm. information was received from Paul Brazier (MNCR, JNCC) and Helen Vine (SAC officer, the Wash and N. Norfolk Coast): during intertidal surveys of the North Norfolk coast, unusual accretions formed by sand masons *Lanice conchilega* were found low on the shore. These were up to 45 cm proud of the surrounding gravelly sediment, and typically up to 1-2 m across (though occasional larger areas were found). They were clearly stabilising the sediment. There was an associated faunal assemblage containing *Sagartia elegans*, which was different to that in the surrounding, more gravelly, substratum. It has been suggested that these might just about qualify as biogenic reefs. *Lanice conchilega* is known to be capable of stabilising sediment and Larsonneur (1994) reported that sand stabilised by sand masons is sufficiently stable to allow subsequent colonisation by *S. alveolata*. However, it is not known how seasonal / stable these features are, and it presently seems unlikely that they are sufficiently solid or altered to qualify as biogenic reefs. They are not considered in this report.

C. REPORT STRUCTURE

This report is divided into similar chapters to the other reports in this series, as follows:

- I. Introduction (including definitions and descriptions)
- II. Distribution
- III. Biology and Ecological Functioning
- IV. Environmental Requirements and Physical Attributes
- V. Sensitivity to Natural Events
- VI. Sensitivity to Human Activities
- VII. Monitoring and Surveillance Options
- VIII. Gaps and Requirements for Further Research
- IX. Synthesis and Application of Information for Conservation Management Relevant to Marine SACs

However, because there proved to be greater differences between the five main types of biogenic reef forming species than might have been initially suspected, each species has had to be treated largely separately within each chapter. Furthermore, because of these differences, compounded by large variations in the level of available information, the sub-headings used for discussion within each chapter are not necessarily consistent between the species, although efforts have been made to maximise consistency as far as is reasonable.

For the reader interested in making comparisons between the species, this can be done mainly in the key points presented at the end of each chapter (where short summaries are given, including, where appropriate, in tabular form) and in chapter IX.

D. DESCRIPTION OF KEY SPECIES AND PHYSICAL CHARACTERISTICS

Although the five species under consideration here share some common features at the level of definition of biogenic reefs presented above, they are each quite distinct in physical form and are therefore described separately below. (This variation is further illustrated in the respective distributions as well as the underpinning environmental and ecological attributes discussed in subsequent chapters).

1. Sabellaria alveolata

S. alveolata creates tubes of coarse sand grains cemented together, dense aggregations of which may be regarded as reefs. Details of tube structure and form are given in Wilson (1971) for Cornish colonies and in Vovelle (1965) for French communities. Wilson (1971) observed that tubes can vary in colour depending on the source of sand grains; shell fragments are taken up in preference to mineral grains though the latter are used where shell fragments are not present. The tubes in Cornwall were found to be up to 20 cm in length and up to around 5 mm in diameter at the external opening. Each tube has an additional cup shaped 'porch' area at the outward end which is up to 10 mm 'deep' and 15 mm across. The head and tentacles protrude into this area when submerged. Single tubes are rarely straight and may be strongly recurved, but aggregated tubes are often less so.

Cunningham et al. (1984), described three forms of aggregations within Britain, based largely on the work of Gruet (1982). These were:

- extensive sheets in which the tubes overlap and lie at an acute angle to the substratum ('placages' *sensu* Gruet, 1982). These occur on low lying, even beaches with more or less homogeneous substratum;
- hummocks in which the tubes radiate out from the initial settlement point ('champignons', *sensu* Gruet, 1982). These are found on more heterogeneous substrata such as large boulders and rock outcrops on sand or shingle. Colonies of this type such as those described by Wilson (1971) in Cornwall can be a metre or two across, though it is sometimes unclear to what extent this overlaps with the third form (below);
- 'reefs', formed of more extensive areas of hummocks fused together, in which strange shapes can result from a combination of further growth, new larval settlement and erosion. There is clearly a likelihood of overlap with the hummock form (above). Reefs of up to around 50 cm thickness have regularly been reported (Wilson, 1971; Gruet, 1982; Cunningham et al., 1984).

For the purposes of this report, all three of the above are considered to fit with the definition of biogenic reef communities, though in the case of the first two there could clearly be some instances in which the designation might not be appropriate.

2. Sabellaria spinulosa

S. spinulosa is very commonly reported to be found in solitary form (e.g. George & Warwick, 1985; Hayward & Ryland, 1990). A number of published records of local marine fauna refer only to the widespread presence of individuals, or at least fail to mention dense aggregations, reefs or accretions (eg around the Plymouth area, MBA, 1957; the Isle of Man, Bruce et al., 1963; and North East England, Garwood, 1982).

Wilson (1971) regarded it surprising that in the Plymouth area *S. spinulosa* is "almost entirely solitary", occurring commonly on stones and shells, while in the North Sea it is "frequently colonial"; he carried out settlement experiments which "lead one to expect them [colonies]".

The following is pers. comm. information from Rohan Holt (MNCR): *Sabellaria spinulosa* appears to be almost ubiquitous on much of the Welsh coast, at least in the north which tends to be more silted or sediment influenced. It occurs from the sublittoral fringe to the circalittoral, with many records from 15-30 m, and seems to be capable of growing on a variety of substrata, including kelp holdfasts, rock and less consolidated sediments such as stony sand or gravel. In some parts of West Wales it grew almost to the exclusion of everything else, and frequently formed sheets up to 2 or 3 cm thick. More often, north west of Anglesey and in other tide swept sites near sediment plains, it forms an underlying thin crust often covered by ascidians and the erect bryozoan *Flustra foliacea*. Thick crusts, sometimes extensive, were found off Northumberland and North Yorkshire by MNCR surveys.

Attrill (pers comm) found large aggregations of *S. spinulosa*, up to approximately 20 cm in diameter, while beam trawling on sand in the outer Thames estuary. In other parts of the Thames estuary it formed the more usual sheets or crusts, though these appeared to be thin and not particularly extensive.

Many records of *S. spinulosa* might just about qualify as biogenic reef communities on the basis of their strong alteration of habitat, but it seems that this species rarely forms substantial

raised areas. Two of the most likely areas in which it may do so are those reported by George & Warwick (1985) in the Severn Estuary, for which detailed descriptions are lacking, and the mouth of the Wash, where true reefs protruding up to 60 cm above the surrounding seabed and extending more or less continuously for hundreds of metres have been seen on underwater video (Foster-Smith, in prep). The latter were described as being somewhat similar to reefs of *S. alveolata* though the arrangement of the tubes is far more irregular.

The only other clear report of truly massive, reef like structures for *S. spinulosa* is that of Linke (1951) in the southern North Sea where he found reefs up to 60 cm thick, 8 m wide and 60 m long (see chapter IV for more details).

There are also few details of density of animals; however, in the Bristol Channel George & Warwick (1985) reported a mean of over 4,000 individuals m^{-2} ; off Lundy an average of 6,800 m^{-2} was found on the wreck of the MV Robert (Hiscock & Rostron unpubl.); and in the south east of England up to 1,600 per individual grab sample has been recorded, although crusts in the Thames estuary contained only up to 228 m^{-2} (both Attrill, pers. comm.).

The worms and tubes themselves are rather smaller than those of *S. alveolata*, and structured, 'honeycomb' like arrangements have never been reported for *S. spinulosa*.

3. Modiolus modiolus

By comparison with *Mytilus*, mussels of the genus *Modiolus* are best described as being adapted to live semi-infaunally with endobyssate attachment to the substratum (Meadows & Shand, 1989; Seed & Suchanek, 1992). However, the ecological niche they can occupy is quite broad, so that they can be found living attached epifaunally in the manner of *Mytilus*, or they may be found hidden within the sediment. With this broad habitat spectrum in mind and in relation to the dynamics and sensitivity of those situations where biogenic reefs form, biotopes where *Modiolus* is important can be divided into a number of primary and secondary sub-divisions, and these are presented, with descriptions, comments and examples, in Table1.

There are gradations to circumstances not qualifying as biogenic reefs but there are two more or less distinct types of end points where the mussels are deemed to truly form bioherms;

- semi-infaunal reefs, which occur in various gradations of density and thickness, and to which it presently seems that the majority of *Modiolus* reef biotopes probably belong. Large accumulations of faecal mud and shell build up, probably over many years so that mounds of a scale visible on echosounders build up. The living mussels in this case form an irregularly clumped layer over the mound, with the largest individuals living with about two thirds of their length embedded in the deposit and small individuals find refuge amongst the byssal threads of the clumps of larger ones.
- infaunal reefs, usually on coarser grounds and in strong currents, where the mussels bind together banks of gravel and live virtually as nested infauna within the coarse deposit. They can form wave-like mounds or bioherms which in the Bay of Fundy have been reported as up to 3 m high and hundreds of metres long. The best described examples of the latter within Britain are those off the north east of the Isle of Man, which contain numerous steep faces up to around 1 m in height, where the *Modiolus* are more concentrated and the associated fauna much richer. Similar areas have recently been found off the Codling Bank, Ireland.

Description	Biogenic reef?	Comments and examples
1. Epifaunal Modiolus		chumples
1A Carpeting steep surfaces by <i>Modiolus</i> . More commonly in the infra-littoral in the cold water parts of the range where it may replace <i>Mytilus</i> at depth on offshore structures.	Not biogenic reef	Parts of Lochs Duich, Long and Alsh?
1B Isolated individuals or small relict clumps of large and probably very old animals. Sometimes these may be at LWS levels on boulder shores.	Not biogenic reef	Widespread
2. Semi-infaunal Modiolus		
2A Massive, nearly continuous beds often forming true bioherm mounds. A range of variation is found both in the way biogenic material is retained to build the mounds and in the mix of associated fauna living on the horse-mussels, in the crevices and in the accumulated soft sediment dominated by faecal material.	Can often be considered as biogenic reef	
2A.1 Low turbidity open sea or sea loch mouth beds in strong tidal streams. Beds in these situations may not retain much of the faeces and pseudo-faeces so that though extensive they may hardly build up sufficient thickness to qualify as reefs.	Not usually biogenic reefs	South east Isle of Man where they do build up thickly in places
2A.2 Higher turbidity areas with moderately tidal streams and where more faeces and pseudo-faeces builds up. Mixed with fine sand swept onto the beds the faecal mud and generations of shell all such beds to mound up several metres above the substratum on which they where founded.	These beds undoubtedly qualify as biogenic reefs.	Off Lleyn Peninsula
2A.3 Sheltered sea loch beds. These are distinguished more by the mix of associated species, but the mounds may not be as massive as those in less quiescent conditions.	Can often be considered as biogenic reef	Scottish Lochs and Voes, Strangford Lough
2B Discontinuous beds on gravel grounds with numerous scattered clumps that may or may not be large enough to be classified as biogenic reefs.	Some areas may qualify as biogenic reefs	Widespread
<u>3. Infaunal Modiolus</u>		
3A Gravel wave or mound deposits in areas of v. strong currents in which abundant <i>Modiolus</i> are almost completely hidden. The mass of mussels "nesting" within the deposit put out byssal threads in all directions, and so bind the deposit, sometimes with much dead shell, into waved mounds. Steep faces up to one metre high and many metres long, with much live & dead shell, well bound & with rich epiphytic biota have been seen.	Steep faces may often qualify as biogenic reef	Several km ² to the north of the Isle of Man found recently (Holt & Shalla, unpubl); also Codling Bank, Ireland.
3B Abundant small <i>Modiolus</i> in offshore coarse sediments that apparently do not survive and grow to produce true mussel beds.	Not biogenic reef	Freq between S Wales & Ireland.
3C Isolated individual <i>Modiolus</i> of moderate size or small clumps living "nested" within coarse sediments.	Not biogenic reef	Widespread.

Densities of *Modiolus* themselves may not necessarily be particularly high in some of these more infaunal reefs, though true figures will only be gained if diver surveys are carried out. Holt et al. (unpubl) estimated maximum densities of large *Modiolus* from photographs as $20 - 40 / m^2$ (probably occasionally more) off the north of the Isle of Man, but it was difficult to pick out the *Modiolus* as only the last few mm of the shells were visible, and the field of view covered by the camera probably varied greatly due to the rough terrain. The combination of these mussels and their byssus threads binding the sediment together, plus often very large amounts of dead shell, nevertheless clearly creates a dramatically altered habitat deserving in many cases to be called a reef. The bioherms described in the Bay of Fundy had similarly low densities (4-78 / m²) but were frequently up to 3m high (Wildish & Fader, in press; Wildish et al., in press).

4. Mytilus edulis

Mytilus reefs are composed of layers of living and dead mussels at high densities, bound together by the byssus threads secreted by the mussels and sometimes overlaying a great deal of accumulated sediment. Subtidal beds have been reported up to 120 cm thick (Simpson, 1977 cited in Seed & Suchanek, 1992). Well developed reefs in most UK sites rarely exceed 30-50 cm, however. Not surprisingly mussel bed thickness and structural complexity increase with age of the bed. Based on observations on beds of *M. californianus*, Suchanek (1979) described *Mytilus* beds in terms of three structural components;

i) a physical matrix of living and dead shells;

ii) a bottom layer of accumulated sediments, mussel faeces and pseudofaeces, organic detritus and shell debris.;

iii) an assemblage of associated flora and fauna.

M. edulis beds and reefs also have these components. The accumulated sediment is called 'mussel mud', and the faeces and pseudofaeces element is often the most important. Nixon et al. (1971) found 14.4 kg m⁻² dry weight of trapped sediment within *M. edulis* beds in Rhode Island, with an organic content of 3.86%. Davies et al. (1980) reported the weight of mussel mud to be 17-19 times the seed mussel production in crab-proofed cages in Morecambe Bay.

Accumulation of sufficient faecal and pseudo-faecal deposits together with dead shell to produce obvious mounds is largely restricted to those places, in estuaries or similar channels and flats, where there is a degree of shelter from wave action, but sufficient flow carrying seston for there to be good growth. Persistent and semi-permanent beds in sheltered locations can in these situations build up an obviously biomediated relief of mounds rising a metre or more above the surrounding seabed. These features can clearly be classified as "Biogenic Reefs".

Large, very raised reef areas often take a hummocked or sometimes ribbon-like form, usually up to a few metres across, often with patches of sediments or cobbles / boulders in between. Sometimes the whole of a mussel bed will have a shape that is obviously aligned with the dominant tidal stream axes in the channel, but superimposed on this there may be a cross tide wave form akin to mega-ripples superimposed on a sand bank. More often, however, the complex of mounds, formed by the patchy and variable growth of the mussels competing for seston and the way they attach byssally to each other, has a more irregular relief. Less projecting areas (especially where only 1-2 mussels deep) may be very extensive and continuous, particularly where they form on more solid substrata. The latter may usually be regarded as beds rather than reefs, and can be over 50 ha in extent (Dare, pers. comm.).

In some cases, for example some of the mussel reefs in Morecambe Bay and the Dornoch Firth, a reef may consist of a single year class of mussels which have settled in very high densities on only moderately sheltered gravel and cobble skears. At first the spat may be almost hidden within the deposit, but as they grow they build up sufficient mud that they emerge as a thin carpet overlaying a layer of mussel mud which may accumulate to a depth of 0.75m in four to five months (Dare, 1976). These areas are much more transient than reefs formed of a large number of year classes, and are often washed away by water movement, particularly during autumn storms (McKay & Fowler, 1997; Dare, pers. comm.).

In many situations, gradations can be seen from those where the mussels merely carpet the substratum to a patchy extent without building substantial mounds, to those where the beds obviously form reefs.

There are situations with stronger water movements where the mussels are on gravel and they so gather and bind together coarse material, rather than their own faecal mud. In beach gravel deposits, particularly where small rivers enter the sea, beds of *Mytilus* have been found on both sides of the Atlantic where the mussels live infaunally in a coarse gravel / small cobble deposit that they themselves stabilise (Stephens & Bertness, 1991).

5. Serpula vermicularis

S. vermicularis usually occurs as individuals encrusted on hard surfaces. A tendency to form aggregations is widely reported (e.g. Hayward & Ryland, 1990; Nelson-Smith, 1967; Zibrowius, 1973) but true reefs have an extremely limited distribution as outlined below. On reefs in Ardbear Lough individual worm tubes had an outside mean diameter of 5.2 mm, and a mean length of 120 mm (up to 180 mm), which is slightly larger than in worms from the open sea (Bosence, 1979). Initial growth is encrusting but after that the worm grows away from the substratum in a sinuous fashion, sometimes intertwining, and reefs develop by continued additions of further worms onto the old. Pieces of reef may fall off into the surrounding sediment where they may continue to grow. In Loch Creran individual reefs are reported to reach up to around 75 cm, in height and 1 m across, but adjacent reefs may coalesce to form larger reefs up to 3 m across (Moore, 1996). Bosence (1979) described reefs up to 2 m in height and 1 m across from Ardbear Lough but implied that aggregated reefs could extend for several hundred metres, although the continuity of such areas was not indicated.

The structure usually appears to be quite open, providing lots of cryptic surfaces and spaces for other organisms. This appears to be related to the regular spacing of the tube apertures of worms at 10-15 mm apart in order to avoid interference of the expanded branchial crowns (diameter 15 mm) during feeding (Bosence, 1979).

E. LINKS TO MNCR BIOTOPE CLASSIFICATION

Table 2 shows those MNCR biotopes which can be considered as biogenic reefs. It also includes a number of biotopes which were considered, but which are do not regarded in this report as biogenic reefs, along with reasons.

Table 2 MNCR biotopes which are potentially relevant to this report with comments relating to their status as biogenic reefs. Biotopes listed are those where the dominant organism is one of the five species considered in detail in this report: *Sabellaria alveolata, S. spinulosa, Modiolus modiolus, Mytilus edulis* and *Serpula vermicularis*.

Sabellaria alveolata			
Higher code	Biotope code	Biotope	Comments
MLR.Sab MLR.Sab		oral Sabellaria (honeycomb worm) reefs Sabellaria alveolata reefs on sand- abraded eulittoral rock	Biogenic reef Sabellaria can perform important stabilisation of habitat usually involving significantly raised structures.
Sabellaria	a spinulo	sa	
Higher code	Biotope code	Biotope	Comments
MIR		DERATELY EXPOSED INFRALITTO	DAL DOCK
	-		
MIR.SedK MIR.SedK	Sanc SabKR	d or gravel-affected or disturbed kelp and Sabellaria spinulosa with kelp and red seaweeds on sand- influenced infralittoral rock	Not biogenic reef. Many associated species capable of growing on the rock whether the <i>Sabellaria</i> are there or not, and no significant raised reef area.
MCR	MO	DERATELY EXPOSED CIRCALITTO	RAL BOCK
MCR.CSab		alittoral Sabellaria reefs	NAL KOCK
MCR.CSab	Sspi	Sabellaria spinulosa crusts on silty turbid circalittoral rock	Not biogenic reef. Many associated species capable of growing on the rock whether the <i>Sabellaria</i> are there or not, and usually no significant raised reef area.
MCR.As MCR.As		dian communities (silt influenced) Dense ascidians, bryozoans, and hydroids on a crust of <i>Sabellaria</i> <i>spinulosa</i> on tide-swept circalittoral rock	Not biogenic reef. Many associated species capable of growing on the rock whether the <i>Sabellaria</i> are there or not, and usually no significant raised reef area.
CMX	CID	CALITTORAL MIXED SEDIMENTS	
CMX	SspiMx	Sabellaria spinulosa and Polydora spp. on stable circalittoral mixed sediment	Biogenic reef - <i>Sabellaria</i> can perform important stabilising function on substratum.

Table 2 (cont	inued)	Relevant MNCR bio	otopes
<i>Modiolus</i>	modiolu	<i>S</i>	
Higher code	Biotope code	Biotope	Comments
MIR		LTERED INFRALITTORAL ROCK	
MCR.M		sel beds (open coast circalittoral rock/n	
MCR.M	ModT	<i>Modiolus modiolus</i> beds with hydroids and red seaweeds on tide- swept circalittoral mixed substrata	Biogenic reef <i>Modiolus</i> creates important alteration of habitat and may form significantly raised structure.
SCR		LTERED CIRCALITTORAL ROCK	
SCR.Mod		tered <i>Modiolus</i> (horse-mussel) beds	
SCR.Mod	ModCvar ModHAs	<i>Modiolus modiolus</i> beds with <i>Chlamys varia</i> , sponges, hydroids and bryozoans on slightly tide-swept very sheltered circalittoral mixed substrata <i>Modiolus modiolus</i> beds with fine hydroids and large solitary ascidians on very sheltered circalittoral mixed substrata	Biogenic reef <i>Modiolus</i> creates important alteration of habitat and may form somewhat raised structure. Biogenic reef <i>Modiolus</i> creates important alteration of habitat and may form somewhat raised structure.
CMX	СШ	CALITTORAL MIXED SEDIMENTS	
CMX	ModMx	<i>Modiolus modiolus</i> beds on circalittoral mixed sediment	Biogenic reef <i>Modiolus</i> creates important alteration of habitat and may form significantly raised structure.
СМХ	ModHo	Sparse <i>Modiolus modiolus</i> , dense <i>Cerianthus lloydii</i> and burrowing holothurians on sheltered circalittoral stones and mixed sediment	Clearly not biogenic reef.
Mytilus ed	ulis		
Higher code	Biotope code	Biotope	Comments
ELR	EXP	OSED LITTORAL ROCK (mussel/bar	macle shores)
ELR.MB	•	lus (mussels) and barnacles	
ELR.MB	MytB	<i>Mytilus edulis</i> and barnacles on very exposed eulittoral rock	Not biogenic reef. This is a typical rocky shore community. Mussels are rarely more than 2 layers deep.
MLR	MO	DERATELY EXPOSED LITTORAL R	OCK (barnacle/fucoid shores)
MLR.MF	Myti	lus (mussels) and fucoids (moderately e	-
MLR.MF	MytFves	Mytilus edulis and Fucus vesiculosus on moderately exposed mid eulittoral rock	Not biogenic reef. Many species capable of growing on the rock whether the <i>Mytilus</i> are there or not (though there may be additional sediment dependent species); usually no significant raised reef area.

Table 2 (cont	tinued)	Relevant MNCR bio	otopes
MLR.MF	MytFR	Mytilus edulis, Fucus serratus and	Not biogenic reef.
		red seaweeds on moderately exposed lower eulittoral rock	As above.
MLR.MF	MytPid	Mytilus edulis and piddocks on	Clearly not biogenic reef.
	5	eulittoral firm clay	5 6
SLR	SHE	I TEDED I ITTODAL DOCK (functional)	horag
SLR SLR.MX		LTERED LITTORAL ROCK (fucoid sl lus (mussel) beds (mixed substrata)	nores)
SLR.MX	MytX	Mytilus edulis beds on eulittoral	Biogenic reef - Mytilus
		mixed substrata	performs important stabilising
			function on substratum.
LMX	LIT	FORAL MIXED SEDIMENTS	
LMX	Mytfab	Mytilus edulis and Fabricia sabella	Not biogenic reef - organisms
		in poorly-sorted muddy sand or muddy	perform some stabilising function on substratum but do not
		gravel shores	form substantial structures.
MIR		LTERED INFRALITTORAL ROCK	
SIR.EstFa SIR.EstFa	Estu: MytT	arine faunal communities (shallow rock/ Mytilus edulis beds on reduced	(mixed substrata) Not biogenic reef. Many species
SIX.Estra	Iviyti	salinity tide-swept infralittoral rock	capable of growing on the rock
			whether the Mytilus are there or
			not (though there may be
			additional sediment dependent species); usually no significant
			raised reef area.
MCR.M	Mus	sel beds (open coast circalittoral rock/m	ivad substrata)
MCR.M	MytHAs	<i>Mytilus edulis</i> beds with hydroids and	Not biogenic reef.
	5	ascidians on tide swept moderately	Associated species almost all
		exposed circalittoral rock	capable of growing on the rock
			whether the <i>Mytilus</i> are there or not, and usually no significant
			raised reef area.
IMX		RALITTORAL MIXED SEDIMENTS	
IMX.EstMx IMX.EstMx	Estu: MytV	arine sublittoral mixed sediments Mytilus edulis beds in variable	Biogenic reef - <i>Mytilus</i>
IIVIX.ESUVIX	lvlyt v	salinity infralittoral mixed sediment	performs important stabilising
			function on substratum; can be
			raised substantially above
			surrounding sediment.
Serpula vermicularis			
Higher code			Comments
inghei coue	code	Biotope	Comments
CMS		CALITTORAL MUDDY SANDS	
CMS	Ser	Serpula vermicularis reefs on very	Biogenic reef Serpula creates
		sheltered circalittoral muddy sand	important alteration of habitat
			and can form large, projecting structures.

F. RELEVANT CONSERVATION INITIATIVES

Due to the range of ecological functioning and biodiversity values associated with biogenic reefs in general, they are featured or implicated for scientific study and/or conservation actions through several initiatives. These are briefly outlined below, and should be considered as distinct in purpose but complementary in application.

1. EU Habitats Directive

Some of the habitats and species covered in other volumes of this series of reports are Annex I or Annex II features. However, although '*reefs*' are an Annex 1 feature, the Habitats Directive makes <u>no mention of '*biogenic* reefs'</u>.

The possible citing of biogenic reefs as a specific reason for selecting SACs is presently under careful review, and it is likely that SACs based on the presence of biogenic reefs will be proposed in the future (Brown et al., 1997).

2. UK Biodiversity Action Plan

Biodiversity Action Plans (BAPs) are being prepared for a variety of species and key habitats, the latter being grouped under different broad habitat types. this work is being carried out by a number of working groups under the direction of the UKBAP Steering Group in support of the UK Government's commitments to biodiversity made at the Earth Summit in Rio de Janeiro. BAPs relevant to this work will be prepared for the following key habitats:

- *Sabellaria alveolata* reefs (broad habitat 'Littoral rock')
- Sabellaria spinulosa reefs (broad habitat 'Inshore sublittoral rock')
- *Modiolus modiolus* beds (broad habitat 'Inshore sublittoral rock')
- *Serpula vermicularis* beds (broad habitat 'Inshore sublittoral rock')

At the time of writing this report the BAPs relevant to *S. alveolata*, *S spinulosa* and *M modiolus* have been produced in draft form, in close co-operation with the production of this report. Final BAP plans are presently understood to be scheduled for production by the end of 1998.

3. OSPAR/JAMP

The Joint Assessment and Monitoring Programme (JAMP) of the Oslo and Paris Conventions for the Prevention of Marine Pollution (OSPAR) is presently developing guidelines for monitoring of marine ecology and biodiversity in relation to human activities. In this respect UK conservation agencies will be reviewing aspects of sensitivity in relation to *Modiolus modiolus* reefs and *Sabellaria spinulosa* reef biotopes, as well as maerl beds, sea pen faunal communities, kelp forests, and seagrass beds (draft already produced). It is anticipated that information in this report will contribute to this process.

G. KEY POINTS FROM CHAPTER I

- Biogenic reefs have been defined for the purposes of this report as "Solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms."
- Many of the reef forming species form extremely variable community types, with obvious gradation between non-reef and reef biotopes. Furthermore, the concept of biogenic reefs has not been an important consideration in past survey work, and community/habitat descriptions by many workers, including to some extent the MNCR biotope classifications, are often inadequate to decide whether a habitat / biotope constitutes biogenic reef. Thus, deciding whether to classify a community or biotope as 'biogenic reef' is often difficult. This is a major problem for many *Modiolus modiolus* and *Sabellaria spinulosa* communities (which seem to be particularly variable in community structure and difficult to observe), less so for the mainly intertidal *Mytilus edulis* (which is also very variable but nevertheless categorisation is often rather easier) and *Sabellaria alveolata* (though there is little experience of categorisation of subtidal *S. alveolata*). Identification of serpulid reefs appears to pose no problem.
- *Sabellaria alveolata* reefs may take the form of extensive sheets, hummocks, or more massive and extensive reefs consisting of fused hummocks.
- Well developed, stable *S. spinulosa* reefs are probably relatively unusual, and have not yet been well described, but probably form extensive areas up to 60 cm proud of the seabed. Less stable, often annual 'crusts' up to a few cm thick seem to be widespread although these probably do not constitute true biogenic reefs.
- *Modiolus modiolus* reef can take two main physical forms: semi infaunal reefs, which grade in density and thickness from continuous dense, raised reefs to scattered clumps which may not actually fit the definition of biogenic reefs; and an infaunal gravel embedded reef community which in Britain can form wave like mounds up to 1 metre high.
- Well developed *Mytilus edulis* reefs generally take the form of hummocks or ribbons, rarely exceeding 30-50 cm in thickness but with very high densities of living and dead mussels, and are often very extensive. They accumulate large amounts of 'mussel mud' (faeces, pseudofaeces and sediments).
- Reefs of the serpulid worm *Serpula vermicularis* in Loch Creran are very discrete structures up to 75 cm high and 1 m across, but adjacent reefs can coalesce to around 3 m across. More extensive reefs have been reported from Ireland. They are formed by calcareous worms tubes up to around 15-20 cm in length growing sinuously upwards in a relatively open structure.
- Reefs of the deep water coral *Lophelia pertusa* are not discussed in this report as they are unlikely to be found in SACs. Reefs of the serpulid worm *Ficopomatus enigmaticus* are not discussed as it is an alien species. Oysters *Ostrea edulis*, the infaunal bivalve *Limaria hians*, the mussel *Musculus discors* and the sand mason *Lanice conchilega* do not constitute reef building species and are not discussed in detail.

II DISTRIBUTION

This chapter gives a general overview of distribution of biogenic reefs, and the species which form them, in global, European and UK terms. This is followed by a discussion of the distribution of biogenic reefs within possible and candidate SACs. Maps and tables are provided summarising, for each species, the known distribution within the UK of biogenic reefs and similar biotopes, both within and outside SACs.

A. DISTRIBUTION OVERVIEW OF BIOGENIC REEFS

All biogenic reefs have a limited distribution within the UK and Europe. The most important known areas of biogenic reefs in the UK are listed in Table 3 with brief descriptions or comments. The locations of these plus relevant biogenic reef MNCR biotopes from Table 2 are given in Figure 2.

1. Sabellaria alveolata

S. alveolata reefs are a southern phenomenon reaching their northerly limit within Britain. Extensive reefs are commonly reported on the French, Spanish and Portuguese Atlantic coasts (Almaca, 1990; Anadon, 1981; Gruet, 1981; Gruet, 1989), and extend as far south as Morocco (Gruet, 1982 cited in Cunningham et al., 1994; Hawkins, pers. obs.). They also occur in the Mediterranean. Within Britain, the range is essentially southern and western (Figure 2a), with reefs not reliably found east of Lyme Regis in the English Channel (Hawkins, pers. obs.), although there are dubious reports from the Isle of Wight (Gubbay, 1988), and none reliably reported north of the Northern Solway Firth (Cunningham et al., 1984). Within Britain and France at least they are usually intertidal, though they have also been reported from the subtidal, sometimes extensively. They are generally limited to areas of hard substratum, including cobble, adjacent to sand and with moderate to considerable exposure to waves (see chapter III). Cunningham et al. (1984) recommended eleven sites for SSSI or SSI status (listed in Table 3) and essentially these remain among the most interesting known intertidal reefs, although those in the Barn Scar and Dubmill Point areas of Cumbria are probably equally valuable. English Nature considered S. alveolata reefs on the Cumbrian coast to be of national importance (English Nature, 1993). However, it is now known that there are also very extensive and rich subtidal reefs in the Severn Estuary which may also be of national importance (Table 3).

2. Sabellaria spinulosa

Published information on world-wide distribution was not found, but in the North East Atlantic *S. spinulosa* has a widespread distribution, which encompasses the whole of the British Isles, including Shetland (MNCR database; Hayward & Ryland 1990) and the Mediterranean Sea (Bhaud & Gruet, 1984), although it is limited to areas with very high levels of suspended sediment.

Areas where dense aggregations have been reported include the Thames Estuary (Attrill, 1996), Dublin Bay (Walker & Rees, 1980), off Lough Foyle, N. Ireland (Erwin et al., 1990), Burrow Head, North Irish Sea (Earll, 1992; Covey in prep), Morecambe Bay (Irving et al., 1996), Hilbre Island, Dee Estuary (McIntosh, 1922 cited in George & Warwick, 1985), Gower

Table 3 A summary of the main known occurrences of biogenic reefs or possible biogenic reef biotopes, concentrating on cSACs and pSACs plus important or well developed areas elsewhere. This table relates only to the five species considered in detail in this report (*Sabellaria alveolata, S. spinulosa, Modiolus modiolus, Mytilus edulis* and *Serpula vermicularis*). Distribution in relation to cSACs and pSACs is given as far as possible.

Sabellaria alveolata		
• -eleven areas recommended for SSSI status by Cunningham et al. (1984) The terms sheets, hummocks and reefs are as defined by Cunningham et al. (1984) (see chapter I)		
Distribution within demor	stration UK Marine cSACs	
Cardigan bay cSAC	• Aberporth - sheets and hummocks (Cunningham et al., 1984).	
Lleyn Peninsula and the Sarnau cSAC	• Shell Island, Mochras - <i>S. alveolata</i> sheets cementing boulders and cobble, with fucoids.	
	• Llwyngwril and Barmouth area - sheets.	
	Less well developed reefs at Criccieth and on the north side of the Lleyn Peninsula.	
	All the above based on information provided by CCW plus Cunningham et al. (1984).	
Morecambe Bay cSAC	Newly discovered small areas off Morecambe frontage which have replaced <i>Mytilus</i> community on boulder scar, plus areas on boulder/cobble around Piel Flats and smaller areas on the West side of Walney Island (C Lumb; J Andrews; B Green, pers. Comm.).	
Solway Firth cSAC	There are numerous extensive areas on the Cumbrian coast but the majority are outside the cSAC. There is a very extensive area of <i>S. alveolata</i> sheets and hummocks on boulder scar at Dubmill point which is on the border of the cSAC and much of this area is likely to be included within the cSAC. A few areas of <i>S. alveolata</i> are known from the Dumfriesshire coast but no extensive ones likely within the cSAC.	
Distribution within other	UK Marine cSACs and pSACs	
Severn Estuary pSAC	Very extensive sublittoral <i>S. alveolata</i> reefs, with some <i>S. spinulosa</i> , on tide swept hard substrata in turbid waters - covering the greater area of the subtidal - 'among the finest and most notable in Britain, with particularly rich associated communities' (CCW). Also some intertidal areas though not very notable according to Cunningham et al. (1984) and unclear if they would qualify as biogenic reefs.	
Drigg Coast cSAC	Drigg coast cSAC includes well developed <i>S. alveolata</i> reefs at Barn Scar and Kookarah. Some nearby to the south eg Tarn Bay/Selker area are probably better examples but are not covered.	
Distribution within other areas		
South west England	 Numerous areas though there is some suggestion of reduction in range in this area, and conspicuously absent from much of West Cornwall. Notable areas listed by Cunningham et al. include: Duckpool, N. Cornwall (hummocks); Dawlish, S. Devon (hummocks); Millook, Cornwall (sheets and hummocks). 	

Table 3 continued	Sabellaria alveolata continued
Wales	 A number of areas identified by Cunningham et al. (1984) including some in Cardigan Bay in the Aberystwyth area, and some on the Gower peninsula, plus: Dunraven bay (unusual reefs and hummocks).
Cumbrian Coast	 As well as those areas mentioned above under Morecambe Bay, Drigg Coast and Solway Firth cSACs, there are many well developed and extensive reef areas on boulder scars on open coasts between the Duddon estuary and St Bees Head, including: Tarn Bay (reefs and hummocks); Annaside Bank (hummocks).
	There are also numerous areas, though probably generally with lower cover, between St Bees Head and Dubmill Point at the entrance to the Solway estuary, particularly in Allonby Bay, including;Crosscanonby.
Northern Ireland	Reefs are reported from the Down Coast at Rossglass (Crisp, 1964) and Glassdrummand Port (Wilkinson et al., 1988). At Glasdrummand they are known to extend into the subtidal.
South west Scotland	• Auchenmaig Bay, in Luce Bay Galloway (hummocks).

Sabellaria spinulosa

There are numerous areas, particularly off North and West Wales but also elsewhere, where crusts of *S. spinulosa* occur but these appear to be largely thin, poorly developed annual features (see text). Only those which seem more likely to represent true biogenic reefs are listed here.

Distribution within demonstration UK Marine cSACs

	<i>S. spinulosa</i> dominated biotopes reported in this area by MNCR but not clear whether they qualify as biogenic reefs nor whether they are actually within the cSAC boundary.	
The Wash and North Norfolk Coast cSAC	Well developed examples have recently been found in the mouth of the Wash within the cSAC boundary (Patterson, pers. comm.). Work is in progress to define these areas more clearly, but they appear to be continuations of areas found outside the cSAC boundary, see below (Foster-Smith, pers. comm.). Sites rich in <i>S. spinulosa</i> have previously been found within the Wash (National Rivers Authority, 1994) though these examples may not have constituted reefs.	
Lleyn Peninsula and the Sarnau cSAC	There are well developed crusts of <i>S spinulosa</i> within the cSAC Lleyn Peninsula and the Sarnau but it is debatable whether they qualify as biogenic reefs (E I Rees, pers. obs.).	
Morecambe Bay	None known, though reportedly there were areas which were lost due to the activities of prawn fishing in the approach channels to the Bay (Mistakidis, 1956; Taylor & Parker, 1993).	
Distribution within other UK Marine cSACs and pSACs None known		

Table 3 continued	Sabellaria spinulosa continued		
Distribution within other	Distribution within other areas		
Bristol Channel	Well developed reefs with associated fauna of relatively slow growing invertebrates reported in the Bristol Channel (George & Warwick, 1985).		
The Wash	Well developed examples have been found well offshore from the Lincolnshire coast, outside the boundary of the Wash and N. Norfolk Coast cSAC. Good video footage shows well developed reef areas protruding up to 60 cm above the surrounding seabed. Extent of coverage is not yet known though video footage covering c 300 m showed almost continuous cover of reefs continuing beyond the videod area (Foster-Smith et al., in prep; Foster-Smith, pers. Comm.).		
Anglesey	There are well developed reefs off the north coast of Anglesey (E I Rees, pers. obs.).		
North Yorkshire & Durham Coasts	<i>S. spinulosa</i> dominated biotopes reported in this area by MNCR but not clear whether they qualify as biogenic reefs		

Modiolus modiolus

Distribution within demonstration UK Marine cSACs

Berwickshire & North	Dense beds reported in the vicinity of the Farne Islands but these are not
Northumberland Coast cSAC	mentioned in draft information on important communities prepared by SNH - extent and density of these is unclear (Helen Davis, English Nature, pers. comm.).
Lleyn Peninsula and the Sarnau cSAC	Clumps of <i>Modiolus</i> have long been known from the North side of the Lleyn Peninsula. In 1993-95 acoustic surveys showed that they form true reefs raised over a metre above the seabed. The BIOMAR team carried out RoxAnn TM surveys in the area in 1995. A detailed acoustic survey of the area was done in 1997 by NW & N. Wales Sea Fisheries Committee for CCW as part of the cSAC demonstration project.
Strangford Lough	There are extensive areas dominated by clumps of <i>Modiolus</i> on a muddy bottom which probably do not qualify as reefs although they support similar communities (Magorrian et al., 1995). Much denser areas which probably do qualify as biogenic reefs exist in places, including between some of the pladdies (islands) (R Holt, M Service, pers. comm.).
Distribution within other Lochs Duich, Long and Ailsh Reefs pSAC	UK Marine cSACs and pSACs Information provided by SNH: "in a number of places, circalittoral boulder slopes support a community typified by the squat lobster <i>Munida</i> <i>rugosa</i> and the horse mussel <i>Modiolus modiolus</i> which forms biogenic reefs in places."
Distribution within other a	areas
Shetland	Numerous areas where <i>Modiolus</i> is important though in many cases may be clumps rather than true biogenic reefs. Busta Voe is thought to have the most extensive and highest quality <i>Modiolus</i> biotopes in the Voes (Alistair Davison, pers. comm.).
Off Humber estuary	Dense beds reported (Murray et al., 1980) though unclear whether they really constitute biogenic reefs.

Table 3 continued	Modiolus modiolus continued
Irish Sea	Numerous areas of coarse bottoms have been known to have clumps or patches of <i>Modiolus</i> , eg much of the area between Anglesey and the Isle of Man. North and north west of Anglesey there may be some more extensive and dense patches.
South east of Isle of Man	Extensive areas reported to be dominated by <i>M. modiolus</i> (Jones, 1951) but thought to be much reduced in density and extent in recent years, due probably to scallop dredging.
North of Isle of Man	At least 6 km ² of seabottom recently discovered where M . <i>modiolus</i> on tide swept gravel and shell creates numerous steep banks up to 1 m high with very rich associated fauna (Holt et al., unpublished).
West of Scotland	<i>M. modiolus</i> forms very dense and beds, though unclear how physically raised, in upper Loch Creran, and in deeper tide swept channels between basins in Loch Leven and Loch Eil (Howson et al., 1994). Numerous other areas where <i>Modiolus</i> is important, though in many these are probably scattered clumps rather than true biogenic reefs.
East coast of N. Ireland and Rep. of Ireland	Probably quite extensive dense beds off the Ards Peninsula, with small areas also reported in Carlingford Lough and at Portrush (Erwin et al., 1986). Unclear in all cases whether they constitute true biogenic reefs. On the southern tip of the Codling Bank off Co Wicklow a gravel embedded type of <i>Modiolus</i> bed was located in 1997 during an Ireland - Wales INTERREG project.

Mytilus edulis

The common mussel is widespread and abundant on many parts of the UKs coasts. There are likely to be numerous, particularly estuarine areas, where *Mytilus* beds develop to the stage where they constitute biogenic reefs, in addition to those mentioned here.

Distribution within demonstration UK Marine cSACs

Berwickshire & North Northumberland Coast cSAC	Large mussel beds exist in the Lindisfarne and Budle Bay estuary area, probably constituting biogenic reef in places.
The Wash and North Norfolk Coast cSAC	In the Wash there are areas which qualify as biogenic reefs. There is a long history of data on stocks and recruitment fluctuations in records kept by Eastern Sea Fisheries Committee and CEFAS.
Burry Inlet	Extensive and well developed reefs form in three main areas within the 'estuary of the three rivers' at Laugharne Sands, Salmon Point Scar and Scott's Bay. Relatively rich associated fauna.
Lleyn Peninsula and the Sarnau cSAC	Areas of cobble on the Sarns have shallow sublittoral beds of <i>Mytilus</i> but unlikely to constitute biogenic reefs.
Morecambe Bay	Mussel beds occur on a number of "skears" within the bay. On some, such as Head Skear in the Walney Channel the beds build up well developed bioherm mounds. On other more exposed skears, such as South America Skear, there are from time to time very dense spat settlements which build up sufficient mud that the mussels detach from the stones and are washed away by storms. Such beds are a very important source of seed for re- laying, for example in the Menai Strait.

Table 3	Mytilus edulis continued
Distribution within other	UK Marine cSACs and pSACs
Dornoch Firth pSAC	Extensive beds which probably constitute biogenic reefs. May have a sublittoral component. (McKay, pers. comm.).
Plymouth Sound and Estuaries cSAC	Mytilus beds which may constitute reefs at the mouth of the Lynher estuary.
Pembrokeshire Islands cSAC	Dense mussels form on tideswept areas but not clear if they form true biogenic reefs (information from CCW).
Solway Firth cSAC	Dense beds/reefs, somewhat transient, occur on some scars & sand banks especially Silloth - Dubmill Point, and may extend subtidally.
Distribution within other a Cromarty Firth	areas
Culbin Sands	
Ythan Estuary	Very dense and extensive reefs. Well studied in relation to bird feeding.
Tayport	<i>Mytilus</i> found sublittorally around the Tay Road Bridge though unclear whether these beds constitute reefs.
Firth of Forth	
South West England and South Wales	Exe Estuary - good examples of well developed beds which form biogenic reefs. Probably also the Teign. Almost certainly many others in the general area (Moore, 1995).
Cumbrian coast	Many extensive boulder scars get heavily covered with <i>Mytilus</i> but probably rarely develops to true biogenic reef status.
Northern Ireland	Lough Foyle - <i>Mytilus</i> forms beds in sand and gravel though debatable whether it constitutes biogenic reefs.
West of Scotland	<i>Mytilus</i> widespread in sealochs on gravel/pebble/cobble; often described as clumped, but forms dense areas which might represent biogenic reefs in freshwater influenced areas at heads of lochs and in tidal narrows.
Serpula vermicula	ris
Distribution within demon None known	stration UK Marine cSACs
Distribution within other None known	UK Marine cSACs and pSACs
Distribution within other a Loch Sween, Scotland	areas Reefs reported previously (Earll, 1982), but recent surveys found only dead colonies (Moore, 1996).
Loch Creran, Scotland	Well developed reefs, particularly in the lower basin but also in the upper (Howson et al., 1994; Moore, 1996).

(Hiscock, 1979), North and West Wales (R Holt pers. comm.; Hiscock, 1984), the Bristol Channel (George & Warwick, 1985), the Solent (Environment Agency South West pers. comm.), Seven Sisters, Sussex (Wood & Jones, 1986), the Wash (Dipper et al., 1989; Foster-Smith et al., 1997; National Rivers Authority, 1994; Warren, 1973), Northumberland and North Yorkshire (Connor et al., 1996 and R Holt, pers. comm.), St Andrews, Scotland (McIntosh, 1922 cited in George & Warwick, 1985), and several locations in the southern North Sea (e.g. Riesen & Reise, 1982; Linke, 1951; Dorjes, 1992). With the exception of Linke (1951), none of the above references seem to describe very massive reefs of the sort created intertidally by Sabellaria alveolata, but 'crusts' or 'sheets' of variable thickness and rarely more than a few cm thick. These may just about fit the criteria for biogenic reefs, at least in some cases, although lack of clear descriptions is a problem in many cases. There are examples of what seem to be true, well developed reefs in the mouth of the Wash (see Table 3) (Foster-Smith et al., in prep February 1998) and possibly in the Bristol Channel (George & Warwick, 1985), though the physical nature of the latter is not well described. S. spinulosa reefs and crusts appear to have a somewhat southerly distribution (Figure 2b) although this may reflect the distribution of suitable habitat, such as perhaps turbidity, rather than temperature.

3. Modiolus modiolus

M. modiolus is a northern species which occurs in both the Atlantic and Pacific Oceans. In the north east Atlantic it occurs from at least the Bay of Biscay north (though occasional specimens may occur as far south as North West Africa) to northern Norway and the White Sea, and occurs off Iceland and the Faeroes (Brown, 1984; Hayward & Ryland, 1990; Roberts, 1975; Schweinitz & Lutz, 1976; Tebble, 1966). Within Britain it is more frequent in northern and western areas (Figure 2c); extensive dense beds do not seem to occur south of the Severn Estuary on the west coast or the Humber Estuary on the east coast. Numerous descriptions of Modiolus communities mention clumps of Modiolus, often scattered on muddy or muddygravel sediments (see chapter III), and in many cases it seems unlikely that these would fit the above description of 'biogenic reefs'. Beds which are probably dense enough or discrete enough to fit the definition of biogenic reefs have been reported from: the south east of the Isle of Man (Jones, 1951); north east of the Isle of Man (Holt et al., unpublished); several parts of Strangford Lough (Magorrian et al., 1995); off the Lleyn Peninsula (Rees, pers. obs.), Lochs Creran, Eil and Leven (Howson et al., 1994), off the Ards Peninsula, relatively small areas in Lochs Duich, Long and Alsh (SNH unpublished information), and the Shetland Voes, and probably occur elsewhere, particular in the Irish Sea and the west of Scotland.

4. Mytilus edulis

The taxonomy of the genus *Mytilus* has been the subject of some debate in recent years, and there is often confusion between three 'species' in particular: *Mytilus edulis, M. trossulus* and *M. galloprovincialis*. The status of the latter has been particularly debated; it was once widely thought to be a separate species but is now regarded by many as a form of *M. edulis* (see e.g. McDonald et al., 1991; Gosling, 1992a; Seed, 1992 for summaries). Nevertheless, *M. edulis* seems to have a broad distribution; it is circumpolar, and reported as far south as Japan and China in the Pacific and to North Carolina in the Atlantic, while in Europe the northern limit is within the Arctic circle, and it is found as far south as the Mediterranean (Clay, 1967). It forms dense aggregations which might fit the definition of biogenic reefs over much of this geographical range.

Mytilus edulis can be abundant all over the UK in intertidal and sometimes subtidal habitats, ranging from fully saline to highly estuarine, and again over much of this range it is capable of

forming dense beds, by embyssment to one another and to underlying substrata, which could justifiably be called biogenic reefs (Figure 2d). In the south west of England it frequently forms hybrids with the more southerly distributed *Mytilus galloprovincialis*, but in more sheltered and lower salinity areas, where true reefs tend to occur, *M. edulis* is much the more dominant form (Gardner, 1994; Gardner, 1996). Hybridisation also occurs on Scottish and Irish coasts, but here there is less intermixing of genes between populations of the two forms than in the south west of England (Gosling, 1992a).

A number of important *Mytilus* reef sites are given in Table 3, but this list is by no means exhaustive.

5. Serpula vermicularis

This species supposedly has a world-wide distribution, but there is a great deal of taxonomic confusion and it is presently thought that the species found within Britain is limited to the north east Atlantic and the Mediterranean. Furthermore, there is a strong possibility that within the Mediterranean it is actually part of a complex of two or three species (ten Hove, pers. comm.). Dr. T. Pillai of the Natural History Museum, London is presently reviewing the genus. S. vermicularis has nevertheless been found throughout Britain from the Shetland to the Channel Islands, particularly on the southern and western coasts (Hayward & Ryland, 1990), but reefs within Britain are reported only from Loch Creran and Linne Mhuirich (at the top end of Loch Sween) (Earll, 1982; Howson et al., 1994). Surveys during 1993 and 1994 failed to find any living reefs in Linne Mhuirich (Moore, 1996). The only other reports found are from two sites in Ireland: Ardbear Lough, Galway; (Bosence, 1973; Bosence, 1979), and Killarey Harbour, Galway (Connor et al., 1997); and 'the Mediterranean' (ten Hove, 1979) where it may not necessarily be the same species. Moreover, the Mediterranean aggregations are "at a smaller scale than in Irish waters" (Zibrowius, pers. comm.). McIntosh (1923) noted that examples of S. vermicularis from the south of England, including Falmouth and Exmouth, were often in massive groups of aggregated tubes attached to Pecten, oysters and other bivalves. Allen (1915), describing the polychaete fauna of Plymouth and South Devon reported that "large masses of this species were obtained by a diver somewhere in the Hamoaze and brought to the laboratory", but there were no other similar reports from this area according to the MBA (1957). The MNCR database includes one reference to abundant S. vermicularis in Loch Glendhoo, north-west Scotland, which comprises dense aggregations on bedrock at the base of a steep cliff. The distribution of reefs in Britain and Ireland is shown in Figure 2e.

B. A PERSPECTIVE ON BIOGENIC REEFS AND SACS

The distribution of major examples of biogenic reefs is given by species in Table 3 and Figure 2, both within cSACs and pSACs, and elsewhere.

No currently proposed SACs were selected specifically on the basis that they contain biogenic reefs. However, biogenic reefs are 'sub-features' of other Annex I features such as 'reefs', 'estuaries' or 'large shallow inlets and bays'. In some cases biogenic reefs are specifically mentioned as reasons why a site is a particularly good example of an Annex 1 habitat e.g. *Mytilus* in Morecambe Bay, *Modiolus* in Strangford Lough, Lleyn Peninsula and the Sarnau and Loch Maddy; *Sabellaria alveolata* in the Solway Firth and Morecambe Bay.

There are candidate SACs selected on the basis of the presence of 'reefs' which do have substantial areas of *Modiolus* reef (Lochs Duich, Long and Alsh, Lleyn Peninsula and the Sarnau), *Sabellaria alveolata* reef (Lleyn Peninsula and the Sarnau); and probably *Sabellaria spinulosa* reef (Lleyn Peninsula and the Sarnau; possibly Berwickshire and the North

Northumberland coast) and *Mytilus* reef (Berwickshire and the North Northumberland coast) (Table 3 and Figure 1).

It is worth noting that an SAC cannot be designated on the basis of an intertidal reef area unless there is also contiguous subtidal reef interest (Brown et al., 1997). In the case of *Mytilus* and *Sabellaria alveolata* reefs, which are usually intertidal but may also occur in the shallow subtidal, they are very likely to occur as interest features of SACs designated as 'estuaries', 'large shallow inlets and bays', or even 'mud and sand flats not covered by sea water' or 'sandbanks which are slightly covered by sea water at all times', (see Table 3 and Figure 1). *Sabellaria alveolata* and *Mytilus edulis* also occur within the Cardigan Bay cSAC, designated on the presence of bottlenose dolphins, *Tursiops truncatus*. The Wash and North Norfolk Coast cSAC almost certainly has *Sabellaria spinulosa* reefs which are probably best regarded as an interest feature under 'large shallow inlets and bays' in Loch Maddy and Strangford Lough.

Serpulid reefs have an extremely limited distribution within the UK (presently known only from one, or possibly two, Scottish sea lochs) and none occur within cSACs or pSACs.

C. KEY POINTS FROM CHAPTER II

- Sabellaria alveolata reefs reach their northerly limit of distribution in the outer Solway Firth, and rarely penetrate further east than Lyme Bay in the English Channel, though they have been found on the Isle of Wight. They seem to be absent from many exposed peninsulas. They are well represented in cSACs though some of the best and most extensive reefs in Cumbria are in unprotected areas.
- Well developed, stable *S. spinulosa* reefs are probably relatively unusual. The only certain occurrence seems to be in the mouth of the Wash, where reefs raised up to 60 cm proud of the seabed extend for hundreds of metres, and occur both within and outside the Wash and North Norfolk Coast cSAC. Reports from the Bristol Channel suggest similar communities may occur there. Less stable, often annual 'crusts' or clumps seem to be much more widespread in turbid sublittoral areas, though few are known from Scottish waters.
- *Modiolus modiolus* has a predominantly northern and western distribution, with few reef areas known south of the Humber or Severn. A number of cSACs include semi infaunal *Modiolus* reefs, but the infaunal gravel-embedded reef community has only been identified in areas outside the UK (Isle of Man and Ireland) which may be more widespread and does not occur in any cSACs or pSACs.
- Well developed *Mytilus edulis* reefs appear to be widespread throughout Britain though the best examples are limited to large shallow inlets and bays, especially estuarine areas. Several cSACs include good examples.
- The only known reefs of the serpulid worm *Serpula vermicularis* within the UK are in Loch Creran. They were also present in part of Loch Sween during the 1980's, although more recent diving surveys found only dead colonies. They occur in sheltered, relatively shallow parts of sealochs, however, and might potentially be found in SACs, for which reason they are discussed here.

III ENVIRONMENTAL REQUIREMENTS AND PHYSICAL ATTRIBUTES

This chapter describes the environmental requirements of the five reef building species under consideration. Where possible these requirements are described specifically in relation to reef communities, but in many cases information is only available in relation to the species in other biotopes or in a more general sense.

Physical strength / fragility of the reefs is also described here, but for more general descriptions of the physical form of the reefs see chapter I.

A. SABELLARIA ALVEOLATA

1. Environmental Requirements

a. Temperature

High summer temperatures are unlikely to be a problem within British waters, but cold winter temperatures can have strong effects. Gruet (1982) reported that growth of *S. alveolata* is severely restricted below 5°C. Crisp (1964) noted that there were many severe losses of *S. alveolata* due to the severe winter of 1962-63, especially in South and North Wales, and in Lyme Bay where some colonies were depleted by half and others lost completely. Not surprisingly, survival was best at lower shore levels. Wilson (1971) found less severe effects at Duckpool in Cornwall, but nevertheless reported almost complete mortalities of some colonies, mainly at the higher shore levels. Further losses of reefs at Criccieth, North Wales were attributed to the cold winter of 1984 (Gubbay, 1988). Frost has been suggested as the factor limiting the upstream distribution of reefs in the Severn Estuary (Mettam, pers. comm. in Bamber & Irving, 1997). Growth rates increase with increasing temperature up to 20°C (Cunningham et al., 1984).

b. Vertical distribution / depth

Reefs form mainly on the bottom third or so of the shoreline and in the shallow subtidal. Those in Duckpool, north east Cornwall were reported to be largely limited to areas exposed only by spring tides (Wilson, 1971), although they do penetrate as far up the shore as MLWN (Hawkins, pers. obs.). On Cumbrian shores hummocks forming at least 20% cover have been reported up to just below MHWN (Allen et al., 1991). The actual distribution on any one shore is probably related largely to substratum distribution and water movement.

True reefs have not often been reported to penetrate far subtidally, but this may to some extent reflect lack of survey data. Extensive shallow subtidal reefs have been found recently in the Severn Estuary (CCW, unpublished information), and in the same area they have been reported to penetrate as far as 20 m depth (Bamber & Irving, 1997). Quite widespread, although patchy, subtidal reefs were found off the Maryport - Dubmill Point area of the Cumbrian Coast by a series of grab surveys, and at Dubmill Point itself very extensive and dense hummocks could be seen extending beyond the level of a very large spring tide (Perkins, 1981). *S. alveolata* reefs are also reported to extend into the subtidal at Glassdrummand, Northern Ireland (Erwin et al., 1990) and also extended subtidally at Hilbre Island in the Dee Estuary in the early 1900's (Herdman, 1919).

c. Suspended sediment

A supply of suspended coarse sediment is a requirement for the development of reefs, and the species has been reported to penetrate into areas such as the Severn Estuary where finer suspended sediments occur (Cunningham et al., 1984). Suspended sediment supply is affected by both the local availability of sediment and the amount of water movement for suspension (see d and e below).

d. Substratum requirements

It is widely reported that *S. alveolata* generally requires hard substrata on which to form, but that these must be in areas with a good supply of suspended coarse sediment. *S. alveolata* reefs can form on a range of substrata from pebble to bedrock (Cunningham et al., 1984). Reefs therefore commonly form on areas of rock or boulders surrounded by sand. Larsonneur (1984), working in the Bay of St Michel in Normandy, noted that the sand mason *Lanice conchilega* can stabilise sand well enough to allow subsequent colonisation by *S. alveolata*. Settlement occurs mainly on existing colonies or their dead remains (see chapter IV).

e. Water movement and hydrography

Water movement of sufficient intensity to suspend coarse sand particles, making them available for building the worms tubes, is a prime requirement. Cunningham et al. (1984) note that this may consist of waves or currents. In many British localities such as the south west of England, much of Wales and the Cumbrian coast the former seem more important, but in others such as parts of the Severn Estuary tidal suspension is probably very important. However, *Sabellaria* is generally absent from very exposed peninsulas such as the Lleyn, Pembrokeshire and the extreme south west of Cornwall, which probably relates to the effect of water movement on recruitment (Cunningham et al., 1984).

The complete absence of *S. alveolata* on the coast of the Isle of Man where there are apparently suitable shores seems odd. Cunningham et al. (1984) considered this as strong evidence of the importance of larval supply to the maintenance of populations (see chapter III). Larval supply itself may be strongly affected by local hydrography.

f. Salinity

No detailed information on salinity requirements or tolerances have been found but the species does not normally seem to penetrate into very low salinity areas. However, Lancaster (1993) found extensive, healthy hummocks of *Sabellaria* overgrown with *Fucus ceranoides* - a fucoid normally found only in estuarine habitats - at Drigg, Cumbria, where there is a large freshwater input from the Drigg BNFL plant.

Larvae are strongly stimulated to settle by the presence of cement secretions of adult or juvenile *Sabellaria* and probably by other calcareous substrata (see chapter IV), though they will clearly also settle on non calcareous substrata.

g. Influence of environmental factors on competitive interactions

Mussels *Mytilus edulis* and *S. alveolata* often occur together, and in many areas one or other may be dominant at different times. The factors affecting this interaction are not understood, though changes in sediment type and water movement are likely to be important factors which may tip the balance one way or another. It can be speculated that salinity and temperature changes could also play a part, since the tolerances of the two species to these are very different. Since both species have variable recruitment and depend upon very heavy recruitment to form dense beds, stochastic factors affecting larval recruitment will obviously also be important.

2. Physical Attributes

Wilson (1971) reports that the porches of the tubes are thin and easily damaged, but that the bulk of the colonies have a consistency resembling soft sandstone, and a considerable resistance to splitting. This seems perhaps to overstate the strength, however, given the experience of Cunningham et al. (1984) who carried out small scale experimental trampling: light trampling was found to be capable of causing obvious damage to the porches; they were able to inflict damage to a depth of up to 6 cm by using heavy pressure, particularly with the heel; and strong kicking caused structural damage to the whole colony, large cracks between the tubes, and the subsequent loss of substantial portion of one colony. Bait diggers appear to have little difficulty in breaking open colonies to collect the worms (Hawkins, pers. obs.). Loss of older colonies does occur during storms, perhaps aided by objects such as logs being tossed against them (Wilson, 1971), but over much of their range they are exposed at least occasionally to some fairly severe storm waves, which many of them clearly survive.

B. SABELLARIA SPINULOSA

1. Environmental Requirements

a. Temperature

Specific information on temperature tolerance was not found for this species, but its widespread distribution, from at least North of the Shetlands to the Mediterranean Sea, together with its predominantly subtidal habit means that *S. spinulosa* is likely to be much less sensitive to temperature changes than the intertidal *S. alveolata*, which has been shown to be severely affected by low winter temperatures - for example, *S. spinulosa* was not affected by the cold winter of 1963 although many *S. alveolata* mortalities resulted (Crisp, 1964).

b. Depth

Although individuals can certainly occur intertidally, very dense *S. spinulosa* is found almost entirely subtidally; there are no reports of intertidal reefs in Britain though sporadic dense intertidal reefs have been reported from the Waddensee, southern North Sea (observations of Linke, 1951 discussed by Wilson, 1971; see chapter IV). Dense crusts are reported in the infralittoral and may occur in only a few metres of water; they are also found in the circalittoral but the maximum depth of dense crusts is unclear. Dense reefs reported by George & Warwick (1985) in the Bristol Channel were in 41 m of water while recently discovered reefs in the mouth of the Wash are in 15-25 m (Foster-Smith et al., in prep February 1998).

c. Suspended sediment and water movement

S. spinulosa requires suspended sand grains in order to form its tubes; reef communities therefore only occur in very turbid areas where sand is placed into suspension by water movement. The relative importance of tidal versus wave induced movements is unclear.

d. Substratum requirements

S. spinulosa reefs or crusts will form on hard substrata but this does not preclude their formation on other substrata (Hiscock, 1991 and pers. comm.).

Several sources suggest that bedrock is not necessary for formation of *Sabellaria spinulosa* crusts and reefs, though a somewhat firm substratum is presumably required. Rees & Dare (1993) describe habitat/ distribution as being typically on shell (especially oyster valves), sandy gravel or rocky substrata with moderate to strong tidal flow. Larsonneur (1994) reported that *Sabellaria spinulosa* dominated communities were present on rock/pebble bottoms in the Bay of Mont St Michel. He also reported sand masons *Lanice conchilega* could sufficiently stabilise sand to allow colonisation by *S. alveolata*. It can be speculated that the same process might be possible with *Sabellaria spinulosa* too, since *Lanice* and *S. spinulosa* are sometimes found together (e.g. Foster-Smith et al., 1997) and extensive *S. spinulosa* colonies are known to occur in essentially sandy areas (see below); this has not been demonstrated, however. Numerous studies have reported high densities of *S. spinulosa* in Day grab or other grab samples which would be unlikely from hard bottoms (Foster-Smith et al., 1997). Hoare & Hiscock (1974) reported the presence of *S. spinulosa* associated with kelp holdfasts (which themselves require a hard substratum).

Larvae are strongly stimulated to settle by cement secretions of adult or newly settled *S. spinulosa* (see chapter IV). In the absence of suitable stimulation metamorphosis and settlement occurs but always more slowly (Wilson, 1970).

There is some suggestion from field observations that established colonies can increase in extent by addition to the existing colony without the need for hard substratum; Warren & Sheldon (1967), Schafer (1972) and Warren (1973) have reported extensive *Sabellaria spinulosa* colonies in essentially sandy areas.

It is likely that stability of the reefs is to some degree a function of stability of the substratum. The more transient crusts probably occur principally on relatively unstable substrata such as mobile sands, while longer lasting reefs could be limited to more stable substrata such as firm mixed sediments.

e. Salinity

Little firm information was found on salinity requirements of *S. spinulosa* although well developed reefs seem to be restricted mainly to deeper waters where salinity would be expected to be more or less fully marine. However, McIntosh (1923) referred to dense aggregations of *Sabellaria* (*alveolata*) being particularly common in estuaries such as the Tees and Humber. Given that his drawings of the aggregates of *Sabellaria* from the Humber looked more like *S. spinulosa* than *S. alveolata*, and the known distribution of the *Sabellaria* species, it seems these aggregations were almost certainly misidentified *S. spinulosa*.

2. Physical Attributes

The fragility, or otherwise, of substantial reefs is unclear, although according to Wilson (1970) the tubes of *Sabellaria spinulosa* are harder and stronger than those of *S. alveolata*. However, *S. spinulosa* reefs in the form of widespread sheets are probably surprisingly fragile. George & Warwick (1985) mention that reefs are broken up sufficiently easily to be sampled by a Day Grab, which is usually unsatisfactory for obtaining samples on hard or stony grounds. Attrill et al. (1996) also obtained samples of *S. spinulosa* reefs which they regarded as quantitative using a Day grab, as did NRA (1994). R. Holt (pers. comm.) has observed that crusts of *S. spinulosa* on cobble and boulders off the Northumberland and North Yorkshire coasts often break up during winter storms. Elsewhere, however, they do seem to be more permanent features, although this may be mainly related to the stability of the physical environment in which they are found rather than any inherent biological difference. The 'balls' of *S. spinulosa* found by Attrill (pers. comm.) are probably considerably more robust, although there is no published evidence for this. There is much evidence that reefs can be very badly broken up by fishing (chapter VI). The fragility, or otherwise, of substantial reefs is unclear.

C. MODIOLUS MODIOLUS

1. Environmental Requirements

a. Temperature

Modiolus is clearly a boreal species, and the fact that dense aggregations seem to reach their southerly limit around British shores suggests a possible susceptibility to a long-term rise in summer water temperatures. Little published information was found on which to make an informed judgement, although it is clear that its upper thermal limit is lower than that of *Mytilus edulis* (Bayne, 1976). Being subtidal it is obviously protected from major short-term fluctuations. It has been suggested that an inability to tolerate temperature changes is one of the factors which prevents *Modiolus* from colonising the intertidal to any extent (Davenport & Kjorsvik, 1982). Low winter water temperatures would not pose any threat to *Modiolus* in a British context.

b. Depth

Dense populations which would represent biogenic reefs seem to be mainly restricted to depths of between 5 and 50 m in British waters, although bioherms have been recorded in over 80 m in Nova Scotia (Wildish & Fader, in press). Individuals have been found at depths of up to 280 m (Schweinitz & Lutz, 1976). Coleman (1973) demonstrated that *M. modiolus* exposed to air has an erratic heart rate, suggesting lack of physiological adaptation to aerial exposure, and loses water rapidly due to an apparent inability to control its gape sufficiently well. Lack of mobility, thin shell and restricted tolerance to changes in temperature and salinity have also been suggested as reasons for its poor ability to colonise the intertidal (Davenport & Kjorsvik, 1982). It is thus not surprising that intertidal occurrences are limited generally to low shore and pools.

c. Salinity

Although dense populations of very young *Modiolus* do occasionally seem to occur subtidally in estuaries, the species is more poorly adapted to fluctuating salinity than many other mussel

species (Bayne, 1976) and dense populations of adults are not found in low salinity areas. Pierce (1970) established tolerance limits of 27-41% for *M. modiolus* based on ventilation behaviour and byssus formation.

d. Substratum requirements

Larval *Modiolus* will settle on a variety of shell and stone substrata, including *Modiolus* shell, and *Modiolus* may occasionally replace *Mytilus* as the main fouler of the deeper parts of offshore structures such as oil rigs. However, survival of small *Modiolus* is often low due to high predation, and there is evidence that the best refuge for juveniles is in the byssus threads of established clumps or aggregations of larger *Modiolus*, which also act as a suitable settlement substratum (Roberts, 1975). In more infaunal *Modiolus* beds it can be speculated that the lack of accessible byssus may be an important factor in reducing recruitment rates; there is some evidence that recruitment in 'infaunal' *Modiolus* reefs to the north of the Isle of Man is very sporadic (Holt & Shalla, 1997). Although clearly requiring some hard substratum for initial formation, *Modiolus* beds and reefs are capable of forming on a variety of sedimentary bottoms ranging from essentially muddy substrata in some sealochs to quite coarse mixed sediments containing much stones and shell.

e. Water movement

Water movement appears to be an important factor in the build up of many of the denser reef areas, the majority being found in areas of moderate to strong tidal currents.

f. Water quality

M. modiolus has been found to be more or less similar in tolerance of oxygen deficiency and hydrogen sulphide to *M. edulis* (Theede et al., 1969), both species being much more tolerant than many other groups such as gastropods, echinoderms and crustaceans. Work in Newfoundland has demonstrated that *Modiolus modiolus* is capable of tolerating intermittent availability of food supplies, reducing feeding activity during periods of low phytoplankton (autumn and winter) and increasing clearance rate during spring and early summer (Navarro & Thompson, 1996). It is also found in a variety of turbid and clear water conditions.

2. Physical Attributes

Fragility of individual *Modiolus* is clearly not particularly high, and the importance of reaching a certain minimum size to avoid predation is mentioned elsewhere. The fragility of reefs is also probably not particularly high, even in those situations where the animals are truly epifaunal; clearly semi-infaunal and infaunal reef areas are less fragile. Clumps upon muddy substrata are presumably more fragile than larger aggregations. Nevertheless, very physical activities such as impacts by towed fishing gear are known to be damaging, not only by disruption and flattening of clumps and larger aggregations, with reduction in the value of the habitat, but also by damage, and presumably mortality, to individual *Modiolus* (see chapter V). It should be noted also that the shells of old individuals can be very brittle due to the activities of the boring sponge *Clione celata* (Comely, 1978).

D. MYTILUS EDULIS

Because of its widespread distribution, intertidal habit, its abundance and ecological importance in many places, its use as a bio-indicator, its commercial importance, and the relative ease with which it can be kept alive in the laboratory, *Mytilus edulis* has been

extremely widely studied. For general information on its biology, ecology and physiology, the reader is referred to Bayne (1976) and Gosling (1992b).

1. Environmental Requirements

a. Temperature

Mussels belonging to the genus *Mytilus* are widely distributed throughout the cooler waters of the world. The *Mytilus edulis* species complex is circumpolar in boreal and temperate waters, in both the southern and northern hemispheres (Soot-Ryen, 1955) extending from the Arctic to the Mediterranean in the North east Atlantic. The most important limiting factor for distribution world-wide is thought to be temperature (Stubbings, 1954).

Damage by extreme low temperatures is minimised in *Mytilus* by the use of nucleating agents in the haemolymph (Aunaas et al., 1988). Even in more temperate sites *M. edulis* is subject to lethal freezing conditions periodically, but they can survive even when tissue temperatures fall below -10° C (Williams, 1970), with large adults surviving laboratory conditions of -16° C for 24 hours (Bourget, 1983). Crisp (1964) observed that *M. edulis* within the British Isles was relatively unaffected by the severe, unexpected freeze of December 1962 to March 1963. Beds in the Wash have survived being buried under ice for up to several weeks in 1963, 1979 and in the mid 1980's (Dare, pers. comm.) on permanently submerged offshore structures. In Sweden, mussels actively ingested seston at -10° C suggesting that they can utilise spring phytoplankton blooms in boreal waters even at low temperatures (Loo, 1992).

Tolerance of high temperatures and desiccation can explain the upper limit of *M. edulis* on the high shore (Seed & Suchanek, 1992). British *M. edulis* have an upper sustained thermal tolerance limit of about 29°C (Almada-Villela et al., 1982; Read & Cumming, 1967).

Recruitment or movement to cracks is known to afford better thermal protection on the upper shore (Suchanek, 1985). It can therefore be speculated that dense reef structures might afford some protection from extremes of temperature to the lower animals. In general, however, given the wide temperature tolerance of *Mytilus*, reefs, which are generally found quite low on the shore, are unlikely to be very sensitive to changes in temperature (but see possible indirect effects of cold in chapter IV).

b. Vertical distribution / depth

Reef areas are normally found on the lower third of the intertidal, and in the shallow subtidal, but can occur down to 10 m in some places such as the Wash and on Caernarfon Bar (Dare, pers. comm.). Dense subtidal populations of *Mytilus* are frequently reported from dock pilings and offshore platforms where low predation may be an important factor.

Lower zonational limits for *M. edulis* are usually set by biological factors, normally predation by starfish, crabs and gastropods (see chapter IV). Lower zonational limits can also be controlled by physical factors. Sand burial has been shown to limit lower regions of *M. edulis* zonation patterns in New Hampshire, USA (Daly & Mathieson, 1977) and this is probably important in some British locations, particularly in the case of cobble or boulder scars in areas of shifting sands such as in Morecambe Bay and the Solway Firth. Upper limits of distribution are set by physical factors, but growth and therefore size of animals is also affected by reduced feeding time at higher levels. It has been estimated that growth would be zero at approximately 55% aerial exposure (Baird, 1966), although clearly this will vary somewhat with local conditions.

c. Salinity

M. edulis is tolerant of a wide range of salinity compared to other biogenic reefs species and may penetrate quite high into estuaries. However, it may stop feeding during short-term exposure to low salinities (Almada-Villela, 1984; Bohle, 1972) and the most well developed reefs therefore usually occur low on the shore in the mid to lower reaches of estuaries.

Almada-Villela (1984) reported greatly reduced shell growth for a period of up to a month or so upon exposure to 16‰ compared to 26 or 32‰, while exposure to 22‰ caused only a small drop in growth rate. In the longer term (in the order of weeks) *M. edulis* adapts well to low salinities (Almada-Villela, 1984; Bohle, 1972), and hence can even grow as dwarf individuals in the inner Baltic where salinities can be as low as 4-5‰ (Kautsky, 1982). Almada-Villela (1984) found that the growth rate of individuals exposed to 13‰ had recovered from almost zero initially, to over 80% of the rate of control animals in 32‰ after one month. It is therefore no surprise that *Mytilus* can do well in brackish lagoons and docks if there is a suitable supply of food.

d. Water quality

M. edulis is widely recognised as being tolerant of a wide variety of environmental variables including salinity and oxygen tension as well as temperature and desiccation (Seed & Suchanek, 1992). It is capable of responding to wide fluctuations in food quantity and quality, including variations in inorganic particle content of the water, with a range of morphological, behavioural and physiological responses (Hawkins & Bayne, 1992). *Mytilus* is not necessarily particularly tolerant of anthropogenic chemicals, however (chapter VI).

Excessive levels of silt and inorganic detritus are thought to be damaging to *Mytilus* once they accumulate too heavily within the reef matrix (Seed & Suchanek, 1992), although the degree to which this might be influenced directly by water quality rather than production of faeces and pseudofaeces is unclear. *Mytilus* is capable of re-surfacing through a shallow covering of sediment. Mussels can colonise unpromising habitats such as former docks (Hawkins et al., 1992; Russell et al., 1983). In these semi-enclosed habitats sheets of mussels up to 30 cm thick can form. Their filtering activity can improve water quality (Allen & Hawkins, 1993; Wilkinson et al., 1996).

e. Substratum requirements

In general the best examples of biogenic *Mytilus* reefs occur on mixed substrata of small boulders, cobble and pebble on sandy or muddy substrata. It has long been suggested that larval *Mytilus* will settle on most substrata provided they are firm and have a rough, discontinuous surface (Maas Geesteranus, 1942). However, settlement is in many cases a two stage process; initial settlement occurs primarily on filamentous substrata such as sublittoral hydroids and algae, with subsequent secondary dispersal and reattachment later in areas with adult beds (see chapter IV).

In wave exposed areas *Mytilus* requires a hard and stable substratum such as rocks, or large boulders on which to form beds.

In sheltered areas infaunal beds may occur on gravel or even quite sandy areas, as reported in Lough Foyle (Erwin et al., 1986), at the mouth of Cookmere Haven, Sussex (E I Rees, pers. obs.), and occasionally in the Wash (Dare, pers. comm.) although it is likely that some harder substratum embedded within the more sandy areas is required. Dense settlement also occurs on cockle shells in the Wash and Burry Inlet, and on *Lanice* in the Wash (Dare, pers. comm.).

In many of these cases the byssus of the embedded mussels do seem to serve a noticeable stabilising function. The authors are not aware of instances where true biogenic reefs have developed on such substrata but the potential may be there given the propensity for *Mytilus* juveniles to settle in the spaces afforded within adult beds (King et al., 1990; McGrorty et al., 1990).

f. Water movement

Mytilus edulis is found in a wide range of exposures, from all but the very most exposed shores to extremely sheltered habitats, but in order to develop large reef structures considerable water movement is required. This provides increased oxygen and food supplies in such areas, and may also help to prevent 'mussel mud' (silt, faeces and pseudofaeces) from building up too quickly. In general, water movement in the best *Mytilus* reef areas is provided mainly by tidal currents, but in some cases wave action may also contribute, as in Morecambe Bay, although these beds tend to be more transient. On some open coasts *M. edulis* may form dense beds on boulder scars, where wave action is the main source of water movement, as on the Cumbrian coast, for example. However, it is debatable whether many of these areas would qualify as biogenic reefs as they tend not to be raised or massive, and are formed on what is essentially an underlying hard (though sometimes unstable) substrate. In general, the more stable reefs occur in smaller, more sheltered estuaries.

2. Physical Attributes

Individual animals have a wide variation in shell strength (Meire & Ervynck, 1986) which is one of the factors which influences mortality due to oystercatcher and crab predation. Shell strength tends to increase with increasing age/size, height on the shore and wave exposure. Large reefs which develop on mixed substrata in fairly exposed sites seem to be much more susceptible to being removed by tidal or wave action than do extensive beds on rock, the latter usually being both much more firmly attached and often less thick. Thicker reefs are attached to the underlying substratum only by the bottom layer of mussels, and accumulations of mussel mud in the deeper layers can kill the bottom mussels, exacerbating the problem. Mussel beds composed of a single year class of mussels may form only a thin layer sitting upon accumulated mussel mud; they are poorly attached to the substratum and are therefore more likely to be detached from the substratum than are mussel beds composed of a large number of years classes (McKay & Fowler, 1997).

Although a bed as a whole may be a persistent feature, the formation of patches within it is a dynamic process (Svane & Ompi, 1993). Those on the outside of patches tend to be larger and there are complex density dependent influences on a small scale on recruitment, growth and mortality (see also 'longevity and stability', chapter IV).

E. SERPULA VERMICULARIS

1. Environmental Requirements

a. Temperature

No definitive published data on temperature requirements of *S. vermicularis* reefs was found. However, its broad geographical range as a species suggests that it is unlikely to be very sensitive to temperature changes in a British context.

b. Depth

As a species Serpula vernicularis has been reported to occur intertidally as scattered specimens and subtidally to depths of over 200 m (Clarke, 1960; Zibrowius, 1973). However, Nelson-Smith (1967) described its distribution as being restricted to shallow water and the lower shore. Moreover, in the only known locality in Britain where living reefs occur, (Loch Creran), these are restricted to depths of 0-14m, are extremely rare outwith the range 1-13 m, and the most well-developed reefs are within the range 6-10 m (Moore, 1996). Similarly in Ardbear Lough, Ireland, they have a restricted depth range of 2-20 m with maximum development between 2 and 15 m (Bosence, 1973; Bosence, 1979). It was suggested by Moore (1996) that the lower limit was restricted by depth, sediment type and substratum availability but that due to correlation between these factors it was not possible to determine their relative importance. There were certainly deep areas where suitable substrata appeared to exist but no reefs occurred. In Ardbear Lough, Bosence (1979) concluded from both observation and from transplant experiments that the lower depth limitation was probably determined by the occurrence of suspended mud and low oxygen levels in the deeper water, while the upper limit was probably due to lowered salinity, competition with algae, and high light levels. However, Moore (1996) quotes Anderson (1887) who described well developed serpulid reefs intertidally among Zostera beds in Loch Creran. Neither the Zostera nor the serpulids occur there now.

c. Salinity

No detailed published information was found on the effect of salinity on *S. vermicularis*. Bosence's work in Ardbear Lough suggested that lowered salinity is in part responsible for the lack of *Serpula* reefs above a depth of 2 m below extreme low water of spring tides, and for a lack of reefs at the head of the Lough where there is freshwater input. Although he produced salinity profiles of the Lough on one spring and one neap tide which suggested that salinities of less than 30 ‰ are probably unusual in the areas of extensive reefs, these are of limited value since such small enclosed loughs can be subject to extremely variable salinity conditions depending on local weather etc. Holt (pers. obs.) strongly suspected that a short-term low-salinity event during the spring killed off experimental cultures of *Laminaria saccharina* and *Alaria esculenta* in the top 5 metres a few hundred metres below the road bridge in Loch Creran, for example. However, *S. vermicularis* reefs were observed in intertidal areas of Loch Creran during the last century. The true effect of variations in salinity is therefore unclear, but some tolerance to short-term lowering of salinity seems to be implied.

d. Water quality

As mentioned above, suspended mud and low oxygen levels prevented development of reefs in deeper areas of Ardbear Lough; conditions were clearly extreme, however, as there was no macroinvertebrate life at all in the deeper areas (Bosence, 1979).

e. Substratum requirements

Serpula vermicularis requires a hard substratum on which to form. It most commonly occurs on bivalve shells (Bosence, 1973; Nelson-Smith, 1967). In Loch Creran it was particularly common on shells of *Pecten*, *Aequipecten* and *Modiolus*, although reefs also formed on bedrock, boulders stones and man-made substrata such as fish farm weights, while large colonies were only rarely found growing on rock (Moore, 1996). Garwood (1982) reported that juveniles were abundant on colonies of the bryozoan *Flustra foliacea* off the north-east coast of England. It is likely that too much sediment on the surface of the rocks or shells would prevent settlement. Reefs form predominantly in areas where there is suitable substratum scattered throughout a muddy or muddy sand bottom. Reef development occurs by repeated subsequent settling of larvae on adult tubes but it is not known whether the larvae are actually attracted to or stimulated to settle on the adult tubes. Clearly there may be a preference for calcareous substrata in general, but this has not been investigated.

f. Water movement

A limited turnover of water in order to facilitate larval retention within the system appears to be a prime requirement for reef development; thus reefs are unlikely to develop and endure except in sheltered sealochs where there are physical barriers at the mouth of the loch limiting tidal exchange of water (Bosence, 1979, Moore, 1996). Shelter from wave action which would be damaging to the reefs would presumably also be a benefit of such an environment.

g. Other factors

Bosence (1979) found settlement was lower on the underside of experimental plates, and noted that a tendency for serpulids to settle in shady areas in preference to brightly lit areas has been reported by several other workers, though the precise causes and implications of this are not understood. Factors other than phototropism, such as temperature, siltation and algal growth, may be important.

2. Physical Attributes

Reefs are clearly very fragile, being reported to spread partly by virtue of pieces falling away and then continuing to grow (Bosence, 1979) and to become more fragile with age (Bosence, 1973). This may in part be due to the activities of the boring sponge, *Cliona celata* (Bosence, 1979). In Loch Creran, Moore (1996) reported localised but severe damage to reefs by the scraping action of chain risers and by the movement of anchor weights. Although many of the individual worms survived and were continuing to feed normally, the value as a habitat was greatly diminished. Moore also suggested that overgrowth of other encrusting organisms could contribute to strengthening the colonies. The overall trend nevertheless seems to be of increasing fragility with increasing age and size.

F. KEY POINTS FROM CHAPTER III

Information from this chapter is here summarised in tabular (Table 4) and textual form (overleaf).

Table 4 Summary information relating to environmental requirements and physical fragility for each biogenic reef species. This information relates as far as possible to biogenic reef biotopes and not necessarily to other biotopes in which the species may be found.

	S. alveolata	S. spinulosa	M. modiolus	M. edulis	S. vermicularis
Temperature	Southern species: may die back intertidally in cold winters Growth restricted below 5°C, maximal around 20°C	Not known to be sensitive in a UK context	Possible susceptibility to high summer water temperatures is inferred from geographical distribution	Not sensitive in a UK context	Not known to be sensitive in a UK context
Depth	Mid-low intertidal and shallow subtidal (occ. to 20m?)	Subtidal (15-50 m?)	Subtidal Mainly 5-50 m	Mid-low intertidal and shallow subtidal (to 10 m)	Subtidal. Dense reefs reported between 1 and 15 m, and from intertidal in the last century
Suspended sediment	Requires suspended sand Probably tolerates some silt	Requires suspended sand Probably silt tolerant	No information found	Tolerates some suspended sand / silt	Possibly intolerant of suspended mud
Substratum	Hard or mixed substrata. Existing tubes of <i>S</i> <i>alveolata</i> (or <i>S</i> . <i>spinulosa</i>) strongly stimulate settlement	Hard or mixed substrata. Existing tubes of <i>S</i> . <i>spinulosa</i> strongly stimulate settlement	Require hard or mixed substrata at least for initial formation. May subsequently spread over softer sediments	Mixed substrata	Require some stones / shells at least for initial formation. May subsequently spread over softer sediments
Water movement / hydrography	Requires moderate wave or current induced movement	Requires moderate water movement	Many denser reefs occur in moderate to strong tidal regimes	Requires strong tidal movements. Transient reefs may develop in areas of moderate water movement	Only known from sheltered conditions with very limited water exchange
Salinity	Does not penetrate far into low salinity areas	Probably does not penetrate far into low salinity areas	Does not penetrate far into low salinity areas	Fully marine and / or estuarine	Possibly some tolerance to short- term lowering of salinity, no detailed information
Physical fragility	Moderate - porches especially can be damaged by light trampling	Moderate? No information specific to well developed reefs but thin sheets can be easily broken up	Moderate (low if very recessed?)	Moderate	Very fragile

KEY POINTS

- Sabellaria alveolata occurs mainly in the form of intertidal (especially the bottom third of the shore), or shallow subtidal, reefs, and is comparatively unusual elsewhere. It is limited to moderately exposed areas or areas of strong tidal influence, where there is a good supply of suspended sand with which to build its tubes, and does not penetrate into very low salinity areas. It requires some degree of hard substratum (stable rocks and boulders or boulder/ cobble scars) on which to form. Settlement is mainly on existing colonies or their dead remains. Areas dominated by *S. alveolata* can cover hundreds of hectares. It is markedly affected by cold winters, with death of large areas of reef reported, particularly at higher shore levels. Reefs are moderately fragile, particularly the porches, which can be damaged by light trampling.
- *S. spinulosa* forms crusts and occasionally well developed, raised reefs sublittorally in turbid waters from a few metres to at least 40 m or so (though intertidal reefs have been sporadically reported from the Waddensee). It seems likely that the best reefs form on areas of sandy sediments with some hard substrata. *S. spinulosa* does not seem to penetrate into low salinity areas. Thin crusts seem to be moderately fragile and are quite easily broken up by storms or physical impacts. Fragility of substantial reefs is unclear although they are probably stronger than those of *S. alveolata*.
- *M. modiolus* occurs in a wide variety of biotopes. Infaunal reefs have been reported in strong tidal waters of moderate depths (15-40 m). Semi-infaunal reefs and beds occur in a variety of situations on mixed or muddy sediments and in a variety of current regimes, and in a range of densities from scattered clumps to large, true reefs or bioherms with many densely packed mussels forming a raised mass. Denser beds / reefs seem to occur between the shallow infralittoral and around 50 m, though they may occur deeper. *Modiolus* reef communities are often patchy but nevertheless extensive, covering many hectares. They are not found in low salinity areas. Fragility of reefs probably varies with the degree to which they are infaunal. Shells of very old individuals may become very fragile due to infestation by boring sponges.
- *Mytilus edulis* is tolerant of a wide range of environmental variables such as temperature, food supply, and water turbidity, but forms large reefs mainly on mixed firm sediments in relatively wave sheltered estuaries where there are strong currents. They form mainly in the mid and low intertidal but can occur down to 10 m in places such as the Wash and Caernarvan Bar. In thick reefs only the bottom layer of mussels is attached to the substratum, and resistance of many reefs to wave and current action seems to deteriorate as the reefs get thicker and accumulate more mussel mud. Beds of only a single year class are also usually poorly attached to the substratum. Shell strength of individuals has been found to be variable.
- *Serpula vermicularis* reefs form initially on a variety of hard substrata such as stones and shells, but can subsequently spread over wider areas. The other main environmental requirements seem to be an enclosed body of water with limited water exchange, allowing for retention of larvae, and probably a lack of competition for space. Siltation and anoxic bottom water can limit downward distribution. The reefs seem to have a moderate tolerance to reductions in salinity. They are very fragile.

IV BIOLOGY AND ECOLOGICAL FUNCTIONING

This section deals with two major aspects of each biogenic reef forming species in turn:

1) biology, which concentrates on:

- reproduction, development and growth, including recruitment processes (but omitting detailed descriptions of reproductive processes and larval development);
- longevity and stability (where individuals and reefs are considered separately if possible, and where seasonal variations are included if appropriate);
- feeding biology; (the details of feeding mechanisms, such as tentacular structure, ciliary mechanisms etc, where known, are not described here as they are not felt to be sufficiently relevant, though appropriate references may be given);
- parasites and diseases.

2) ecological functioning, which discusses:

- the habitat created by biogenic reefs, including information on the range of species associated with them; (the diversity of habitats which is often created by biogenic reefs, and the resulting increase in richness and / or diversity of the community, are among the most important reasons for which they are identified in general terms as being of conservation interest);
- any wider effects on the environment;
- the importance of known predators;
- competitive interactions with other species.

A. SABELLARIA ALVEOLATA

1. Biology

a. Reproduction, development and growth

The most detailed work done on *S. alveolata* reproduction within Britain is that of Wilson (e.g. Wilson, 1971) in Cornwall.

i. Spawning season

Wilson (1971) reported a short summer spawning period around July.

ii. Larval development and settlement

The larvae probably spend anything between 6 weeks and 6 months in the plankton (Wilson, 1968b; Wilson, 1971) so that dispersal could potentially be widespread. Slight settlement has been observed in all months except July, but in 14 years of close observations (1961 to 1975), Wilson (1976) observed only three heavy settlements, in 1966, 1970 and 1975. All were in the period from September to November or December. Observations elsewhere also support the observation that intensity of settlement is extremely variable from year to year and place to place (Cunningham et al., 1984; Gruet, 1982). Settlement occurs mainly on existing colonies or their dead remains; chemical stimulation seems to be involved, and this can come from *S. spinulosa* tubes as well as *S. alveolata* (Cunningham et al., 1984; Gruet, 1982; Wilson, 1971).

iii. Growth rates

Growth is rapid, and is promoted by high levels of suspended sand and by higher water temperatures up to 20°C. A mean increase in tube length of up to 12 cm per year has been reported for northern France (Gruet, 1982). Cunningham et al. (1984) stated that growth is probably lower than this in Britain due to the lower water temperatures, although Wilson (1971) reported growth rates (tube length) of 10-15 cm per year in several colonies at Duckpool, North Cornwall for first year colonies, and around 6 cm in second year worms.

iv. Maturation

Wilson (1971) reported that in good situations the worms mature within the first year, spawning in the July following settlement.

b. Longevity and stability

A typical life span for worms in colonies forming reefs on bedrock and large boulders in Duckpool was 4-5 years (Wilson, 1971), with a likely maximum of around 9 years (Gruet, 1982; Wilson, 1971). However, it is suspected that there are many colonies on intertidal cobble and small boulder scars on moderately exposed shores where shorter lifespans are likely due to the unstable nature of the substratum. Wilson (1971) reported that it was possible to age the worms to some degree by measuring the diameter of the tube (but not the wider 'porch' at the top of the tube).

Cunningham et al. (1984) reported that no observations appear to have been made on the longevity of actual reefs rather than individual worms, although in fact Wilson's observations at Duckpool, North Cornwall do contain some useful information in this regard, as do some less detailed studies by other workers. There is plenty of evidence that intertidal reefs, at least, are in many cases unstable, and there frequently (but by no means always) appears to be a cycle of development and decay over periods of up to around five years (Gruet, 1985; Gruet, 1986; Gruet, 1989; Perkins, 1986; Perkins, 1988; Perkins et al., 1978; Perkins et al., 1978). Exceptionally, Wilson (1976) observed one small reef from its inception as three small individual colonies in 1961, through a period between 1966 and 1975 where it existed as a reef rather greater than 1 metre in extent and up to 60 cm thick, with major settlement of worms occurring in 1966 and 1970. This reef finally 'died' in the autumn of 1975, ironically a period of intense new settlement elsewhere the same beach (Wilson, 1976). In the long term, areas with good *Sabellaria* reef development tend to remain so.

c. Feeding

S. alveolata is a filter feeder, but no information on feeding biology or mechanisms in this species was found. Wells (1970) described briefly the feeding structures and mechanisms of the related intertidal reef builder *Sabellaria kaiparaensis*. There was no information on particle size preferences or the effect of external factors such as food availability or turbidity on feeding, but a crude sorting mechanism was described, whereby particles too large to be ingested glide over the mouth and are transferred via the ventral lips to specialised pads which incorporate them into the walls of the tube. It was also mentioned that the worms did not feed continuously without aeration because suspended matter would foul the ciliary mechanism under stagnant conditions. In the absence of more specific information it has to be assumed that these observations also apply to *S. alveolata* and *S. spinulosa*.

d. Parasites and diseases

No information was found on this subject.

2. Ecological Functioning

a. Reef habitats

No information was found regarding community structure of subtidal *S. alveolata* reefs, and the following information therefore relates entirely to intertidal reefs.

Intertidal *S. alveolata* reefs are not particularly diverse communities, though they do nevertheless provide some increased diversity of habitat, and older reefs have somewhat more diverse associated communities than younger ones.

Sheets of S. alveolata appear to enhance algal diversity, apparently by providing barriers to limpet grazing (Hawkins, pers. obs. in Torbay and Cunningham et al., 1984). A number of studies have reported that older reefs provide a variety of habitats for other species, often in crevices. Wilson (1971) noted that Fucus serratus, F. vesiculosus, Palmaria palmata, Polysiphonia sp, Ceramium, sp, and Ulva lactuca are frequently associated with older Sabellaria colonies, and small polychaetes such as Fabricia sabella and syllids have been found living within the colonies. Cunningham et al. (1984) carried out limited quantitative quadrat surveys of S. alveolata reefs and noted up to eighteen associated animal species and twenty associated plant species, mainly on older colonies. The important animal species were all epifauna, including barnacles Chthamalus montagui, C. stellatus and Semibalanus balanoides, limpets Patella vulgata, P. depressa and P. aspera, mussels Mytilus edulis, dogwhelks Nucella lapillus and serpulid worms. There were few crevice fauna. The important plant species were Ceramium sp, Fucus vesiculosus, F. serratus, Ulva lactuca, Laurencia sp, Palmaria palmata, Corallina elongata, Enteromorpha sp, and Lomentaria sp. They found that algal colonisation, particularly of Ulva and Enteromorpha, was higher on reefs with a *placages* (sheet) structure, which they attributed to the fact that the worm tubes grow more longitudinally than in other reefs, so that algal sporelings are less likely to be disturbed by the growth or feeding activities of the worms. It is suspected that detailed studies would reveal other differences between the various physical forms of S. alveolata reefs.

Most studies have suggested that dense young colonies of Sabellaria alveolata are not very diverse communities. Wilson (1971) noted that barnacles, serpulid worms, encrusting algae and smaller tufted algae are overgrown and smothered out of existence by S. alveolata, that even algae do not do well where the Sabellaria are in their prime, and that where Sabellaria are dominant other species are suppressed. He stated that the reefs were at their 'best and cleanest' (i.e. well developed, contiguous reefs not overgrown by encrusting or attached fauna and flora) when a majority of worms in them were aged around 2 years. At Risehow Scar in Cumbria it was observed that "it has covered much of the scar and by firmly cementing gravels, shingle cobbles and boulders into a coherent layer it has reduced diversity and abundance of fauna eg littoral fish, small crabs and molluscs which have nowhere to shelter when the tide is out" (Perkins, 1988). Cunningham et al. (1984) reported that actively growing Sabellaria colonies are able to outcompete all other littoral species for space, and noted that young sheets of S. alveolata may reduce the diversity of shores by reducing the number of crevices available, but that as the sheets get older and break up the range of habitats provided increases. Thus the overall diversity of the community seems in general to be closely related to the developmental cycle of the reefs, as noticed also on French shores by Gruet (1982).

Cunningham et al. (1984) also noted that placages may impede the drainage of the shore, creating pools of standing water where there would otherwise be none. Further habitat modification they reported included the stabilisation of mobile sand, shingle, pebbles, and

small boulders, for example on the Cumbrian coastline, and increased habitat heterogeneity of exposed barnacle dominated shores and sand scoured rocks.

No rare or unusual species have been reported to be associated with *Sabellaria alveolata* reefs.

b. Predators

There is little detailed mention in the literature of predation on *Sabellaria alveolata*, although *Carcinus maenas* was a troublesome predator of transplanted portions of reefs in Somerset (Bamber & Irving, 1997), and remains have been found in the stomachs of the shore crab *Carcinus maenas* and the blenny *Blennius pholis* on shores at Sellafield, Cumbria (Taylor et al., 1962). Herdman (1919) mentioned that flatfish such as plaice and sole could easily obtain the worms by crunching up the brittle sand tubes but this appears to be supposition. Since the worms are known to be able to retract considerable distances down into the tubes (Cunningham et al., 1984; Wilson, 1971), it would appear to be difficult for predators to extract worms easily from compact reef masses. Bird predation has never been mentioned in any reports found by the authors, so it seems likely that the main predators are marine organisms. Wilson (1971) seemed to regard predation on *S. alveolata* reefs in North Cornwall as of little overall importance.

c. Competitors

Stability of *Sabellaria* reefs is influenced not only by stability of the substratum on which they are settled, but perhaps also by interactions with other species. It has been reported that heavy mussel settlement on reefs in Cumbria caused some deterioration in the quality of the reefs (Perkins, 1988). It has also been observed in Brittany that small mussels dislodged from nearby cultivation ropes lodge in the reefs and break up the surface as they grow (Mitchell, 1984). Cunningham et al. (1984) noticed large numbers of mussels particularly on older *Sabellaria* colonies, and suggested the existence of a *Sabellaria / Mytilus* succession, though they conceded that long-term observations were necessary to confirm this. Further support for this theory has come in recent years from Heysham, in Morecambe Bay, where *Sabellaria* reefs have developed on a boulder scar which has for around thirty years normally been populated by mussels *Mytilus edulis*. It is suspected that changes in sediment regime, including increased availability of coarse sand, as a result of a number sea defence developments, have allowed *Sabellaria* to outcompete the mussels, though this is unproven (Chris Lumb, Neil Fletcher and Jim Andrews, pers. comms.).

It is also suspected that on older reefs dense growths of seaweeds, mainly *Fucus*, can cause reefs to be torn up, particularly on less stable substrata.

d. Wider effects on the environment

No information was found on this subject with regard to S. alveolata.

B. SABELLARIA SPINULOSA

1. Biology

a. Reproduction, development and growth

i. Spawning season

Reproductive seasonality is unclear, but spawning probably occurs largely over winter and settlement in early spring. George & Warwick (1985) found major settlement in the Bristol Channel to occur in March, which is in agreement with the observations of Wilson (1970; 1971) working in the Plymouth area, who generally found a spawning period from January - March and a settlement period from March to April. Bhaud (1972) reported larvae of *Sabellaria spinulosa* in the plankton from December - March in Mediterranean populations. However, according to Garwood (1982) on the north-east coast of England larvae were found in the plankton from August to November. The MBA (1957) reported the breeding season according to three separate authorities as "May", "September", and "Jan-Sept, fertilisations made and larvae reared" in the Plymouth area.

ii. Larval development and settlement

The larvae spend between six weeks and two months in the plankton (Wilson, 1970) and so dispersal range is likely to be considerable.

Experimental lab work by Wilson (1970) showed that *Sabellaria spinulosa* larvae are strongly stimulated to metamorphose and settle by cement secretions of adult or newly settled young *S. spinulosa*. Scallop shells, especially *Pecten maximus*, appeared also to have some slight settlement inducing properties; oyster shells, with which *Sabellaria spinulosa* are often associated in the southern North Sea, were not tested. While *S. alveolata* larvae were stimulated to metamorphose by cement secretions of *S. spinulosa*, the opposite was rare; *S. spinulosa* are clearly more choosy in this respect. It appeared that in the absence of suitable stimulation metamorphosis and settlement sometimes occurred but always more slowly.

Rees and Dare (1993) considered that *Sabellaria spinulosa* had low recruitment, awarding it 1 on a four point scale. Evidence from the Bristol Channel (George and Warwick, 1984) and the southern North Sea (Linke, 1951; Michaelis, 1978) suggests that fecundity and recruitment may be very variable, at least in some areas (see also under longevity and stability, below).

iii. Growth

Detailed reports were not found but growth appears to be rapid. Where *S. spinulosa* acts as an annual species sheets up to 2-3 cm thick develop during a single growing season (essentially spring and summer) (R. Holt pers. comm.). Very rapid growth is also implied by the observations of Linke (1951) as translated by Wilson (1971).

iv. Maturation

Linke (1951) reported that spawning of intertidal *S. spinulosa* reefs in the southern North Sea took place during the first and second years.

b. Longevity and stability

From survey work on the Northumberland and North Yorkshire coasts, R Holt (pers. comm.) suggests that *Sabellaria spinulosa* often acts as a fast growing annual. Areas where *S. spinulosa* had been lost due to winter storms appeared to recolonize quickly up to the maximum observed 2-3 cm thick sheet during the following summer. Many thin crust-like

forms of *S. spinulosa* are probably annual or transient features of this sort, but there are reports of more stable communities, as below.

The melon sized aggregations found in sandy areas by Attrill (pers. comm.) appeared to be of too great a diameter to be created in one year. However, it is also possible that they are seasonal features which are added to each year, whether or not individual worms are perennial.

The reefs found recently in the mouth of the Wash are clearly accumulations created over a number of years as they stand up to 30-60 cm proud of the seabed, and there is a well developed infauna and epifauna, but no detailed information on reef development is available (Foster-Smith, pers. comm.).

George & Warwick (1985) made seasonal observations in the Bristol Channel. They concluded that in the year of study the juvenile settlement was low and that the observed density of adults could not be maintained by that degree of recruitment. They reported that the majority of the reef was composed of *S. spinulosa* over one year old, but gave no further indication of potential ages. However, they observed that most of the species found within the reef matrix were slow growing and long-lived with a very low turnover rate, implying that the reef itself must have been relatively old and stable. They also pointed out that, since *Sabellaria alveolata* can live for nine years (Wilson, 1971), it is quite possible that *S. spinulosa* could also be long-lived.

Wilson (1971) also discusses the observations of Linke (1951, original reference not seen by present authors) on Sabellaria spinulosa in the southern North Sea. Linke apparently described the sudden appearance of massive colonies on stone-work of protective groynes uncovered at low water on the island of Norderney, Fresian islands. In 1943 no colonies were present (time of year of this observation is unknown) but by September 1944 there were reefs 6-8 m wide and 40-60 cm high stretching for 60 m along both sides of three groynes and for 10 m around their broad ends. Linke assumed that settlement took place in 1944. In the summer of 1945 many colonies were dead and those remaining ceased growth in the autumn. Spawning took place in both their first and second years. Small scattered clumps were alive in 1946 but it is not known if they were from the 1944 settlement. Local fishermen confirmed that such reefs did occur annually here and there in other localities, though Linke (1951) observed that in this particular locality there had been only scattered individuals for decades. Wilson (1971) attributed the mass settlement to a swarm of larvae which were induced into settling after having been washed into the area of the scattered individuals. This suggests that perhaps the ability of newly settled young to stimulate settlement of larvae can "accelerate" the settlement process once it has started.

Michaelis (1978) reports that during the 1950s such intertidal populations became rare in this area but gives no explanation. He mentions that *S. spinulosa* was still present subtidally in the area, however.

Neither of these authors appears to have considered the possibility that these reefs could have been *Sabellaria alveolata* misidentified as *S. spinulosa*. *Sabellaria alveolata* has not been reliably reported on the east coast of England (Cunningham et al., 1984) and so it must be assumed that the identifications were correct.

c. Feeding

S. spinulosa is a filter feeder, but no detailed information on feeding was found (but see information on feeding in the related species S. kaiparaensis in the section on S. alveolata above).

d. Parasites and diseases

No information on this subject was found.

2. Ecological Functioning

a. Reef habitats

The thicker, and probably more permanent, crusts or reefs seem to have a considerable influence on the benthic community structure (e.g. Connor et al., 1996). George & Warwick (1985) mentioned that *Sabellaria spinulosa* reefs contained a more diverse fauna than nearby areas, and NRA (1994) found sites in the Wash associated with *S. spinulosa* to have more than twice as many species and almost three times as many individuals (excluding the *Sabellaria* themselves) as sites with low, or no, *S. spinulosa*. In the NRA survey sites the distinction between '*S. spinulosa* sites' and 'low or no *S. spinulosa*' was made at only 100 individuals per 3 grab samples (covering 0.3 m²), raising the possibility that even relatively sparse *S. spinulosa* communities with attached *Polydora* tubes, and with an infauna of typical sublittoral polychaete species, as well as the bivalves *Abra alba* and *Nucula nitidosa*, and an epifauna including tubeworms, pycnogonids, hermit crabs and amphipods. All of the species reported are found widely in other communities.

The well developed reefs of *S. spinulosa* found recently in the mouth of the Wash (see chapter II) appear to have a rich associated infauna and epifauna, although detailed studies of the associated biota have not yet been published. A report on recent surveys is in prep (Foster-Smith et al., in prep) but has not been seen by the authors; the following is from Foster-Smith (pers. comm.). From a combination of video footage and grab sampling, errant polychaetes and crabs appear to be particularly numerous within the reef itself. Sedentary species such as anemones were also seen although these were not so obviously important. High densities of shrimp like organisms, probably mysids, could be seen immediately above the reef on video footage. There was an obvious increase in richness of the associated infauna and epifauna with increasing *S. spinulosa* cover.

It is clear that there is often a rich and probably diverse community associated with well developed *S. spinulosa* reefs but there are presently few details.

Pink shrimp *Pandalus montagui* are often closely associated with *S. spinulosa* reefs, to the extent that fishermen pursuing *Pandalus* have been reported to use small trawls to search for lumps of *S. spinulosa* which they regard as an indication of good fishing grounds (Warren & Sheldon, 1967).

b. Predators

Warren (1973) and Warren & Sheldon (1967) reported that *Sabellaria spinulosa*, probably along with other associated organisms, can be an important food source for pink shrimp *Pandalus montagui*. The likely importance of this in terms of potential influences on the reef or associated species is not known. No further information on predators was found.

c. Competitors

George & Warwick (1985) have suggested from observations in he Bristol Channel that growth recruitment of *S. spinulosa* could be inhibited or even prevented, and fecundity possibly reduced, by dense populations of the brittle star *Ophiothrix fragilis*.

d. Wider effects on the environment

No information on this subject was found.

C. MODIOLUS MODIOLUS

1. Biology

a. Reproduction, development and growth

Many aspects of the reproduction, development and growth of *Modiolus* seem to be highly variable.

i. Spawning season

The spawning season is often ill defined, and may vary greatly with depth (Schweinitz & Lutz, 1976) and probably with latitude (water temperature). Populations in Strangford Lough showed no pronounced annual cycle, with a slow release of gametes throughout the year (Brown & Seed, 1977; Seed & Brown, 1975; Seed & Brown, 1977). The geographically very close population off the south east of the Isle of Man showed clear annual cycles in gonad development and in recruitment, with a likely maximal spawning in spring and summer, although probably occurring to some degree all year (Jasim & Brand, 1989). Populations in Scotland also showed variable reproductive seasonalities, and again some showed strong seasonality, with spawning occurring typically in the spring and early summer (Comely, 1978; Comely, 1981). Reproduction in populations in northern Norway and Sweden seems to be controlled by temperature, with a strong peak of spawning in June (Brown, 1984).

ii. Larval development, settlement and recruitment

Little is known about larval stages but the planktonic stage is thought to be extremely long (Ocklemann, 1965), suggesting that recruitment may be possible from distant populations (Brown, 1984). Preliminary genetic work using enzyme electrophoresis on a population off the south east of the Isle of Man appeared to support this, since the results suggested that recruitment came from several different parent populations (Lewis, unpubl.).

Recruitment of juveniles (spat) is very variable, not only seasonally, but probably also very much between years in many populations. Most early work on recruitment was inferred from size distribution within populations, which is very difficult in such a long-lived and (for much of its life) slow growing species. Bimodal size distributions have usually been found. In some populations such as Strangford Lough, where there does seem to be regular recruitment, this is simply a result of size specific variation in growth and mortality (eg Seed & Brown, 1978), since young *Modiolus* tend to grow quickly in the early years (see below). This was also the case for *Modiolus* in two areas off the south east of the Isle of Man (Jasim, 1986; Jasim & Brand, 1989). Other populations do seem to undergo very irregular recruitment, however. Recent work on the *Modiolus* reef areas to the north east of the Isle of Man suggested that recruitment in many years has been negligible. Very irregular recruitment, with

gaps of many years, has also been reported for Norwegian (Wiborg, 1946; Dahle, 1984 cited in Jasim, 1986) and Canadian populations (Rowell, 1967).

Intuitively it seems likely that enclosed areas, such as the Strangford Lough cSAC, and Scottish sea lochs and Voes, must be largely self sustaining, but this may not be the case for more open areas such as the Lleyn Peninsula and the Sarnau cSAC. Preliminary unpublished genetic work at Port Erin Marine Laboratory has suggested that the beds off the south east of the Isle of Man may recruit largely from other areas in a somewhat sporadic way.

Settlement can be very dense, as sometimes seems to occur in populations in the Bristol Channel. Recruitment to adult populations is very strongly limited by predation in the early years however; the Bristol Channel juveniles do not seem to recruit well, for example.

iii. Growth

Studies by Anwar et al. (1990) showed that growth is very rapid in the first four to six years, at which age they reach a length of 35-40 mm, after which they are less vulnerable to attack by predators. Only the very largest crabs and starfish can open mussels over 50 mm in length, and large *Modiolus* are thought to be relatively predator free.

A wide variety of growth rates has been reported, with some relatively fast growing young populations (eg on rigs in the Bravo Forties oil field in the North Sea), where fast growing populations of animals up to 10 years old occur. Particularly slow growing populations have been reported in the Firth of Lorne (Comely, 1978), and in nearshore populations off the south east of the Isle of Man (Jasim, 1986), where average lengths of 70 mm or less are reached at an estimated age of around 20 years. In many populations animals seem typically to reach a length of 100 mm at ages of roughly 12-18 years (eg several populations is the West of Scotland, Shetland, Strangford Lough and around the Isle of Man; (Comely, 1978; Comely, 1981; Holt & Shalla, unpublished; Jasim, 1986; Seed & Brown, 1975)). Maximum sizes in British waters are generally thought to be around 200 mm (Anwar et al., 1990; Brown, 1976).

Rates of development of reefs are not known. There would appear to be some potential for spread of existing bioherms where these take the form of very dense raised beds, as off the Lleyn Peninsula, as a result of clumps of mussels dropping off from the edges, which are often quite discrete. This would undoubtedly be a very slow process taking probably many years per metre of spread. Spread or recovery of more infaunal types of reefs would presumably be slower still, although this is purely speculative.

iv. Maturation

Sexual maturity occurs at around 35-40, and the mussels are able to divert more resources to reproduction and less to growth (Anwar et al., 1990). The age at which the majority of animals reach sexual maturity has been reported as:

- 3-4 years (Isle of Man; Jasim, 1987);
- 5-6 years (Norway; Wiborg, 1946);
- 4 years, but reaching full gonad maturity at 7-8 years old (Canada; Rowell, 1967).

b. Longevity and stability

Occasional mussels aged up to 35 years are reported in most British populations and ages in excess of twenty five years seem to be very frequent. Maximum ages are likely to be well in excess of 50 years (Anwar et al., 1990).

Dense reefs and beds are thought in general to be very stable in the long term, despite somewhat intermittent recruitment in some cases. This is based upon observations that reefs are consistently found in the same place over long time periods, but to what degree the *Modiolus* population structure, physical nature of the reefs, or the associated community structure might vary does not appear to have been studied. The variable nature of recruitment in at least some populations demonstrates that some variation in *Modiolus* population structure, but this has not been described in any detail.

c. Feeding

Modiolus is a filter feeder, although considerably less work has been done on mechanisms and influences on feeding rates than in *Mytilus*. It has been shown that *Modiolus* remove particles over a wide size range, and that considerable amounts of pseudofaeces as well as faeces can be produced (Navarro & Thompson, 1997). See *Ecological Functioning* below for further information.

d. Parasites and diseases

No detailed information was found on this subject regarding *Modiolus*, although it is known that the boring sponge *Cliona celata* can badly damage the shells of old *Modiolus* (Comely, 1978).

2. Ecological Functioning

a. Reef habitats

The communities associated with *Modiolus* are known generally to be extremely rich and diverse. There are clearly variations in composition of associated species. No species are known to be limited in distribution only to *Modiolus* reefs.

i. Richness and diversity

Brown & Seed (1977) recorded 90 invertebrate taxa associated with *Modiolus* clumps in Strangford Lough, with most of the major groups well represented. Holt & Shalla (unpublished) found 270 invertebrate taxa associated with *Modiolus* reef areas to the north east of the Isle of Man, and suggested that this was likely to be an underestimate, particularly in terms of sponges and infauna.

In the Gulf of Maine it has been found that the diversity of other benthic species increased as *Modiolus* clump size and number increased (Ojeda & Dearborn, 1989). From limited data plus subjective observations it seems likely that this would be the case in British waters, and moreover that reef areas would have a more diverse fauna than non-reef areas, but at present this has not been conclusively demonstrated.

ii. Community and habitat descriptions - general

Apart from the infauna, the *Modiolus* community in Strangford Lough has been described as consisting of mainly three components (Magorrian, 1996), and this description probably applies to any *Modiolus* reef community:

A) Very dense aggregations of living and dead *Modiolus* shells which form the frame work in a single or multiple layers

B) A rich community of free living and sessile epifauna and predators.

C) A very rich and diverse small community which seeks shelter in the crevices between the *Modiolus* shells and byssus threads and flourishes on its rich sediment.

Sponges, ascidians, *Alcyonium digitatum*, *Chlamys varia*, *Aequipecten opercularis*, hydroids, and *Ophiothrix fragilis* are all frequent or abundant in some, but not all, *Modiolus* communities. Urchins, starfish and whelks are numerous on most. In shallower areas red seaweeds such as *Phycodrys rubens* and corallines may also be present. It has long been suggested that many *Modiolus* bed communities contain an infauna similar in composition to the Boreal Offshore Gravel Association of Jones (1950), equivalent to the 'deep *Venus*' community (Mackie, 1990) occurring in coarse sand/gravel/shell sediments at depths of 40-100m, with typical species including the urchin *Spatangus purpureus* and bivalves *Glycymeris, Astarte sulcata*, and *Venus* spp.

iii. Community and habitat descriptions - detailed

The MNCR marine biotope classification (Connor et al., 1997) lists many of the epifaunal major species associated with the four *Modiolus* biotopes which could represent biogenic reefs (see Table 1). Indeed, the distinctions between the biotopes are made partially on the basis of the associated communities.

In very sheltered sealochs and Shetland Voes with only slight tidal movement the MNCR has identified a community of '*Modiolus modiolus* beds with fine hydroids and large solitary ascidians' (SCR.ModHas) on very sheltered circalittoral mixed substrata where there is often a high mud content. Decapods such as spider crabs *Hyas araneus*, *Aequipecten opercularis*, and brittlestars such as *Ophiothrix fragilis*, *Ophiocomina nigra* and *Ophiopholis aculeata* may be common. The biotope ModCvar (*Modiolus modiolus* beds with *Chlamys varia*, sponges, hydroids and bryozoans on a slightly tide-swept very sheltered circalittoral mixed substrata), so far reported only from Strangford Lough (a cSAC), is a richer version with far more sponges including several species of *Mycale*, *Haliclona* spp, *Spanaplion armaturum* and *Iophon hyndmani*, hydroids, and *Chlamys varia*. No descriptions of the infauna of these communities were found.

The other two relevant MNCR communities (MCR.ModT; *Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata and CMX.ModMx; *Modiolus modiolus* beds on circalittoral mixed sediment) are also similar to each other, being distinguished mainly by the presence in the latter of much sediment in which venerid bivalves typical of the 'deep *Venus*' infaunal community occur. Sponges such as *Hemimycale columella*, hydroids such as *Sertularia argentea*, *Hydrallmania falcata* and *Abietinaria abietina*, *Alcyonium digitatum*, barnacles, tubeworms *Pomatoceros triqueter*, bryozoans such as *Alcyonidium mytili* and ascidians such as *Dendrodoa grossularia* tend to be typical of the epifauna. These community (MCR.ModT) appears to be widespread, being reported from the Shetland Voes, the Humber, the Bristol Channel, the Lleyn Peninsula (within the cSAC), Northern Ireland, including off the Ards Peninsula, and some of the Scottish

Sealochs including within the Loch Duich, Long and Alsh cSAC. The latter is reported off North East England (this probably occurs within the Berwickshire and North Northumberland cSAC, though this is unclear on presently available information), off the Ards peninsula and south east of the Isle of Man.

The reefs north east of the Isle of Man seem to combine elements of both of the above communities (MCR.ModT and CMX.ModMx), with the addition of considerable numbers of *Chlamys varia* and smaller numbers of *Chlamys distorta* and *Aequipecten opercularis*. The more prominent free living epifauna identified by Holt & Shalla (unpublished) included whelks, topshells, nudibranchs, starfish, sea urchins, brittle stars, and many decapods. Sessile epifauna included many prominent hydroids and bryozoans, anemones, *Alcyonium digitatum*, serpulid worms, barnacles, saddle oysters and sponges. There were also several species of fish including numerous dragonets (*Callionymus lyra*) lesser spotted dog fish (*Scyliorhinus caniculus*), butterfish (*Pholis gunnellus*) and occasional sea scorpions (possibly *Taurulus bubalis*).

iv. Possible roles as nursery grounds

The possible role of *Modiolus* reef communities in providing a nursery refuge for other species is occasionally mentioned but does not appear to have been investigated. Dense growths of bushy hydroids and bryozoans could conceivably provide an important settling area for spat of bivalves such as *Pecten maximus* and *Aequipecten opercularis*, adults of which are often abundant in nearby areas.

b. Predators

Predators are significant mainly in young animals, and appear to be of great importance in determining survival of juveniles to adulthood. Predation in the early years is probably largely by crabs and starfish, which are very numerous on most *Modiolus* beds and reefs, and it is suspected that survival is greatly enhanced by juveniles living within the mass of adult's byssus threads where predators can not easily get them (Anwar et al., 1990). Only the very largest crabs and starfish can open mussels over 50 mm in length, and large *Modiolus* are thought to be relatively predator free. *Modiolus* grows rapidly in the early years, which is thought to be important in enhancing survival to adulthood (see earlier).

c. Competitors

No mention of competitors of *Modiolus* was found during this study. However, it is known that the brittle star *Ophiothrix fragilis* can occur in high densities in similar areas to *Modiolus* reefs; that it is prone to large population fluctuations;, and that high densities of *Ophiothrix* are strongly suspected to have reduced growth and recruitment of *Sabellaria spinulosa* reefs in the Bristol Channel (see also 'food limitation', chapter V).

d. Wider effects on the environment

Modiolus reefs may be very extensive, and often include many other filter feeders such as sponges, hydroids, bryozoans, soft corals, brittlestars, bivalves and ascidians, and so are probably of great importance in channelling organic material between the plankton and the benthos (usually referred to in the literature as 'benthic-pelagic coupling'), although there appear as yet to have been no detailed publications on this aspect of *Modiolus* reefs in British waters.

The majority of the work on this subject has been concentrated in the Bay of Fundy by Wildish and co-workers and is briefly summarised here. *Modiolus* in this area forms

'bioherms', often with relatively low densities of actual *Modiolus* (see chapters I & II), but covering extensive areas. Mixing processes allow *Modiolus* to feed on live phytoplankton down to 100 m depth, and it is the largest contributor to secondary benthic production (Wildish & Fader, in press); biodeposition via faeces and pseudofaeces (up to 41 mg dry weight per animal per day, mainly in the form of large diatoms) is a major mechanism in providing organic material and other nutrients to deposit and suspension feeders (Navarro & Thompson, 1997). It has been suggested from flume tank experiments that seston concentrations will be depleted directly over dense *Modiolus* beds where water flow is low, and that this can be identified in the field by a decrease in mussel bed density (Wildish & Kristmanson, 1984; Wildish & Kristmanson, 1985). No comparable work was found on British *Modiolus* communities, although similar suggestions have been made for *Mytilus*.

D. MYTILUS EDULIS

1. Biology

a. Reproduction, development and growth

A discussion of the reproductive biology of *Mytilus edulis* is found in Seed & Suchanek (1992), including an account of larval ecology (Lutz & Kennish, 1992).

i. Spawning season and fecundity

Many populations of *M. edulis* exhibit some spawning all year round, with major peaks of spawning in spring and often a number of further 'opportunist' spawnings later in the summer, with more restricted spawning periods where adult feeding conditions are poor. Spawning on the west coast of Britain occurs a few weeks earlier than on the colder east coast (Seed & Suchanek, 1992). Reproductive output (see below) is size and site related, and is also influenced by temperature, food supply and tidal exposure; 10-fold variations in reproductive effort have been recorded from six contrasted sites on the English and Welsh coasts (Bayne et al., 1983). Fecundity also varies from year to year, probably reflecting adjustments to energy allocations according to variation in food supply (Thompson, 1979, working in the North west Atlantic).

ii. Larval development, settlement and recruitment

Larval growth to metamorphosis during spring and early summer, at around 10° C, normally takes about 2-4 weeks (Lane et al., 1985; Seed, 1976; Seed & Suchanek, 1992; Widdows, 1991). Under optimum conditions it may take 20 days or less (Bayne, 1965; Seed & Suchanek, 1992; Sprung, 1984a; Sprung, 1984b). Temperature is probably the main influence on the duration of metamorphic delay, with longer delays at lower temperatures (Strathman, 1987), but salinity, food supply and non-availability of suitable substratum may also delay settlement, and larval life may last for up to three months (Widdows, 1991) or even over six months in some cases (Lane et al., 1985). Once the larvae reach the pediveliger stage and they are competent to settle metamorphosis can be delayed for up to 7 weeks. Upon settling the young mussels are known as spat.

M. edulis has a two-stage extended dispersal strategy. A primary settlement of post-larvae usually settles onto sublittoral filamentous substrata such as hydroids and algae. Then, after growing to around 1-2 mm in length, the spat detach and move to the adult beds, aided by the secretion of long byssus threads which help the young mussels to drift in the water until a secondary settlement site is found. In some cases beds of filamentous algae such as *Polysiphonia, Corallina* and *Mastocarpus* seem to provide a pool of young mussels which might account for some of the sporadic recruitment seen in some places. However, it has

become apparent recently that sometimes only a single settlement may occur, directly onto adult beds (e.g. King et al., 1990), and further study is needed to fully understand settlement and recruitment processes (see Seed & Suchanek, 1992 and Lutz & Kennish, 1992 for further information and references).

Spatfall and recruitment in some beds of mussels is very variable year on year. An exceptional (at least for the area concerned) spatfall on parts of the Cumbrian coast was reported to consist of densities of up to 175,500 m⁻² (Perkins, 1987; Perkins, 1988). Unlike some other invertebrates, high densities of the adults do not inhibit the settlement of spat (Commito, 1987). Persistent stable beds can be maintained by relatively modest spat recruitment into the crevices and shelter of the byssal threads of the adults. McGrorty et al. (1990) demonstrated that in stable beds in the Exe Estuary, recruitment to adult populations was relatively unaffected by very large variations in spatfall - during the period 1976 - 1983 spat recruitment varied by a factor of 17 (min - max), but adult numbers varied by only 1.5 suggesting strong damping over the first year (McGrorty et al., 1990). First winter mortality averaged 68%. The adults suffered large losses (mean 39%) after spawning and 24% winter mortality mainly due to bird predation.

There have been several co-operative attempts to compare recruitment at different locations along European coasts (see Dijkema, 1992), though there are staff resource implications in doing this. Recruitment is favoured by cold preceding winters caused by decreases in predator populations and delays in the arrival of newly settled crabs and shrimps on the flats which allows the spat to reach a larger size before the onset of predation.

iii. Growth and production

Growth and production rates within Mytilus biogenic reefs can be extremely high. In a population in Morecambe Bay, which is characterised by high rates of mortality, the production by two year classes was calculated as 2.5 to 3 times their maximum standing crop; most of this was by first-year mussels and production had virtually ceased after sixteen months, with few mussels surviving beyond the third year (Dare, 1976). Low shore mussels in favourable areas can grow to 3.5 - 4 cm in 30 weeks (Orton, 1914) and to 60-80 mm in length within 2 years (Seed, 1976). Such rapid production and turnover seems to be a characteristic of many of the biogenic *Mytilus* communities in estuarine and other enclosed areas. Over a one year period Craeymeersch et al. (1986) estimated production on an intertidal bed in the Eastern Scheldt to have been 156g AFDW / m^2 and the P:B ratio to have been 0.5. By means of cage exclosure experiments Egerrup & Laursen (1992) estimated that annual predation on a mussel bed in the Danish Wadden Sea was 116 g AFDW / m^2 from a mean annual biomass of 740 g AFDW / m^2 . This was equivalent to 17% of the biomass and 81% of the secondary production. The most important predators were eider and oystercatcher. Crab predation was thought to have been insignificant in this experiment on an established bed. Self-thinning as mussels grow is also reported as there are limits to multilayered packing (Hughes & Griffiths, 1988), although in flat bed situations, the fate of displaced mussels is not clear. It is possible that they can wash to locations where they can embyss again.

The above figures contrast with rates on higher rocky shore areas where *M. edulis* might only reach 20-30 mm after 15-20 years (Seed, 1976).

iv. Maturation

In contrast to Modiolus, Mytilus can reproduce in its first year of life (Seed & Brown, 1977).

b. Longevity and stability

i. Longevity of individuals and reefs

Mussels are capable of living to very old ages in certain conditions and *Mytilus edulis* has been reported as reaching 18-24 years in the Danish Wadden Sea (Thiesen, 1968). However, it seems likely that the majority of animals in biogenic reef areas are very young, since these reefs have a tendency to grow rapidly and be detached by water movement when they become well developed. There are areas in Morecambe Bay, and probably elsewhere, which regularly (though not invariably) receive heavy juvenile recruitment but which rarely develop into true beds, losses probably being attributed to a mixture of predation and loss to wave action later in the year. Many biogenic reefs probably consist largely of mussels up to two or three years of age (Dare, 1976; Seed, 1976) (see also chapter I). In some cases heavy predation by starfish and birds is probably also partly responsible for this (see later). However, more stable reefs do occur in smaller, sheltered estuaries (see the example of the Exe Estuary in the discussion on recruitment, section a).

Over time, beds in particular places may for natural reasons vary in the positions they occupy on the continuum between thin, patchy beds and well developed reefs. Particularly at times when the biomass of mussels is high, mounds may form. When stocks are low for whatever reason the mounds may barely be detectable. Because mussel mud is highly cohesive, once it has consolidated, the deposits may last for years after the mussels have largely gone.

ii. Long-term stability

Four surveys of the extent of intertidal mussel beds in the German part of the Wadden Sea since 1949 showed that the distribution of the beds remained rather constant, although the abundance of the mussels varied considerably due to irregular mass spatfalls, ice drift, storm surges and parasitism (Obert & Michaelis, 1991). During the 1980s the mussel populations declined due to the co-occurrence of increasing eider predation, intensification of the mussel fishery and a series of ice winters. Niels & Thiel (1993) using aerial surveys make a clear distinction between persistent beds in relatively sheltered situations and beds in exposed situations in the Schleswig-Holstein part of the Wadden Sea. Using records from 1937, 1968 and 1978 to compare with those from 1989-1991 they indicated that there were great similarities in the extent of the persistent beds over the long-term. In the Dutch parts of the Wadden Sea the distribution of the beds also remained relatively constant over the 1949 - 1988 period, though figures given by Dankers & Koelemaij (1989) indicate the overall biomass of mussels varying by a factor of over 30.

In the Danish part of the Wadden Sea Jensen (1992) showed that there no obvious differences between macrobenthos populations present in the 1930s and in the 1980s. There was no difference at all in cockle growth rates between the 1930s and the 1980s in situations not directly influenced by terrestrial run-off, but some observations suggested that mussels had extended their range along the low water line.

iii. Small scale movements

It is widely recognised that *Mytilus*, although apparently sedentary, can actually move appreciable distances to readjust positions within clumps or to resurface when covered by sand. However, when Raffaelli et al. (1990) created large numbers of small bare patches ($5-140 \text{ cm}^2$) in dense mussel beds in the Ythan estuary, to simulate patches made by feeding eider, they observed that mussels rarely encroached back onto them over 30-50 day periods.

c. Feeding

There has been a great deal of work on the feeding ecology of *Mytilus*. For an introduction to this subject and other aspects of *Mytilus* physiology the reader is referred to Hawkins & Bayne (1992). *M. edulis* is a filter feeder capable of removing particles down to 2-3 μ m with 80-100% efficiency (MØhlenberg & Riisgåd, 1977), and which shows a great range of adaptations to changing conditions, including the ability to regulate filtration rates, ingestion rates and the production of pseudofaeces dependent upon the quantity and quality of plankton and other particulate matter in the water (with a near immediate response), physiological adaptations to changing nutrient conditions (usually taking days or weeks), and morphological changes to filtration apparatus (months). Organic and bacterial food sources adhering to particles and resuspended benthic algae and other organic matter may also be important as food sources.

d. Parasites and diseases

There is a wide range of known diseases, and more especially parasites, of *Mytilus* which probably represents the amount of work carried out on *Mytilus* rather than any special susceptibilities. These have been reviewed by Bower (1992). Those which are, or have been, considered to be most important are considered below.

i. Trematodes

It is thought that trematodes of the families Bucephalidae and Fellodostomidae, which use mussels as primary hosts, are among the more serious parasites. Some of these are known to cause a wide range of problems including parasitic castration and death, (Cousteau et al., 1990; Feng, 1988), and on occasion mass mortalities (Munford et al., 1981) in *Mytilus edulis* and other mussels. Mussels higher on the shore contain have a higher incidence of parasitism by a trematode for which the oystercatcher is the next host, but the true importance of this parasite is unclear. The supposition that mussels suffer less in general from parasites (and diseases) than oysters is probably an artefact of the shorter history of intensive cultivation (Bower, 1992).

ii. Polydora ciliata

Another important parasite is the polychaete *Polydora ciliata*, which burrows into the shell, weakening it and rendering the mussel more susceptible to predation by birds and shore crabs. This may cause particular problems for mussels greater than 6 cm in length (Kent, 1989), which when healthy are normally relatively free of predation, and can cause substantial mortalities (Lauckner, 1983).

iii. Mytilicola intestinalis

The parasitic copepod *Mytilicola intestinalis* is widely prevalent in *M. edulis*, and mass mortalities of cultivated mussels have often been attributed to it, but a ten year study carried out in Cornwall suggested that *M. intestinalis* may be a commensal rather than a harmful parasite (Davey, 1989), and the true position is unclear (Bower, 1992).

2. Ecological Functioning

a. Reef habitats

The associated biota of *Mytilus* reefs has been little studied, but does not appear generally to be particularly rich or diverse in comparison with stable subtidal biogenic reefs such as those of *Modiolus* or *Serpula vermicularis*, *S. alveolata* in the Severn Estuary, and possibly the more stable examples of *S. spinulosa* reefs. Nevertheless, these often represent the only hard

substrate communities in the area, so that they may be regarded as important in terms of increased habitat heterogeneity. A variety of small infaunal invertebrates is found within the accumulations of mussel mud, with some larger mobile animals such as *Littorina littorea*, *Gammarus* spp, polychaetes and small *Carcinus maenas* in between the mussels and dead shells. These are hunted by foraging birds such as turnstones, curlews, redshank and gulls. The shells themselves may support encrusting fauna such as barnacles, and algae, particularly *Fucus vesiculosus* and sometimes green algae such as *Enteromorpha*, may be frequent. Briggs (1982) found at least 34 species associated with the matrix of partly-infaunal mussel beds in Lough Foyle, of which almost half were crustaceans. Dense beds in intertidal mussel communities in the southern North Sea had only 12 associated species (Asmus, 1987), and this might be more typical of the rapidly growing communities present in the larger *Mytilus* reefs, especially in estuarine areas, although production rates of associated species might still be high.

In other areas, more stable and long-lived *Mytilus* beds such as those found on moderately exposed rock surfaces probably build up much more diverse associated communities, with typically 50-100 species (see Seed, 1996 for a review) although many of these would probably not be regarded as biogenic reefs.

A consequence of enhanced biodeposition of labile organic matter is that mussel mounds have more deposit feeding oligochaetes than the surrounding flats (Dittmann, 1990).

Newcombe (1935) pointed out that sediments below dense mussel beds can become more anoxic, leading to the loss of some infaunal bivalve species such as *Mya arenaria*.

It has also been suggested that the high rate of suspension feeding in the mussel mounds favours species that reproduce with cocoons, brood the young, or which disperse as juveniles rather than as planktonic larvae (Commito, 1987).

b. Predators

On permanently submerged offshore structures, fewer predators and the opportunity for continuous feeding are thought to be the factors which accounts for the success of M. *edulis* in creating very dense aggregations of large mussels. It is possible that relative lack of predators in some enclosed, especially more estuarine, areas might thus be partly responsible for the build up of reefs in these areas.

i. Invertebrates

A number of invertebrate predators can be very important in regulating *Mytilus* populations, particularly crabs and starfish. On parts of the east coast of England the lower limits of *M. edulis* beds are controlled by predation by *Asterias rubens* and *Nucella lapillus*, although the latter may be more important in exposed than in sheltered areas (Seed, 1969); gastropods, unlike starfish, were not regarded as important predators of *Mytilus* in Morecambe Bay (Dare, 1976) nor in the Wash (Dare, pers. comm.) or the Danish Wadden Sea (Thiesen, 1968). In Ireland *Liocarcinus, Carcinus, Nucella* and *Marthasterias* are thought the most likely candidates to control the lower limits of mussel beds (Kitching & Ebling, 1967). Crab-proof cages on the shore in the Menai Strait resulted in good survival of *M. edulis* whereas in unprotected control areas there was very rapid loss of all live mussels due to predation by *Carcinus maenas* (Davies et al., 1980). Work in Nova Scotia has demonstrated that there is an upper size limit of around 70 mm in length for predation by *C. maenas* on *M. edulis*, although in the UK most mussels longer than 45 mm are probably safe (Davies et al., 1980) In Washington State Suchanek (1981) observed 'herds' of roaming starfish *Pisaster ochraceus* eliminating large beds of *M. edulis* in days. Similar rapid destruction of *Mytilus* beds by

Asterias has been observed on rocky shores in Europe (Seed, 1969) and on boulder scars around MLWST in Morecambe Bay. In the latter case, *Asterias* has been found at densities up to 450 m⁻², and the swarm, which covered up to 2.25 ha at one time, may have cleared up to 4,000 tonnes of first year mussels between June and September (Dare, 1976; Dare, 1982). In the Wash, *Asterias* destroys most sublittoral settlements each year, and also attacks cultivated plots at or below MLWST. These predatory species are sensitive to desiccation so that mussels have a spatial refuge on the shore above MLWNT.

Invertebrate predators of reef-forming bivalves including Mytilus are reviewed in Seed (1993).

<u>ii. Flatfish</u>

Other important predators include flatfish; in Morecambe Bay, flounders were found to contain the remains of up to 570 (average 150) small mussels (up to 15 mm in length) per fish, and plaice and dabs were similarly important (Dare, 1976). Flounders have also been found to be important predators of mussels in Liverpool Docks (Hawkins, pers. comm.)

iii. Birds

Bird predation on mussels can also be important, and may significantly affect the development of reefs. It has been studied extensively (see reviews in Seed & Suchanek, 1992, and Meire, 1993). Oystercatchers and eider ducks are very widely reported as feeding extensively on Mytilus, and may be responsible for heavy mortalities in wave protected bays and estuaries (Seed & Suchanek, 1992). Eider are also sometimes regarded as a nuisance on submerged mussel farms. More than 60% of the adult eider diet may consist of mussels (Seed & Suchanek, 1992). Knot, turnstones, sandpipers, herring gulls and even crows are also known to feed on intertidal mussels, while scoters also dive for small mussels. In Morecambe Bay, Dare (1976) identified oystercatchers, herring gulls, eider ducks and knot as major sources of Mytilus edulis mortality. There were differences in the size range of Mytilus taken, with knot being important when the mussels were only a few mm long, herring gulls at around 3-20 mm length, and oystercatchers and eiders at larger sizes. For eiders, Raffaelli et al. (1990) reported a rather smaller preferred size of 10-25 mm in the Ythan estuary, where over a 60 day period a flock of 500 removed approximately 36% of the larger mussels (6-30 mm). They also reported that eider feed by removing large clumps, leaving bare patches on the rock. Many of the *Mytilus* which are shaken from these clumps but not eaten may die later. Taking this into account, they calculated that a flock of around 500 eiders probably removed around 4,000 m² of mussels (around 25% of the mussel bed under study), during November of the study year. Eiders are known to be present all year around, but there are reduced numbers during winter and a rapid rise during spring, often to over 4,000, when females especially feed voraciously, in preparation for a long fast over their incubation period (Baird & Milne, 1981; Raffaelli et al., 1990). Baird & Milne (1981) reported that in the Ythan estuary, bird predation accounted for 72% of the annual M. edulis production (other predators being negligible in these terms) with flocks of over 4000 eider being responsible for 42% and oystercatchers and herring gulls 15% each. It was concluded by Raffaelli et al. (1990) that direct and indirect mortality caused a significant impact upon the population dynamics of *M. edulis*, although there was surprisingly little evidence of significant impact upon the associated invertebrate community. The likelihood that areas of mussel beds from which clumps had been removed could be more susceptible to subsequent removal by water movement was not mentioned, perhaps because the Ythan is a sheltered estuary, but this would appear to be a possibility; the disruption of the integrity of mussel clumps on mussel ropes is recognised as an important side effect of eider predation. Hosomi (1984) noted that the tendency of M. galloprovincialis to recruit strongly around edges as well as upon individuals of established beds might serve to reduce the removal of mussels by wave action.

Mytilus is often a staple food of oystercatchers in the winter. In the east Scheldt, Holland, 40% of the annual mussel production is consumed by oystercatchers (Meire & Ervynck, 1986), and mussel production is probably the major limiting factor for density of overwintering flocks (Craeymeersch et al., 1986). In Conway, North Wales, oystercatchers were found to consume up to 574 mussels (average length 25.7 mm) or 186 mussels (average 37.5 mm) each in a low tide (Drinnan, 1958). Considerable selection by oystercatchers has been shown against mussels which are barnacle encrusted, thick shelled or otherwise difficult to open (Leopold et al., 1989; Meire & Ervynck, 1986).

It is clear that bird predation may significantly affect the quality of biogenic reefs.

iv. Effects of cold winters on bird predation

Crisp (1964) noted that, although *M. edulis* was relatively unaffected by unusually low temperatures, there was an increased mortality due to predation on mussels by birds in parts of South Wales. It was thought that the cold may have rendered some species, including mussels, too torpid to resist attack by birds. In the same paper it was observed that there were heavy mortalities of cockles *Cardium edule* in the Solway Firth caused by oystercatchers and gulls "for whom they offered during one period the only accessible food", and heavy predation on moribund cockles by oystercatchers in Morecambe Bay was noted. The possibility of increased foraging in intertidal areas by birds during extremely cold weather must therefore also be considered.

v. Other predators

In addition to the species already mentioned, a wide variety of other organisms have been found to be important predators on mytilids in some circumstances, including limpets, predatory gastropods, *Cancer*, lobsters, urchins, fish, otters, seals and even walrus and turtles (see relevant references in Seed & Suchanek, 1992), and pink shrimp *Pandalus montagui* take spat in the Wash (Dare, pers. comm.) but none of these are likely to be of major importance in the main areas of biogenic *M. edulis* reefs.

c. Competitors

Possible competitive interactions between *Mytilus* and *Sabellaria alveolata* have been discussed in the relevant section above on *S. alveolata*. These interactions tend to occur on more exposed boulder scars where mussel have less tendency to form well developed reefs, and so are probably more important with regard to the *Sabellaria* reefs than *Mytilus* reefs.

d. Wider effects on the environment

i. Effects on the water column

It has often been established that the efficient removal of particles in *Mytilus* beds can deplete the seston available in the benthic boundary layer downstream of them. In some bays the mussel beds are of a scale such that by their filter feeding they play a particularly important role in energy flow over much wider areas than the actual beds. At one level they compete for phytoplankton with beds of cockles that are often on flats inshore. "Rain shadow" effects have been reported. Mussel beds result in significant depletion of phytoplankton at the bottom of the water column (Frechette & Grant, 1991) and function as systems, not just as populations of mussels (Dame & Dankers, 1988). Using a canalised flume system installed on a natural bed in the Wadden Sea, Asmus & Asmus (1991) measured a 37% uptake of phytoplankton passing through the 20 m flume in summer. An equivalent high nutrient release from the bed was also measured. Using a benthic seston sampler Muschenheim & Newell (1992) estimated that on an ebb tide a mussel bed was capable of processing the water over the bed to a depth of 7 cm but allowing for significant refiltration the effective feeding zone was of the order of 3.5 cm. They fed preferentially on high concentrations of resuspended benthic diatoms.

ii. Effects on the sediment

Mytilus reefs have a strong stabilising effect on sediment, for periods varying from a few months to many years, and it has been suggested that in their absence large scale changes to whole estuary complexes may occur (McKay, pers. comm.).

Mussel beds are extremely important in the generation of organically enriched biodeposits that provide nutrition for wide ranges of deposit feeding invertebrates not just in them but over wide areas of tidal flats around them. In the Northern Baltic, Kautsky & Evans (1987) estimated in situ biodeposit production per gram of mussel (dry weight including shell) as 1.76 g or 0.33 g AFDW. During the growing season (April - September) the biodeposit had a higher organic content and a higher nitrogen content than naturally sedimenting material. With the ecologically similar *M. chilensis* the mean annual deposition rate was measured at $234g/m^2/day$ of which 21% was organic matter (Jaramillo et al., 1992). Modification of the benthos and the redox discontinuity under mussels cultivated in suspension has been shown in Gallicia and in Sweden (Mattsson & Linden, 1983). Parallels may be drawn with the generalised patterns of macrobenthic succession accompanying organic over-enrichment as postulated by Pearson & Rosenberg (1978).

75% of the >2mm carbonate fraction of sediments in the Wadden Sea consists of fragmented shells. Eiders crush *Mytilus* internally when feeding and Cadee (1994) suggests that a third to a half of the shell fragments could have been produced in this way.

iii. Bird populations

Mytilus in reefs and beds are clearly of great importance as food for bird populations, particularly eiders and oystercatchers for which *Mytilus* is a stable food for at least part of the year. The interrelationships between birds and mussels are discussed in the sections on predators and competitors above, and reported detrimental effects of low mussel stocks on oystercatchers and eiders are mentioned in chapter VI.

E. SERPULA VERMICULARIS

1. Biology

a. Reproduction, development and growth

There is relatively little published information on reproduction in *Serpula*, and most of what there is comes from non-reef situations.

i. Spawning season

Spawning seems to occur in the summer: Elmhirst (1922) reported that spawning occurs in June to August in the Clyde Sea area, and Allen (1915) found ripe specimens in the Plymouth area in August and September.

ii. Larval development and settlement

In Ardbear Lough, Bosence (1979) found dense settlement of larvae onto plates in August, but did not carry out investigations at any other times. Nelson-Smith (1967) states that no serpulids settle in winter in temperate areas, though settlement may extend throughout the summer. Length of the planktonic stage is unknown but comparison with other serpulids suggests it may be between six days and two months, although in other species the period has

been shown to vary with season, salinity or food availability, and delayed settling may cause reduced discrimination of substrata during settling (see ten Hove, 1979 for additional references). Settlement preferences have been discussed in chapter III.

iii. Growth rates

Growth and development of individuals seem to be relatively fast. Bosence (1979) found a mean tube growth of 9 mm in length over a one month period (August 1972), and described growth as periodic due to the presence of trumpet like enlargements on the tubes. It seems likely that these would be annual features, suggesting a lifespan of several years, but no published evidence to support this supposition has yet been found. Moore (unpublished) found that initially bare substrata could support dense aggregations of up to an estimated 15 cm in height after around three months.

Nothing has been published on the development rates of *S. vermicularis* reefs, which presumably take many years.

iv. Maturation

Given the rapid growth rates achieved, it seems likely that the worms would reach adult size, and probably maturity, within one year, as is normal within the serpulids. Orton (1914) observed that ten month old specimens in the south west of England could successfully reproduce.

b. Longevity and stability

The longevity of reefs is unknown, but it appears that they must take many years, and possibly decades, to develop to the extent of the larger reefs observed. Nothing is known about the proportion of small colonies which actually succeed in developing into large reefs. From the external growth structures on tubes it seems likely that individual worms seem to be capable of living for several years (see above).

c. Feeding

S. vermicularis is a filter feeder and the arrangement of its tubes in reefs is such that interference between adjacent crowns is avoided. No details have been found regarding the mechanism of feeding or the type of food taken but the presence of laminarase, chitinase and cellulase in its digestive system (Michel & De Villez, 1978) suggests that quite large detrital particles may form an important part of the diet.

d. Parasites and diseases

The boring sponge *Cliona celata* appears to significantly weaken the reef structure as the colony ages, but the main result of this seems to be that sections of older reefs fall away and form a nucleus for subsequent colonisation and growth, thus allowing reef development on areas where there may have previously been no suitable substratum (Bosence, 1979). Worms on fallen sections were reported to respond by growing away from the substratum.

a. Reef habitats

S. vermicularis reefs act as a substratum for a wide variety of other organisms. These include numerous sessile organisms such as boring, encrusting sponges and massive sponges, ascidians and hydroids, the serpulid Pomatoceros triqueter, spirorbid and other tube worms, numerous encrusting bryozoans, the anemone Metridium senile, and numerous bivalves such as Monia patelliformis, Modiolus modiolus, Chlamys distorta, C. varia and Aequipecten opercularis (though many of the pectinids may only be temporary inhabitants) (Bosence, 1979; Howson et al., 1994; Connor et al., 1997). In shallow water dense growths of the red alga Phycodrys rubens may occur on the reefs. Mobile inhabitants which have been reported include numerous crab and other crustacean species, the urchins Echinus esculentus and Psammechinus miliaris, the brittle star Ophiothrix fragilis, the starfish Asterias rubens, and the whelk Buccinum undatum. The richness of the associated community is not surprising given the relatively open structure of the reefs and the lack of hard substrata in the areas where it is found. The MNCR marine biotope classification lists 34 species as occurring in at least 40% of records for S. vermicularis reefs. A further species, the tunicate Pyura microcosmus, reportedly occurred in only 20-40% of records but was described as highly faithful (i.e. found only in this or very closely related biotopes). Knowledge of associated biota is largely limited to macrofauna which can be observed on the outside of reefs. Investigations including more cryptic fauna are likely to reveal an even greater richness and diversity than presently known. Even very small 'heads' of serpulids (Pomatoceros spp), such as form on single shells in many sublittoral areas, have been reported to contain up to 68 taxa (Kaiser et al., in press); many of these were polychaetes, though isopods, amphipods and sipunculid worms were also important.

Bosence (1979) estimated that in Ardbear Lough, Ireland, about 5% of the Lough floor would have been hard substrate in the absence of reefs, but that the development of reefs had increased this to around 25%.

b. Wider effects on the environment

Other than the relatively local increase in hard substrate (see previous paragraph) no information on this subject was found. Given that reefs seem to develop only in enclosed areas with very limited water exchange, wider effects can only be expected within these limited areas, if at all. Since *S. vermicularis* is a filter feeder, extensive areas might have the potential to have effects on phytoplankton levels, but this is merely speculation.

c. Predators

d. Competitors

Although no competitors are known in relation to existing reefs, lack of competition for space was suggested by Bosence (1979) as one of the factors leading to reef development in enclosed sea lochs, along with limited water exchange leading to increased larval supply. The implication is that space occupiers such as algae, barnacles or mussels might, in some circumstances, prevent development of reefs.

F. KEY POINTS FROM CHAPTER IV

Information from this chapter is here summarised in tabular (Table 5) and textual form (overleaf).

Table 5 Summary information relating to environmental requirements and physical fragility for each biogenic reef species. This information relates as far as possible to biogenic reef biotopes and not necessarily to other biotopes in which the species may be found.

	S. alveolata	S. spinulosa	M. modiolus	M. edulis	S. vermicularis
BIOLOGY					
Reproduction, development and growth	Sexually mature in 1st yr. Recruitment very variable. Settlement strongly induced by contact with adult tubes (living or dead). Growth rapid.	Sexually mature in 1st yr. Recruitment often seems variable. Settlement induced by contact with adult tubes, living or dead. Growth rapid.	Sexual maturity at 3- 6yrs. Recruitment often variable Juveniles survive best within byssus of adults. Growth rates variable, rapid in first 4-6 years.	Sexually mature in 1st year. Settlement often in 2 stages. Recruitment highly variable. Growth rapid, measured production rates high.	Sexually mature in 1st yr. Preferential settlement on calcareous structures. Growth rapid.
Longevity and stability	Typically worms reach 4-5 years but can be 9-10. Reefs v. variable in extent & cover though tend to recur on the same shores in the long term.	Individuals can be more than 1 yr old but max unknown. Many communities are annual but more stable reef areas do seem to occur, though rarer.	Individuals commonly over 25 years and may be over 50 in some cases. Reefs seem to be very stable	<i>Mytilus</i> can be 18-24 yrs old but many reefs are largely of mussels up to 2-3 yrs. Density of beds varies, but tend to occupy same areas in long term.	Presumably reefs take many years to develop and are reasonably stable.
Feeding biology	Filter feeder, little information available.	Filter feeder, little information available.	Filter feeder, capable of removing particles over a wide size range.	Filter feeder, takes particles down to 2- 3 μ m. Wide range of long & short-term adaptation to changing conditions	Filter feeder, little information available.
Important parasites and diseases	None known	None known	Shell boring sponge <i>Cliona celata</i> can weaken old shells	Trematodes; shell- boring polychaete Polydora ciliata; copepod Mytilicola intestinalis??	Shell boring sponge <i>Cliona celata</i> can weaken reef but may not be deleterious.
ECOLOGICAL	FUNCTIONING				
Reef habitat / community	Species poor when colonies are young, somewhat richer when older. Often provide increased diversity of habitat.	Stable reef areas probably species rich but annual areas probably less so. More info required.	Very rich & diverse communities of epifauna and infauna.	Generally species poor but provide diversity of habitat in essentially sedimentary areas.	Epifauna & large mobile fauna v. rich & diverse. Info required on cryptic fauna which may also be v rich.
Wider effects on environment	None known	None known	Large areas may reduce phytoplankton levels?. Some possible importance as nursery grounds?	May reduce plankton levels (competition with cockles). Stabilise sand over wide areas, important as food for birds & invertebrates.	None known
Predators	Not known to be v. important on natural reefs. Crabs preyed heavily on trans- plants.	Little info, possibly Pink shrimp <i>Pandalus</i> <i>montagui</i> could be important.	Crabs and starfish important when young, (4-6 yrs), little predation once >50mm long.	Many - starfish, crabs & flatfish on smaller mussels, & birds (esp eider & oystercatchers) on larger ones.	None known
Competitors	<i>Mytilus</i> can be an important competitor.	Dense brittle stars can reduce / inhibit growth & recruitment, presumably by	None known; it can be speculated that dense brittle stars could have detrimental effects	Sabellaria alveolata may compete in some areas, but is of limited importance	Lack of competition for space thought to be a required for reef development,

	preventing feeding and possibly by feeding on larvae.	similar to those on <i>S. spinulosa</i>	in relation to biogenic reefs.	but has not been demonstrated.
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KEY POINTS

- S. alveolata spawn in July. Larval life seems to be long, with settlement occurring mainly over autumn and winter. Settlement is strongly stimulated by the presence of Sabellaria tubes. The worms themselves probably have a typical life cycle of 4 or 5 years (up to 9 or 10) although this might be less on unstable substrata. S. alveolata reefs experience very variable recruitment, which can be extremely heavy on occasion, and undergo cycles of development and decay over a few years, with rapid growth and development of reefs in the first year. Recruitment can be poor for many years, however. In the long term there appears to be a moderate stability, with reefs being found largely in the same areas. There are examples of more transient reefs, however. The richness and diversity of the associated community do not seem to be very remarkable, and seem to vary with the developmental cycle, being very low on dense, young reefs and somewhat higher, with up to 38 species reported on older reefs. There is some evidence of differences in community structure between the different reef forms. Reefs can lead to increased heterogeneity of mobile sediments and stones, exposed barnacle dominated shores and sand scoured rocks, and sheets may impede drainage to form pools. There is little information on predators, which do not seem to have important effects. There is little information on any aspect of subtidal communities.
- S. spinulosa seems in many cases to act more like an annual than S. alveolata, but on more stable reefs the animals seem to be able to live for a few years. Reproductive seasonality is unclear, but spawning probably occurs largely over winter and settlement in early spring. Settlement is stimulated by the presence of S. spinulosa tubes, but not as strongly as in S. alveolata. The commercially valuable pink shrimp Pandalus montagui seems to have a strong association with S. spinulosa reefs. Recruitment is probably variable and can be greatly reduced by dense brittle stars Ophiothrix fragilis, which can also reduce growth and fecundity. Associated communities on reef areas are noticeably richer than surrounding areas but there is presently a lack of detailed information on this subject.
- *M. modiolus* is a very long-lived species and animals in reef communities are frequently 25 years old or more. Spawning seasons are variable, some populations spawning in summer and others more or less all year round. The larvae spend a long time in the plankton and recruitment is slow and sometimes very sporadic, with poor recruitment over a number of years. Although reefs in enclosed sea lochs are probably self recruiting, those from more open areas may not be. Predation rates, especially by crabs and starfish, are high in the early years. *Modiolus* does not mature sexually until it is 3-6 years old, allowing all of its efforts to be directed into rapid growth in the early years. Beyond about 35-40 mm in length predation rates become markedly lower, and sexual maturity occurs around this time. Survival is also enhanced by the habit of *Modiolus* are at a disadvantage in this respect. *Modiolus* has a very strong structuring influence on the sediments in which reef areas usually occur, and extremely rich associated faunas containing hundreds of species have been found.
- *Mytilus edulis*, in contrast to *Modiolus*, spawns in its first year. Under favourable feeding conditions there are a number of spawnings in spring and summer, and settlement occurs usually within a month or so. In some populations there is a primary settlement on filamentous substrata followed by detachment, and subsequent reattachment on adult beds. Recruitment is highly variable from year to year in most places. *Mytilus* can be very long-lived but reef populations are usually only up to two or three years old, with rapid growth

- and high rates of production. Predation is usually very high; fish and invertebrates are important on the lower shore, and often prevent the extension of *Mytilus* beds into the subtidal. Intertidal bird predation, especially by eiders and oystercatchers, can be responsible for up to 72% of the annual mussel production, and mussels form an important part of the diet of these birds. The communities associated with large mussel reefs in bays and estuaries are much less rich and diverse than the older, more stable beds on moderately exposed rocky shores, or than subtidal biogenic reef communities (*Modiolus, S. spinulosa* and *Serpula*), and contain no remarkable species, but may represent the only hard substrate communities over wide areas. They can also provide nutrition in the form of organically enriched biodeposits for wide ranges of deposit feeding invertebrates over wide areas of tidal flats as well as within the reefs. Mussels reefs may have the ability to locally deplete the phytoplankton and may compete with cockle beds in this way.
- Based on limited information, *Serpula vermicularis* probably spawns in summer, and settlement would be expected to be maximal in late summer and early autumn. Growth rates seem to be fast, and *S. vermicularis* probably spawns in its first year. Rate of accumulation of reefs is presumably very slow, requiring many years to reach the maximum sizes observed in Loch Creran. Little is known about feeding ecology. The reefs, being relatively long-lived and stable, and with a relatively open structure affording much crevice habitat, seem to have a very rich associated fauna, but only limited video and diver recording studies have been done. The tunicate *Pyura microcosmus* is reportedly limited largely to this habitat. Predators of *Serpula* include two species of wrasse, and the starfish *Asterias rubens*. Urchins can destroy the tubes but probably not the worms themselves.

V SENSITIVITY TO NATURAL EVENTS

Following Holt et al. (1995), McLeod (1996) and Hiscock (in prep) both sensitivity (the likelihood that an organism or community will suffer damage or death when exposed to an external factor) and vulnerability (the likelihood of exposure to an external factor) have been taken into consideration under the general heading of 'sensitivity' here.

Some repetition between this chapter and chapter IV (biological and ecological functioning) is unavoidable, though this has been minimised as far as possible. In the main, only instances where ecological events or conditions seem likely to have important effects on biogenic reefs are considered here.

A. SABELLARIA ALVEOLATA

1. Factors Affecting Recruitment

Sabellaria alveolata is well known to be extremely variable in recruitment but the reasons for this are not known. A number of possibilities can be mooted speculatively, such as:

- Lowered fecundity due to environmental factors such as temperature, food supply
- Reduced larval supply due to loss of reefs in neighbouring areas
- Lack of larval supply due to the vagaries of water movements

2. Changes to Sand Supply

By virtue of its dependence upon hard substrata adjacent to good supplies of suspended sand, *Sabellaria alveolata* lives in areas which are subject to large scale changes in sand supply, for example as a result of storms. Wilson (1971) reported regular changes in sand depth of a metre or two metres at Duckpool, North Cornwall. *Sabellaria* reefs survived short-term burial for days or even weeks but were killed by long-term burial which is probably a frequent occurrence. Burial of reefs has been recorded on the Cumbrian coast (Perkins, 1967) and is almost certainly a common occurrence elsewhere.

In the Mediterranean Gulf of Valencia, Porras et al. (1996) reported losses of *S. alveolata* reefs due to siltation form river floods and natural accumulation of sand, but that the reefs recovered rapidly (within a few years) in comparison to situations where sand accumulated as a result of human activities.

3. Cold Winters

There were numerous losses of *S. alveolata* due to the cold winter of 1962-63, particularly in North and South Wales and Lyme Bay (Crisp, 1964). Most appeared to have fully recovered by 1984 (Cunningham et al., 1984). *S. alveolata* in Criccieth in North Wales was badly affected by the cold winter of 1984 (Gubbay, 1988). Recent information suggests that recovery may have been only limited by 1995 (CCW, unpublished), although due to the variable and sometimes cyclic nature of *S. alveolata* reefs this conclusion may not be valid if regular monitoring was not carried out in the intervening period. Extensive intertidal reefs are known to have been present in the Dee Estuary (Hilbre Island) in the late nineteenth and early

twentieth centuries (eg Herdman, 1919) but were absent when resurveyed during the 1940's (Craggs, 1982) and 1980's (Cunningham et al., 1984).

Extreme temperatures may also have the potential to indirectly alter community structures. In the North east Pacific, Paine (1986) observed a change between the dominance of M. *californianus* before a severe freeze and M. *edulis* (which is much more tolerant of low temperatures) after. Since there seems frequently to be some competition between S. *alveolata* and *Mytilus edulis*, and these have different temperature tolerances, it is possible that low temperatures might play a part in determining which of these species dominates.

4. Predator Densities

There is little knowledge of predators of *Sabellaria alveolata*, (chapter IV). Sensitivity to changes in predator populations is therefore unclear, but seems unlikely on present knowledge to be an important consideration.

B. SABELLARIA SPINULOSA

Thin crusts of *Sabellaria spinulosa* often act as a fast growing annual and appear to be resilient phenomena. *Sabellaria spinulosa* is often referred to as a pollution indicator (see chapter VI) and seems unlikely to be particularly sensitive to changes in water quality except perhaps in the unlikely event of the supply of sand with which to build its tubes being removed. No published evidence of any strong sensitivity to natural events has been found.

Well developed, more stable reefs seem to be very unusual, and this apparent rarity suggests that an unusual set of environmental factors and/or circumstances is required for their formation. It might, therefore, be expected that they would display sensitivity to some factor or factors, but there is little information from which to gain any insight into this, and the following points are therefore rather speculative.

George & Warwick (1985) have suggested that growth and recruitment of *S. spinulosa* can be inhibited or even prevented by dense populations of the brittle star *Ophiothrix fragilis*, which can occur at very high densities thus preventing adequate food particles from reaching the worms. This is thought to have been the reason behind very low recruitment and growth of *S. spinulosa* in an area of the Bristol Channel in 1976. Fecundity of the adults in the colony was also severely reduced, possibly for the same reason. The possibility that the larvae themselves could be filtered out by very dense *O. fragilis* (or other filter feeders such as *Mytilus*) was not mentioned but should be considered. Using historical data, Holme (1983) found that brittle star beds off Plymouth have undergone large scale changes in density due to the changing fortunes of a predatory starfish, *Luidia ciliaris*, which in turn might be explained in terms of changes in the penetration of oceanic Atlantic water into the English Channel (the 'Russell cycle').

It is likely that stability of the reefs is to some degree a function of stability of the substratum, which could be affected by frequency of storms, for example. The more ephemeral reefs probably occur principally on relatively unstable substrata, while longer lasting reefs might be limited to more stable substrata. Depth and water movement as well as substratum might affect this. It is also possible that regularity of recruitment might be a factor, but there is presently little knowledge of influences on fecundity and recruitment, although they do seem to be variable, at least in some instances (see chapter IV). (Given the long planktonic phase of six weeks to two months, and the probable need for a dense swarm of larvae to be stimulated

to settle by the presence of existing tubes, some variability in recruitment would not be surprising).

Thicker, more established reefs, however initiated, would be more likely to resist breaking up, and possibly more attractive as a settlement substratum, so increasing their likelihood of long-term survival. Given that the worms may live for several years, such reefs might be expected to survive despite occasional years of poor recruitment, as suggested for the Bristol Channel populations studied by George & Warwick (1984). No detailed studies on this topic have been carried out, however, and this is therefore rather speculative.

There is little knowledge of predators of *S. spinulosa* on which to assess likely sensitivity to changes in predator populations.

Michaelis (1978) mentions that during the 1950s *S. spinulosa* "withdrew from the intertidal area of Niedersachsen" (the Waddensee), where "Formerly the 'reefs' of this worm were frequently found on the head of the groins around the East Friesian Islands", but unfortunately offers no explanation. However, the reefs were always apparently sporadic, and intertidal reefs of this worm have not been reported elsewhere (See chapter IV for a summary of Linke's observations in this area during the 1940s).

C. MODIOLUS MODIOLUS

1. Introduction

This section is aimed principally at that part of the range of biotopes containing *Modiolus modiolus* where the horse mussels build up substantial mounds or bioherms, although some aspects may be applicable to biotopes with lower densities of *Modiolus*.

2. Physico-Chemical Events

Spawning and recruitment may well be affected by physico-chemical changes, for example due to resulting affects on feeding conditions (phytoplankton levels), but we have found no detailed information regarding specific sensitivity on this subject, other than basic information already given in chapter III.

3. Biological Events

a. Food limitation

It has often been established that the concentrations of suspension feeders in *Mytilus* beds can deplete the seston available in the benthic boundary layer downstream of them. Wildish & Kristmanson (1984, 1985) measured this effect in flumes with *Modiolus* as well. Thus food limitation of growth might be a problem in years with poor phytoplankton production. Further considerations in this respect might include the effects of *Ophiothrix fragilis*, which often occurs in very dense beds in the same areas as *Modiolus*. Given that *Ophiothrix* are extremely efficient filter feeders, and that this species is prone to large fluctuations in population, it might be speculated that long-term smothering by *Ophiothrix* beds could occur, leading to an inability of the *Modiolus* to feed. George & Warwick (1985) suggested that this was the reason behind very low recruitment and growth of *Sabellaria spinulosa* in the Bristol Channel in 1976.

b. Predation

Predation of young *Modiolus* by crabs and starfish in particular appears to be important, and it is known that at least intertidally predation by *Asterias* particularly can be devastating to *Mytilus* beds. Factors affecting the proportion of young *Modiolus* surviving through to the size at which predation appears no longer to be a serious threat have not been studied, although in comparison with *Mytilus* reefs, which are composed of much younger animals, the effect of one or two 'bad years' of recruitment would be far less serious. It is suspected that juveniles living within the mass of adult byssus threads have greatly enhanced survival, in which case infaunal *Modiolus* could be at a disadvantage since the byssus may be largely inaccessible.

c. Parasites and diseases

We have no knowledge of this subject regarding *Modiolus*, although it is known that the boring sponge *Cliona celata* can badly damage the shells of old *Modiolus* (Comely, 1978).

D. MYTILUS

1. Introduction

Although concern here is primarily with mussel beds as "Biogenic Reefs" of intrinsic conservation interest in their own right, it is recognised that in many places the mussels are of as much importance directly as food for birds and invertebrate predators, or as key functional features of the ecosystems of the large shallow embayments. Responses to natural events here are reviewed primarily in the context of the intrinsic interest of the reef features, but these other contexts also need to be borne in mind.

The presence and scale of the mussel bed mounds is governed by the complex interplay of features that on the one hand cause them to build up and on the other break them down. Stock density is influenced by recruitment, predation and density dependent mortality, together with factors that affect feeding; the production of faeces and growth all build up the mounds. Waves, currents, predation and sometimes ice scour or sand burial, limit, erode or carry away the mounds.

The dynamics and sensitivity of mussel beds forming biogenic mounds under various conditions needs to be considered at the various different levels of scale. In the long-term, persistent mound forming beds tend to remain in the same place, though patches and individual mounds within them are very much more dynamic. Above the scale of the individual, consideration has also to be given to dynamics at the scale of clumps. Differences in recruitment, growth and mortality are likely to occur at all scales and similarly in the associated fauna and flora.

Far less is known of the dynamics and sensitivities of the 'gravel deposit' type of bed than the commercially exploited estuary channel beds.

In general, *Mytilus* is considered to have a strong ability to recover from disturbance (Seed & Suchanek, 1992).

2. Physico-Chemical Events

a. Short-term

Many mussel reefs are vulnerable to total destruction by storms and tidal surges in the Wash, Morecambe Bay and the Wadden Sea, and on occasion this may involve hundreds of hectares. The number of mussel beds in the Schleswig-Holstein part of the Wadden Sea mapped by aerial survey decreased from 94 in 1989 to 49 in 1991 as a result of severe storms in early 1990 (Nehls & Thiel, 1993). Storms were a major factor in limiting persistent mussel beds to the shelter of the islands while in more exposed areas the beds were highly dynamic. Young (1985) demonstrated experimentally that mechanical agitation stimulated byssus production in mussels. Erratic storms are likely therefore to be more damaging than where equivalent wave forces are the norm on exposed rocky shores.

Ice flows can sweep away beds in the Wash and the Wadden Sea in the most severe winters. Sand burial of *Mytilus* reefs occurs occasionally in Morecambe Bay (Dare, pers. comm.). Large scale sand movements are also common in other places, such as parts of the Cumbrian Coast and Solway Firth (e.g. Perkins, 1967; 1968; 1970; 1971; Perkins et al., 1980), and can be expected to bury *Mytilus* beds and reefs on occasion.

b. Long-term climate change

Beukema (1992) used the observed macrobenthos changes in the western part of the Wadden Sea over mild winters in the 1969-1991 period to forecast responses to warming in the long term. Mild winters resulted in greater weight loss by individuals over the winter followed by poor recruitment in the following summer and subsequent problems both for the fishery and dependent predators such as eiders. In part, recruitment failure after mild winters is thought to be due to greater numbers of predatory small crabs on the flats at the crucial time of settlement. On the other hand, severe ice cover over hard winters can also greatly reduce mussel densities, e.g. in the Wadden See (Nehls & Thiel, 1993) and the Wash (Dare, pers. comm.). Increased mussel predation by birds was reported for several areas during the harsh winter of 1964 (see chapter IV).

3. Biological Events

a. Predation

Predation is an important influence on all mussel populations and has been discussed in detail in chapter IV. See also the effects of mild winters on crab predation in the paragraph above. However, Nehls & Thiel (1993) considered that bird predation was less important in causing losses of entire adult mussel populations than factors such as storm loss.

b. Phytoplankton blooms

Dense phytoplankton blooms can, on occasion, be detrimental to *Mytilus edulis*, although serious effects at the population level have only occasionally been reported. Dense blooms of a non-flagellated chrysophycean alga in North America caused heavy mortalities in *M. edulis* (Tracey, 1988). Blooms of the toxic dinoflagellate *Gyrodinium aureolum* have been reported to cause some mortalities of *M. edulis* in Norway (Tangen, 1977), and sublethal toxic including acute effects on clearance rate and marked cellular damage to the gut in *Mytilus* in the UK (Widdows et al., 1979), although, in general, reports of *G. aureolum* blooms seem to suggest that kills of fish, lugworms and other invertebrates are more frequent and widespread

than are kills of mussels (Boalch, 1979; Helm et al., 1974; Tangen, 1977). A bloom of the flagellate *Phaeocystis poucheti*, which produces copious amounts of glutinous material, caused reproductive failure in *Mytilus* in the Dutch Wadden Sea as a result of the inability of the mussels to feed (Pieters et al., 1980).

E. SERPULA VERMICULARIS

There are few studies of serpulid reefs, and a complete absence of any form of monitoring, upon which to base any interpretation of sensitivity, and the following is therefore largely supposition.

Asterias rubens has frequently been seen feeding on reefs in Ardbear Lough (see chapter IV) and it is known that it can sometimes occur in very dense waves which can destroy *Mytilus* beds in a short time (see chapter IV). It is therefore presumably possible that it is capable of great damage to serpulid reefs, although the muddy substratum usually found between reefs would presumably prevent rapid spread of starfish.

F. KEY POINTS FROM CHAPTER V

- *S. alveolata* is subject to extremely variable recruitment but the reasons for this are not known. It often suffers from burial as a result of large movements of sand, a feature of its preferred environment, which it can tolerate for periods of days or even weeks, although this severely hampers its growth. Longer term burial kills it. Colonies can die back for many years as a result of cold winters. In many parts of its range it seems to compete for space with mussels *Mytilus edulis*, interactions with which are not fully understood. There is little knowledge of predators of *S. alveolata* but they do not appear to be important.
- Recruitment processes in *Sabellaria spinulosa*, and the factors affecting them are little known. Given that many *S. spinulosa* crusts (reefs?) are more or less annual features, it seems likely that stability of substratum is a factor in determining whether they develop into more stable, permanent structures. Interactions with brittle stars *Ophiothrix fragilis*, which can reduce recruitment, growth and probably fecundity of *S. spinulosa*, may be important. *S. spinulosa* is probably generally tolerant of changes in water quality, although the associated fauna may not necessarily be. As with *S. alveolata*, there is little knowledge of predators on which to judge likely sensitivity to changes in predator populations.
- In general *Modiolus* beds seem to be persistent features over decadal time spans, and there is little documented evidence of sensitivity to particular natural events. However, predation is extremely important on young *Modiolus*, and probably combines with erratic spawning and larval settlement to produce the very variable and sporadic recruitment to sexually mature age classes seen in some areas. It can be speculated, therefore, that density and age structure within reefs might vary considerably over periods of years or decades, although no studies have been carried out which might prove or disprove this. It can also be speculated that infaunal beds might be more subject to predation than semi-infaunal reefs due to the greater inaccessibility of the byssus threads, which are thought to be very important in providing shelter to young *Modiolus*. It is also possible that increased densities of *Ophiothrix fragilis*, known to have highly variable population densities in some areas, might be detrimental to *Modiolus*. Finally, in the long term, rising sea temperatures could conceivably be a problem given that the species is near its southern limit. There is little knowledge of parasites and disease.
- *Mytilus* has been much more extensively studied than other biogenic reef species, and as is often the case the factors affecting it appear to be more complex, probably simply because more is known. In less sheltered areas *Mytilus* reefs are subject to removal by storms. In places massive predation by *Asterias* has been reported to wipe out large beds. Bird predation is also extremely important and changes in bird populations appear to have the potential to alter mussel communities, although this is probably a less important factor than storms. Recruitment is thought to be favoured by cold preceding winters as a result of decreased predation on the spatfall, although loss of entire beds due to ice scour has been reported in the Wash. Phytoplankton blooms have been reported to cause mortalities in *Mytilus* but are probably less important than storms, predation and winter temperatures. Overall, however, mussel beds are resilient, with a strong ability to regenerate after losses (but see potential for losses on a wider scale, chapter VI).
- There is little information upon which to base an assessment of the sensitivity of serpulid reefs to natural events.

VI SENSITIVITY TO HUMAN ACTIVITIES

Following Holt et al. (1995), McLeod (1996) and Hiscock (in prep) we have tried to consider both 'sensitivity' (the likelihood that an organism or community will suffer damage or death when exposed to an external factor) and 'vulnerability' (the likelihood of exposure to an external factor) under the general heading of sensitivity here.

Although not strictly within the remit of this report (sensitivity and dynamics) fisheries regulations clearly have management implications for *Mytilus*, which constitutes an important fishery in terms of collection of wild stocks, relaying of 'seed mussels' for ongrowing, and true aquaculture. A brief mention of relevant fisheries regulations is therefore included in this section.

A. SABELLARIA ALVEOLATA

1. Changes in Sediment Regime

It would be expected that this species would be sensitive and vulnerable to changes in sediment regime, and this certainly appears to be the case. There is some evidence that newly constructed groynes off Morecambe have resulted in a coarser sediment regime which has allowed *S. alveolata* to colonise boulder and cobble grounds in place of *Mytilus* which was previously dominant (Lumb, pers. comm.; Andrews, pers. comm.).

In the Mediterranean Gulf of Valencia, Spain, 23 sites at which *S. alveolata* reefs had been reported since 1989 were resurveyed in 1994. Reefs were found at only 13 sites, and of these there was clear evidence of reduction in extent in three and increase in extent at four (Porras et al., 1996). They reported that the most frequent cause of losses was sand level rise as a consequence of the construction of sea walls and marinas / harbours, and beach nourishment projects. Although reef losses were also attributable to natural causes such as river floods or natural sand accumulation, in these cases, recovery after perturbation events had been recorded on many occasions between 1989 and 1994.

On more open coasts, where shore defences on one stretch of coast are able to reduce sand supply to neighbouring areas, it may be speculated that this might lead to reduced availability of sand and therefore reduced development of *S. alveolata* reefs. Parts of the Cumbrian and Welsh coasts might conceivably be susceptible to such changes. Modern policy tends to be not to carry out activities which might result in dramatic reductions in sediment supply to neighbouring areas, but the possibilities should nevertheless be borne in mind.

2. Physical Damage

Trampling and, possibly, bait digging have been identified as possible impacts (e.g. Cunningham et al., 1984). Cunningham et al. (1984) showed rapid recovery from single trampling events of a light or moderate nature. More extensive damage to colonies (i.e. chunks being removed) was less evident in the short term, but some such damage did occur and was subsequently enlarged by wave action. Mitchell (1984) observed that in Brittany damage on popular beaches was minimal and limited to trodden gaps for access through the reefs. Damage to colonies has been observed by people breaking open the tubes with knives

and removing the worms for use as fishing bait, though nowhere has this been seen on any intensive scale (Cunningham et al., 1984; Hawkins, pers. obs.).

3. Aquaculture

In Brittany intensive mussel cultivation on ropes wound around intertidal oak stakes affected nearby *S. alveolata* reefs in three ways: they were smothered with faeces and pseudofaeces, (though it was not clear if this resulted in any harm); small mussels dislodged from the ropes then lodged in the reefs and broke up the surface as they grew; and commercial collection of these mussels from the reef caused trampling damage (Mitchell, 1984). However, mussels are extremely common in cSACs where extensive *Sabellaria* reefs are found and nearby cultivation activities (which would probably be limited to relaying) seem unlikely to have detrimental effects. Relaying directly on top of *Sabellaria* reefs would, of course be detrimental but seems unlikely to be attempted.

4. Chemical Contaminants

Mitchell (1984) stated that one of the prime reasons for initiating the research carried out by Cunningham et al. (1984) was "reports of the species vanishing from some areas due to pollution" but no further information on this has been found. *S. alveolata* were, however, common at the turn of the century at Hilbre Island in the mouth of the Dee Estuary, but disappeared for reasons unknown; siltation, cold winters and pollution have all been quoted as possibilities (Craggs, 1982), though there was no apparent justification for the latter.

S. alveolata appears to be present at lower abundance on that part of the Cumbrian coastline where industrial and sewage effluents are most concentrated (around the Whitehaven - Workington - Maryport area) than elsewhere on the Cumbrian coast, but to some extent this might simply represent a lack of suitable habitat (Hartnoll et al., 1998).

Possible evidence of sensitivity to detergents used in oil spill events was found for the larvae of *S. spinulosa*, to which is closely related (see below), though no references were found for *S. alveolata* itself.

Overall there is little evidence for any unusual sensitivity to chemical contaminants.

5. Cooling Water Discharges

Studies at Hinkley Point, Somerset, found that growth of the tubes in the winter was considerably greater in the cooling water outfall, where the water temperature was raised by around 8-10°C, than at a control site, although the size of the individual worms themselves seemed to be unaffected (Bamber & Irving, 1997).

B. SABELLARIA SPINULOSA

The sensitivity of *S. spinulosa* to man induced change was summarised in a recent report (Holt et al., 1997a). This section draws heavily on that report.

1. Fishing

Berghahn & Vorberg (1993) have suggested that *Sabellaria spinulosa* in it's absence is a good indicator of fishing intensity in the Wadden Sea. Subtidal *S. spinulosa* reefs are reported to have been lost due to physical damage in at least five areas of the north east Atlantic. In the Waddensee, Riesen & Reise (1982) reported that extensive subtidal *S. spinulosa* reefs were lost from the Lister Ley, island of Sylt, between 1924 and 1982; they reported that local shrimp fishermen claimed to have deliberately destroyed them with "heavy gear" as they were in the way of the shrimp trawling. Reise & Schubert (1987) reported similar losses from the Norderau area, and attributed them to similar causes. Shrimp trawling still occurs in these areas and the *S. spinulosa* have not reappeared, but have effectively been replaced by mussel *Mytilus edulis* communities and assemblages of sand dwelling amphipods (Reise & Schubert, 1987). The mussels are also exploited.

Dorjes (1992) reported complete loss by 1987 of almost two km² of *Sabellaria spinulosa* reef in Jade Bay, North Sea, the distribution of which had been described by Schuster (1952, ref not seen), and suggested that this was probably as a result of fisheries activities.

In Morecambe Bay fisheries for pink shrimp *Pandalus montagui* have been implicated in the loss of subtidal *Sabellaria spinulosa* reefs in the approach channels to the Bay (Mistakidis, 1956; Taylor & Parker, 1993). EU LIFE funded surveys in appropriate areas during May 1998, using grabs, small beam trawls and anchor dredges, as well as interview with local divers, found no evidence of *Sabellaria spinulosa*, although there were numerous pink shrimp, and some subtidal *S. alveolata* were found adjacent to known intertidal reefs (Fletcher, pers. comm.).

Warren & Sheldon (1967), discussing the pink shrimp fishery of the Thames Estuary and the Wash, reported that "it has been the accepted practice among commercial fishermen to search with a small hand dredge for the polychaete worm *Sabellaria spinulosa* and then trawl for shrimp in areas where this was found." Warren (1973) reported "In recent years ross (*Sabellaria spinulosa*) has been found only in small clumps in the Wash where the bottom is predominantly sandy, particularly towards the offshore end of the fishery. No reefs of ross are known to exist."

Graham (1955) assumed that trawling would damage *Sabellaria spinulosa* reefs but did not back this up with any direct evidence. He also assumed that recovery would be rapid as the worms were 'effectively annual'.

Rees & Dare (1993), using a four point numerical scale of assessment of "risk of extinctions through natural and anthropogenic factors" for a number of benthic species, considered that the risk for *S. spinulosa* from trawl/dredge effects was high, scoring the maximum 4.

2. Aggregate Extraction

Clearly it is certain that at least in the short term *Sabellaria spinulosa* reefs would suffer severe direct damage by extensive aggregate dredging activities, and that aggregate extraction is very likely to occur in areas where *S. spinulosa* is found, as expected from the distribution and habitat requirements of the species. This has been noticed in practice by English Nature and others (e.g. various licensed dredging areas, Gilliland pers. comm.; East Anglia, Attrill pers. comm.). The extent of important *Sabellaria* reef structures, and speed of recovery from this damage, are presently unknown. Compared to fishing impacts, gravel extraction is likely to be more limited in extent, more controlled, and less likely to continue for very long time periods, so that although direct damage would obviously be severe, recovery from adjacent undamaged areas seems more likely. The likelihood of damage due to sediment plumes in areas adjacent to gravel extraction is presently less clear, since there is no knowledge of the effects of differing particle sizes upon *Sabellaria*, for example, although it would be surprising if damage was other than very localised given the preference for somewhat turbid waters.

3. Water Quality

Sabellaria spinulosa appears to be generally tolerant of changes in water quality. Hoare & Hiscock (1974) investigated the distribution of marine organisms around the outfall from a bromide extraction plant in North Wales. The effluent had a pH of 4 and among other contaminants contained free halogens. Species richness and diversity was markedly reduced within 150 m of the outfall both intertidally and subtidally, with red algae, *Antedon bifida* and *Helcion pellicidum* being particularly sensitive. However, *S. spinulosa* was found closer to the outfall than any other organism, and was found in larger numbers at intermediate distances than further away. Hoare & Hiscock (1974) also reported that other workers had described *S. spinulosa* as a pollution indicator but unfortunately did not give relevant references.

Furthermore, in a report on surveys of Dublin Bay in relation to sewage discharge and dumping, Walker & Rees (1980) reported that "In the dumping area and in the south-east of the bay downtide of the dump site, where depths are greater, the faunas resembled the *Nucula/Sabellaria* [*spinulosa*] community of Caspers. As well as having pollution indicator species, this latter community generally had greater faunal densities and diversities than elsewhere in the bay (except low diversities at the dump sites in 1971). Apart from a possible effect of depth, this suggests that the dumping was having an enriching rather than a degrading effect, although the probable sediment change since 1874 may imply a change in community type".

4. Chemical Contaminants

S. spinulosa was relatively unaffected by an outfall containing free halogens (see 3. Water Quality, above).

The only other information found was the following work on oil dispersants. Larvae of *Sabellaria spinulosa* were killed after several weeks in a 1 ppm concentration of an oil dispersant (detergent BP1002) while larvae in uncontaminated control experiments all survived (Wilson, 1968a). A 2.5 ppm concentration killed the larvae within a day or two. Since the toxicity of detergents varies enormously and no other species were tested, it is not known whether this represents a strong sensitivity to such chemicals on the part of *S. spinulosa* or not. Further experiments using heavier concentrations suggested that detergent adsorbed onto the sand particles forming the tubes of *S. spinulosa* and caused the death of larvae settling

onto them, but that the effects lasted only a few days (Wilson, 1968c). No studies on the effects of oil or oil and detergent mixes were found, nor on more modern detergents.

Overall S. spinulosa seems unlikely to show any special sensitivity to chemical contaminants.

C. MODIOLUS MODIOLUS

Knowledge of sensitivity to human impacts is limited to very few direct studies. However it can be assumed that recovery from physical impacts will depend on the spatial scale of the impacts. Recruitment is slow and sporadic. Spat survival to adulthood occurs best where the spat shelter amongst the mass of adults. Thus, where impacts are so severe that extensive areas are cleared of horse mussels, recovery is unlikely even in the medium term. The time taken for small breaks in a bed to close up by the growth of surrounding clumps is not known, nor is the survival of clumps torn away from the main bed.

1. Fishing

At present there seems to be no large scale *Modiolus* fishery in the UK, but there have been small *Modiolus* fisheries in Scotland (Rohan Holt, pers. comm.) where it appears to be widely eaten, and also used for fishing bait, on a local scale (McKay, pers. comm.). Occasional local use in the west of Scotland was also mentioned by Comely (1978) and *Modiolus* may also have been taken on a very small scale from Loch Creran recently (D. Donnan, pers. comm.). *Modiolus* has occasionally been seen on markets in Lancashire (Bill Cook, pers. comm.). In Norway *Modiolus* is rather more important as a fishery in some areas, although no information on fishing methods or their effects has been found. Given the sporadic and low recruitment of *Modiolus* in UK populations, direct fishery activity obviously has potential to be very damaging, and should be prohibited from important biogenic reef areas unless it can be conclusively demonstrated that it is sustainable.

Scallop and queen scallop dredging has been implicated in the dramatic reduction in density and extent of the widespread and often dense areas of Modiolus bed, (probably representing true biogenic reef) which was described by Jones (1951) off the south east of the Isle of Man. The scallops and queens are fished using heavy metal dredges, usually with large prominent metal teeth along the leading edge. The beds of *Modiolus* have become progressively much more scattered and less dense over the years (skipper of R V Roagan, Port Erin Marine Laboratory, pers. comm.). Unfortunately no surveys of these beds have been done since Jones's initial descriptions. The effect on associated communities has also not been studied, although it is known that the very large barnacle Balanus hameri, which used to be abundant on this particular community, has not been found there recently (Rees, pers. obs.; skipper of R V Roagan, Port Erin Marine Laboratory, pers. comm.). It is unlikely that scallop or queen fishing would be very viable over very dense reef areas, and it has therefore been assumed that many years of fishing on adjacent areas have to some extent 'nibbled away at the edges' of the denser beds. Scallop and queen dredging is known to be damaging to a variety of epibenthic organisms, including many found in association with Modiolus, such as Alcyonium digitatum, spider crabs such as Hyas and Inachus, Cancer, Echinus esculentus, Psammechinus miliaris and to a lesser extent Buccinum undatum (Hill et al., 1997) and probably others including particularly sponges (Veale, pers. comm.).

Scallop dredging on the very rough *Modiolus* reef areas to the north of the Isle of Man has apparently never taken place, presumably because the ground is too rough. In this area the *Modiolus* create numerous banks and reefs up to 1 m high (see earlier chapters).

Obvious damage including severe damage to *Modiolus* (ie the majority broken), flattening of emergent *Modiolus* clumps, and loss of the majority of epifauna, especially emergent species such as *Alcyonium*, was observed as a result of queen trawling in Strangford Lough (Magorrian et al., 1995) where the *Modiolus* seem frequently to occur as clumps on a muddy substratum.

It is suspected that fishing for queen scallops has taken place over *Modiolus* reef areas in upper Loch Creran recently but no details are yet available (D. Donnan, pers. comm.). Video footage of these areas taken during 1996, and showing the reefs to be in apparently good condition, is held by SNH. Queenie dredging was widespread in the Shetland Voes in the 1970's and 1980's and may conceivably be responsible for the apparent existence of *Modiolus* there mainly in clumps rather than dense beds or reefs (McKay, pers. comm.).

Whelk fishing using pots is frequently carried out over rough ground, so might be assumed to be relatively common on *Modiolus* dominated areas. Strings of several hundred pots can be used on *Modiolus* beds to the north of the Isle of Man and off the Lleyn Peninsula. Damage is not likely to be severe, and it is suspected that the emergent epifaunal bioherms of the Lleyn are probably more sensitive than the more infaunal reef / bank areas off the north of the Isle of Man.

2. Oil and Gas Exploration and Production

On the 'infaunal' *Modiolus* reef areas to the north east of the Isle of Man drilling of a single oil/gas exploration well from a jack up rig using water based drilling muds was carried out recently. Drill cuttings disposal was carried out close to the seabed in an attempt to minimise the cuttings pile. Short-term studies using mainly video surveys, with limited anchor dredge sampling, revealed no very obvious impacts to *Modiolus* reefs, including cover of *Alcyonium*, hydroids and sponges, even within 50 m of the wellhead, although the survey design was such that only very obvious effects would have been detected (Holt & Shalla, unpublished). Contamination by barium from the drilling muds was detected in all *Modiolus* sampled (up to 250 m away) but there was no apparent contamination by any other metals or hydrocarbons even at the wellhead location. No long-term studies were carried out. Direct effects of the rig legs were assumed to be severe but no damage was detected by towed video. No long-term studies were carried out. No other studies on *Modiolus* communities in relation to oil and gas exploration are known.

3. Cable and Pipelaying

Information on the effects of laying or trenching in cables or pipelines through *Modiolus* beds was not found. Intuitively it is assumed that cables laid on the surface will be soon be covered over, but scars caused by trenching are more likely to remain. Associated with pipelaying there would probably also be disturbance caused by lay-barge anchors and mooring wires to consider.

4. Spoil and Waste Disposal

Effects of offshore disposal of dredge spoil and other solid wastes are little known. In a bed off the Humber long-term changes in contaminant loads associated with spoil disposal were detectable in the shells of these very long-lived animals. While this indicates survival of the mussels within a dispersal zone around a disposal ground, information on loss of condition, as occurs when *Mytilus* are subjected to excessive sediment loads, is not available. Deposition of capital dredgings such as barge loads of boulder clay which will initially settle as a mass will almost certainly smother the patch it lands on. From such spoil mounds the material

usually disperses, but there are no case histories to indicate rates of sediment accretion that *Modiolus* clumps can keep up with. Exploratory benthos sampling off North Wales in the 1960s showed that there were *Modiolus* beds in or near the ground for which FEPA licences are presently issued for disposals from Holyhead. No monitoring is known to have been done.

5. Aquaculture

Although no studies relating to the effects of aquaculture on *Modiolus* have been found, intuitively there must be some potential for damage in enclosed sea lochs and Voes where both occur together. In terms of SACs the place most likely for this to be an issue would be the Lochs Duich, Long and Alsh cSAC, where intensive salmon and mussel farming are carried out, though in fact there are few sea loch systems now unaffected by salmon farming (Black, 1996). Salmon farming in particular is known to produce large quantities of detritus, with localised deoxygenation leading to death of much of the benthos (Brown et al., 1987; Gowen & Bradbury, 1987). The majority on studies have been carried out on macrobenthic infauna, and effects in some instances have been reported to be detectable up to 45 m (Brown et al., 1987) or even 150 m or more (Weston, 1990). It is worth mentioning that, despite currents running for part of the tidal cycle from salmon farm cages to a *Mytilus edulis* bed, Taylor et al. (1992) were unable to demonstrate an influence of waste salmon food on mussel growth. Until studies specific to *Modiolus* have been carried out, it is impossible to predict with any certainty the likely effects of salmon cage aquaculture, but there is nothing presently to indicate that any wider effects than those reported above on macrobenthic infauna would occur.

D. MYTILUS EDULIS

1. Exploitation

a. Local fisheries

In virtually every cSAC location round Britain where mussel beds form mud-mound reefs, the mussels have been fished or are fished now. Such fisheries have been managed by Sea Fisheries Committee (SFC) byelaws for the past 100 years. In the Wash several thousand tonnes are fished by dredges in good years. In the past, intertidal mussel beds were often exploited by hand using a variety of simple hand tools. These artisanal fisheries still persist on a small scale and, in the absence of adequate recruitment, can significantly deplete the biomass on the most accessible beds. Where the beds extend into low water channels, as in the Conwy Estuary, long-handled rakes or long handled tongs may be used to lift clumps from the seabed into a boat. With hand-working, initial selection takes place on the beds, but when working against tide, weather or daylight constraints, the catch often has to be sorted again to remove undersized shellfish. The discards are returned to the beds but not always to the particular bed from which they came. When fished by hand at moderate levels by men with traditional skills the biogenic reefs will probably retain most of their intrinsic biodiversity. Many of the same species may even survive in good numbers under cultivation regimes. Natural mussel beds are, however, vulnerable to over-exploitation; indeed many sea fisheries committees have long had powers to close beds either when stocks fall to low levels or protect undersized shellfish.

Mussels are also taken on quite a large scale by hand for use as angling and long-line bait, although the latter is now in less demand than in the past. Anglers tend to have most impact where the beds are adjacent to roads leading to favoured shore fishing locations or to harbours

where they board charter boats. A small mussel bed adjacent to a road causeway in Anglesey was virtually eliminated over a period of years by anglers collecting mussels for bait and digging over the gravel for ragworm, in spite of a Sea Fisheries Committee bylaw which has long prohibited digging in mussel beds.

Mussel dredging results in temporary resuspension of sediment in the vicinity of the activity. Rieman & Hoffman (1991) showed that $1470g / m^2$ dredged was temporarily re-suspended, but that most of this was redeposited in the first 30 minutes and turbidity returned to background levels after 60 minutes. The elimination of sand from within the mantle cavities of mussels disturbed by dredging was measured by De Vooys (1987). Three phases were distinguished, rapid discharge in the first 15 minutes, an exponentially decreasing rate over the next 4 hours followed by slow release over 48 hours. Although this study was concerned with the harvested product, the information is relevant to disturbance in the field due to fishing and civil engineering projects. It should be noted that *Mytilus* reefs typically inhabit areas of high natural turbidity.

Mytilus is probably less affected by incidental damage due to fisheries for other organisms than are other biogenic reef communities. Reise & Schubert (1987) reported that reefs of *S. spinulosa*, lost from areas of the southern North Sea due to shrimp fishing, were replaced by *M. edulis* communities and assemblages of sand dwelling amphipods (Reise & Schubert, 1987). The mussels are also now exploited in addition to the shrimps.

b. Re-laying

The biggest yields from mussel fisheries in England and Wales now involve a measure of cultivation known as relaying, in which young seed mussels are transplanted onto plots (lays) in the low intertidal or very shallow sublittoral, where they grow well. This movement and the subsequent harvesting is now often done with quite large purpose built dredging vessels capable of carrying 12 tonnes of mussels or more. The entire enterprise is dependent on the availability of sufficient seed in circumstances where it can be dredged. Hence seed that grows so densely that it accumulates mud and lifts off the stones on which it settled is particularly valuable. The stony skear known as 'South America' within the Morecambe Bay cSAC is one such location. The Dornoch Firth is another good source of these seed mussels. There may be a narrow weather window between the build up of the seed into dredgeable condition in summer, and it being washed away by storms.

Nehls & Thiel (1993) make a distinction between persistent mussel beds and more dynamic beds in more exposed situations (such as the 'South America' skear) and suggest that the impact of mussel fishing will be quite different in persisting and dynamic beds. In particular, they considered that fishing of persistent beds could remove the crucial reserves which mussel feeding birds such as eiders and oystercatchers need in times of low mussel populations.

The operators of re-laid beds aim to spread the mussels out at around 50-100 tonnes / ha so that there is less density dependent depression of growth. The clumps build up some mounds in these on-growing plots but not to the extent found on undisturbed beds. Great differences can occur over short distances within cultivation plots in the rates of growth and the rates of predation. *Carcinus maenas, Asterias rubens* and oystercatchers are important predators both on natural mussel beds and on mussel lays, so in spite of the growth of the individual mussels the operators have to be satisfied with yields that are only about equal to the gross weight of seed laid. Various techniques have been used to ameliorate starfish predation, including the use of mop type tangles and roller dredges, as well as temporary movement of the mussels to higher intertidal locations where gulls can prey on the starfish.

The mussel cultivation industry is an established feature of several of the large embayments now listed as cSACs, notably in the Wash, Poole Harbour and the Dornoch Firth. The activity has increased the total area of ground covered by mussel beds, but these are often only temporary beds. The fishing of seed is usually controlled by systems of permits under Sea Fisheries Committee bylaws and sometimes through Regulating Orders. Protection for the ongrowing cultivated stocks is achieved through leases of Several Fishery Order plots.

c. Over-exploitation at the level of regional recruitment cells

There is concern that it is possible to so overexploit the stocks of mussels within particular embayments that this reduces subsequent recruitment. The sizes of areas from which stocks may come for recruitment is unknown, and relationships between stock and recruitment are poorly understood. There is nevertheless some historical evidence to support intuitive views that a precautionary approach needs to be taken. All delays in development and settlement of larvae decrease chances of survival.

Gross declines in stocks within intertidal mussel beds either through repeated recruitment failure, over-exploitation, or a combination of circumstances can result in knock-on consequences over wider areas. For example in the Dutch Wadden Sea in 1990 mussel stocks declined to unprecedentedly low levels resulting in eiders dying or leaving the area, and oystercatchers seeking alternative prey such as first year and older cockles, adult *Macoma balthica* and juvenile *Mya arenaria*, which then suffered particularly high rates of mortality (Beukema, 1993). There were also consequences for fishing pressures in other areas, including Britain, through international market demand and prices.

d. Cultivation

A useful review of cultivation was produced by Bayne (1991) in a volume published following an international symposium on the biology and cultivation of mussels. A review on cultivation by Hickman (1992) shows world production of 1.1 million tonnes in 1988 most of which is of farmed mussels.

Raft-and-line cultivation of mussels within the UK is limited mainly to Scotland. Despite early predictions of enormous potential, and the high quality of product, tonnages have not increased anywhere near as dramatically as once anticipated, being generally less than 1,000 tonnes per year (McKay & Fowler, 1997), mainly from sheltered sea lochs in the Strathclyde and Highland regions.

Raft-and-line mussel farms may have impacts on the local benthos (see McKay & Fowler, 1997 for a summary) but do not generally impact directly onto *Mytilus* biogenic reef areas.

There is evidence from Scotland and Europe that, where shellfish rafts cover 10% or more of sea lochs in areas of poor water exchange, the filtering activity of mussels can severely reduce plankton levels, with potential effects on wild filter feeders (McKay & Fowler, 1997). McKay & Fowler also point out that in the one instance in Scotland where such reduced plankton levels were suspected (Caol Scotnish, Loch Sween), the production of the farm itself suffered to such an extent that cultivation was discontinued. They also pointed out that most Scotlish mussel farms are small and unlikely to have serious effects on plankton levels.

The possibility of the inadvertent transfer of toxic or nuisance phytoplankton with shipments of bivalve spat was demonstrated in a preliminary study by Scarratt et al. (1993).

e. Fisheries regulations

Fisheries regulations vary greatly in different parts of the UK. The regulatory considerations in terms of mussel fisheries management are complex and a reasonably comprehensive summary is presently in preparation (Wilson, in prep). Useful information on Scottish Legislation is given in McKay & Fowler (1997). The following very brief summaries draw on these plus personal communications from D. McKay (Scotland, England & Wales) P. Dare (England & Wales), J. Andrews (England & Wales) and B. Magorrian (N. Ireland).

i. England & Wales

Mussel fisheries may be removed from the public fishery by the granting of Several and Regulating Orders¹ by MAFF to commercial companies or to Sea Fisheries Committees, who in turn grant licenses to commercial companies or individuals. These may extend for up to 60 years in some instances, although 30 years is more usual. Several Orders grant the rights to mussel fisheries to individuals or companies and are issued principally in those areas where relaying and ongrowing of seed mussels is important. Regulatory Orders allow the granting of numerous licenses to individuals or companies to fish an area for mussels but give no control over where, or how much, any individual fishes, although they may stipulate the method of fishing. Hybrid orders - essentially Regulating Orders where the grantee has the power to assign Several fishery plots within the area - can also be assigned.

A fundamental consideration with Several and Regulating Orders is that the holder is obliged to manage the fisheries in such a way as to <u>develop</u> the fishery.

¹Several, Regulating and Hybrid Orders may be assigned for any shellfisheries including crustacea

In many places Sea Fisheries Committees may also pass by-laws which can cover public fisheries and regulated fisheries, for example to regulate the size of mussels taken, to regulate physically damaging activities such as pipelaying, or to prevent fishing altogether at times of low stocks.

ii. Scotland

The majority of all mussels are managed by the Crown Estate Commissioners who grant leases for their exploitation. Few such licenses have been issued in recent years, and SNH have been consulted on all applications. In many cases the Crown has ceded rights of ownership to others such as local landowners, for example in the Dornoch Firth where the rights to manage and exploit mussels is now held by the Highland Council. There is no right of Public Fishery for mussels. Although Several and Regulated Fisheries Regulations were extended to cover Scotland in 1986, it is thought that these may have little, if any, relevance to mussel fisheries in Scotland due to the absence of a public fishery.

iii. Northern Ireland

Any registered fishing vessel is entitled to fish for mussels in NI waters. DANI awards licences to individuals or companies to relay seed for ongrowing, and to subsequently dredge the mussels. Closure of wild mussel beds because of low stocks is not a management option which is presently pursued, mainly because there is no legal mechanism currently in place. In all cases there are also stringent public health regulations with regard to the sale of mussels for human consumption, but these are not considered here.

2. Chemical Contaminants

a. Introduction

The bioaccumulation of environmental contaminants and their effects on the physiology of mussels was reviewed by Widdows & Donkin (1992). At the molecular and cellular level the effects were reviewed by Livingstone & Pipe (1992). An example of the use of mussels in monitoring the bioavailability of contaminants released by dredging sediments from a harbour was given by Bergen et al. (1993) #247]. They also give bioconcentration factors for six PCB congeners from the seawater.

The survival time of mussels in air is a simple to measure yet sensitive response to pollution induced environmental stress (Smaal et al., 1991). Survival was significantly lower after 6 weeks experimental exposure in contaminated parts of the Western Scheldt (Smaal et al., 1990), particularly when the mussels accumulated higher tissue concentrations of the lower PCB congeners. Clearance rates were also reduced at the highest tissue concentrations.

As part of the US Mussel Watch, histological examination for neoplasias was included as well as chemical analyses. Significant increases were found in the incidence of neoplasias where there were higher concentrations of combustion related PAHs, cis-chlordane pesticides and cadmium (Hillman, 1993).

b. Specific contaminants

i. Diesel

Mesocosm experiments over two years with the water accommodated fraction of diesel showed that *Mytilus* was more sensitive than many of the other common intertidal invertebrates such as *Carcinus maenas* and *Littorina littorea*, being lost from mesocosms dosed with $30.1 \mu g/L$ and above (Bokn et al., 1993).

ii. PCBs

When mussels from areas where they had been exposed to PCBs were moved to a clean location, little depuration occurred over 3 months until gametogenesis (Hummel et al., 1990). Accumulated PCBs decline when mussels spawn, but different congeners are not all lost at the same rate, suggesting differential partitioning in different tissues or lipid pools (McDowell Capuzzo et al., 1989).

<u>iii. TBT</u>

A number of studies have demonstrated toxic effects of TBT, including mortalities, at concentrations in water of $0.4 \ \mu g \ L^{-1}$ or less (see Widdows & Donkin, 1992 for a summary).

iv. Sunflower Oil

Even substances that generally seem relatively benign sometimes cause unexpected impacts. In 1991 a special products tanker carrying sunflower oil was wrecked off the Anglesey coast. Mussels ingested droplets of the vegetable oil, with consequences for their reproductive metabolism resulting in mortality some months later when they spawned (Mudge et al., 1993).

c. Mixed effluents

In general, it is thought that bioaccumulation and toxicity of mixtures of organic compounds is additive, although antagonistic interactions (where the combined effects of toxicants is less than would be expected from simple addition of the effects of the separate toxicants) have sometimes been reported (see Widdows & Donkin, 1992, for a summary). Studies of interactions between structurally unrelated toxicants petroleum hydrocarbons and copper have revealed a simple additive effect (Widdows & Donkin, 1991), although this contradicted earlier work by Stromgren (1986), who found antagonism. Antagonism between the effects of TBT and hydrocarbons has been reported in laboratory studies (Widdows & Donkin, 1991), and this was supported by field observations which found mussels surviving with high tissue levels of TBT at sites thought to have hydrocarbon contamination (Page & Widdows, 1991). Reports of synergistic effects of combinations of toxicants were not found during preparation of this report.

d. Comparisons of larval and adult sensitivity

Although there is a widespread supposition that larval stages of invertebrates are more sensitive to pollutants than adults, this may not be the case, at least in *Mytilus*; scope for growth studies have suggested that adults are around 10 times more sensitive than larvae in respect of copper (Beaumont et al., 1987), hydrocarbons (Widdows et al., 1987) and sewage sludge (Butler et al., 1990) and around 4 times for TBT (Page & Widdows, 1991). Results of toxicity studies of these and other contaminants from a variety of studies, in adult and larval stages, are summarised in Widdows & Donkin (1992), as also are the measured levels of a variety of contaminants within adult mussels.

e. Generalising about sensitivity to chemical pollutants

Mussels were missing from a wider area of a Cumbrian shore than were other organisms around a large, phosphate rich outfall, the effluent from which was contaminated by a number of heavy metals (Pope et al., 1997). On the other hand, distribution of shore organisms around other industrial or mixed outfalls has shown mussels to be among the least sensitive shore organisms (eg McKenzie & Perkins, 1979). Laboratory based toxicity tests tend to give the same mixed results, with few organisms, including *Mytilus*, being consistently tolerant or sensitive. Attempts to generalise about sensitivity to chemical pollutants are probably unwise (Holt et al., 1997a; Holt et al., 1997b).

3. Eutrophication and Phytoplankton Blooms

It is known that blooms can sometimes cause problems, including mortalities, in *Mytilus* (see previous chapter). Long-term nutrient enrichment and increasing phytoplankton production have been reported in the southern North Sea (De Jonge, 1997; Smayda, 1990) (though interestingly production off the East Anglian Coastline has been reported by Tett at al., 1994, to be only around one quarter of that off the Wadden Sea) and the Irish Sea (Allen et al., in press). Trends in the frequency of problematic phytoplankton blooms are more difficult to establish due to lack of historical data, but blooms appear to be increasingly frequent on the west of Scotland (McKay, pers. comm.) and probably in the southern North Sea (Smayda, 1990). An associated problem is that enrichment often appears to be associated with changes in the species composition of phytoplankton, often favouring smaller groups at the expense of diatoms (Smayda, 1990) and this could have unknown consequences for all filter feeding organisms including *Mytilus*.

4. Parasites

During a period when there was considerable capital dredging in progress in the Conwy Estuary, the shell boring parasite *Polydora ciliata* became unusually frequent resulting in both loss of condition and higher vulnerability to predation by crabs (Ambariyanto & Seed, 1991). Mass mortalities of farmed mussels have been attributed to the parasite *Mytilicola intestinalis* but this was considered by Bower (1992) to be unsubstantiated (see chapter IV).

5. Introduced Species

The mytilid *Aulocomya ater*, a native of South America, has recently been found in the Moray Firth (McKay, pers. comm.). It is thought that this species has stronger byssal attachment than *Mytilus edulis* and may replace it in more exposed areas if it reproduces successfully.

6. Salmon Farming

Despite currents running for part of the tidal cycle from salmon farm cages to a mussel bed, Taylor et al. (1992) were unable to demonstrate an influence of waste salmon food on mussel growth.

E. SERPULA VERMICULARIS

There are a number of activities which are known to damage, or have the potential to damage *Serpula* reefs, the majority of these are mentioned in Moore (1996) on which the summary below is largely based.

Scale is an important consideration. The reefs are small and extremely limited in distribution so that damage which might be considered modest in another community could be regarded as serious in the case of serpulid reefs.

1. Moorings

The reefs are clearly fragile enough to be very easily damaged by physical impingement. Severe damage, albeit on a very local scale, caused by movement of mooring blocks and chains has been seen in parts of Loch Creran. One mooring had reduced colonies to rubble within a radius of about 10 m, while further extensive damage was caused within about 50 m of salmon cages. Although many worms survive such damage, the integrity of the habitat, and its value to other species, is grossly reduced. In Loch Creran, limiting moorings to areas with a depth greater that about 15 m, together with careful choice of ground tackle and limited length of riser chain to reduce movement would minimise or avoid damage.

2. Fishing

Fishing is an activity which could potentially be very damaging. Moore (1996) reported that at the time of his study fishing was limited to occasional *Nephrops* trawling, which was of low risk as it occurred in deeper, muddier areas where serpulid reefs were not found, and there was no evidence from extensive dive surveys of damage that appeared to be caused by bottom fishing. Dredging/trawling for queen scallops, of which stocks seems to be present in Loch Creran, had not been observed but has taken place since, at least in upper Loch Creran (Donnan, pers. comm.). There is clearly potential for damage to reefs although though there is

no present knowledge of the extent of damage, if any, to date. Moore reports that reef areas often contain reasonable stocks of queen scallops. More detailed information on the overall distribution of queens, so that the proportion of the stock found inside and outside reef areas, would help in the preparation of a management strategy for fishing. It is strongly recommended that, if possible, fishing with potentially damaging gear such as dredges or trawls is prevented in areas of dense reefs.

3. Collection by Divers

Moore (1996) has pointed out that physical removal by divers, particularly for commercial aquaria, already occurs in Loch Creran. It is likely that this could be easily sustainable on a small scale, as seems to occur at present, but even rough estimates of the maximum sustainable rate of removal are not presently possible, making predictions of the effects of increased collection difficult.

4. Organic Enrichment

Around 1 km of the south side of Loch Creran around the dump site for an alginate factory (at Barcaldine) was found to be totally devoid of reefs. However, conditions are likely to have been quite severe in the locality, since the discharge consisted of thousands of tonnes per annum of organically rich de-alginated seaweed residue deposited into a poorly flushed loch, and a thick bacterial mat was observed on the seabed within this area (Moore, 1996). It does not therefore follow that this absence of reefs indicates any special sensitivity to organic pollution. If detailed historical information on water quality in the area is available through either the owners of the factory (Kelco Nutrasweet) or the appropriate authority, and or studies of the distribution of other marine organisms in the same area, a better assessment of its likely sensitivity could be made.

Since the discharge of seaweed residue ceased in October 1996 (Richard Searle, Kelco Nutrasweet, pers. comm.), this represents an ideal opportunity to study the rate of recolonisation of the area (see chapter VII) on which there is currently little information.

5. Regeneration Potential

Artificial methods of regenerating reefs in areas where they have been lost have also not been studied, although an opportunity clearly exists in the area around Barcaldine. There is evidence that successful methods might be relatively easily devised for those areas where there is still already a viable population to provide larvae; dense aggregations of *Serpula* quickly cover many artificial surfaces left in Loch Creran, and 'mini reefs' up to around 15 cm in height can appear within three months or so (Moore, pers. comm.). Bosence (1979) successfully moved small pieces of reef to new areas within Ardbear Lough, with no apparent mortalities after a month or so, so long as the new area was not within the anoxic deeper parts of the Lough, but longer term monitoring of these transplants was not carried out. There thus seems to be potential for enhancement of reef areas by placement of suitable substratum in areas known to have good recruitment, with subsequent transfer to other areas if necessary, but this potential is as yet unproven.

In areas where there is no longer a viable population to provide larvae, as may now be the situation in Loch Sween, reefs will clearly not regenerate naturally. Unfortunately, given the apparent requirements for dense larval supply, as encouraged by low turnover of water, it currently seems likely that regeneration by artificial means such as transfer of young established colonies from other areas, while perhaps technically feasible, would need to be

carried out on a scale which would be impractical in reality. Further information on growth and recruitment processes is needed to clarify this issue.

F. KEY POINTS FROM CHAPTER VI

Information from this chapter is here summarised in tabular (Table 6) and textual form (overleaf).

Table 6 Summary information relating to sensitivity to human activities for each biogenic reef species. This information relates as far as possible to biogenic reef biotopes and not necessarily to other biotopes in which the species may be found.

	S. alveolata	S. spinulosa	M. modiolus	M. edulis	S. vermicularis
Fishing					
Direct exploitation	Occasionally taken for fishing bait, Seems inconsequential on present scale.	None	Very limited at present	Very important. Over-exploitation can cause, or contribute to, decline in stocks on a local or wide scale. Traditional methods of harvesting may retain more of the biodiversity than mechanical harvesting.	Occasionally taken by divers for commercial aquaria, probably sustainable on present scale but effects of increased collection difficult to assess.
Trawling/ Dredging for other species	Irrelevant	Widespread loss of reefs due to prawn trawling eg Morecambe Bay, the Wash, and southern North Sea. Recovery seems to be poor even after cessation of fishing.	Widespread damage by queen scallop dredging known to have been caused in Strangford Lough and suspected SE of Isle of Man and possibly elsewhere eg Shetland Voes.	Irrelevant	None carried out at present but remains a possibility which would undoubtedly cause extensive damage.
Potting for other species	Irrelevant	Probably minimal effects.	May be some damage to semi- infaunal reefs.	Probably inconsequential even on subtidal reefs	None known to occur at present but fragility of reefs means damage would be likely.
Other activities					
Serious deleterious effects known or strongly suspected to be possible	Coastal developments (sand burial, possibly also sand loss).	Aggregate extraction	Oil & Gas exploration & production? More information needed. Cable/pipe-laying Spoil and waste disposal Aquaculture especially salmon farming in sealochs	Chemical contaminants including diesel and sunflower oil.	Moorings if badly planned Organic enrichment (at least if severe).
Minor or very local deleterious effects likely	Trampling Bait digging Mussel farming		Oil & Gas exploration & production? More information needed.		Diver collection if levels increase.
Activities known to have positive effects	*Cooling water discharge	*Sewage discharge? *Discharge from bromide extraction plant?			

* Although positive effects on the reef forming species in question have been reported, it seems likely that there would be deleterious effects on associated communities.

KEY POINTS

Fishing activities:

- By their nature biogenic reefs are likely to be sensitive to strong physical disturbance. Fishing is the most widespread and damaging activity in a variety of biogenic reef types. *Mytilus* is the only one which itself is an important fishery, (although *Modiolus* is edible and taken on a local scale in places, and more commercially in Norway). Natural mussel reefs harvested by hand seem to retain their biodiversity, but are vulnerable to over-exploitation, particularly when combined with recruitment failure. They generally seem to recover well when managed correctly, but there is a strong suspicion that over-exploitation on a very wide scale can greatly hinder recovery. The habit of relaying mussel seed may have increased areas of dense mussel bed in many areas, but these are not allowed to develop into true reef areas. In many cases the 'seed' mussels taken for relaying would be unlikely to persist if left alone.
- *Modiolus* and *Sabellaria spinulosa* reef areas have both almost certainly suffered widespread and long lasting damage due to the activities of bottom fishing. Reports of *S. spinulosa* reef losses are more widespread than *Modiolus* reefs, probably because of the link between the *Sabellaria* reefs and the pink shrimp, *Pandalus montagui*, which seems to be associated with it. In both these cases recovery is impossible while the fishery activities persist in the area. The likelihood of recovery in the absence of the fishery is rather an unknown quantity in both cases; recent surveys suggest recovery of *S. spinulosa* has not occurred in Morecambe bay despite the cessation of fishing many years ago, and this seems most likely to be due either to lack of larval supply, or to permanent or ongoing alterations to the habitat. Recovery of *Modiolus* reefs would undoubtedly be very slow at best. Infaunal *Modiolus* reefs are likely to be both less sensitive and less vulnerable to fishing by towed bottom gear than more epifaunal reefs. Most of the serpulid reefs in Loch Creran are probably protected from bottom fishing by virtue of the topography of the areas in which they live; if areas are identified where this is not so, steps would need to be taken to prevent fishing for queen scallops which would potentially be very damaging.

Other activities:

- Sabellaria alveolata is potentially vulnerable to changes in sediment regime as a result of shoreline development plans; both large scale increases and decreases in sand could be potentially damaging, although it is likely that in most cases this would be on a local scale only. *S. alveolata* is also moderately susceptible to trampling damage in recreational areas, and on a very small scale perhaps to collection of worms for bait. *S. alveolata* appears to be favoured by elevated winter temperatures (8-10°C) associated with cooling water discharges. Sensitivities of subtidal reef areas can only be guessed at at present, but are likely to be similar to those of *S. spinulosa*.
- *S. spinulosa* occurs in the type of area which is often of value for marine gravel extraction. Direct damage would clearly be heavy, and there is presently little knowledge of recovery. It seems likely that damage to adjacent populations of *Sabellaria* by resulting sediment plumes would not be particularly high, but nevertheless this has yet to be demonstrated conclusively. Moreover damage to associated fauna and flora on particularly rich reefs may be more significant. *S. spinulosa* itself seems generally quite tolerant to changes in water quality. Similar arguments would apply to other physical activities such pipelaying and cable trenching.

- *Modiolus* reefs are likely to be susceptible to any physical activity such as pipelaying, trenchlaying and use of jack up oil rigs and recovery times would be long. Limited short-term surveys in connection with drilling of a single oil well using water based muds detected barium contamination up to at least 250 m from the well but no obvious damage to gravel-embedded reefs. Sensitivity to many impacts may depend on the nature of the reefs concerned, including the current regime. In sheltered sealochs there may be some sensitivity to organic enrichment from aquaculture, particularly salmon farming.
- *Mytilus* has been shown to be sensitive to some pollutants, including TBT, diesel and sunflower oil. It is known to bioaccumulate a wide variety of contaminants, often with sublethal effects, although whether it is any more sensitive than other marine organisms in this respect is unclear. Greatly increased sediment levels as a result of dredging activities have been shown to result in loss of condition and increased predation by crabs.
- Serpulid reefs are physically fragile and therefore easily damaged by moorings, as has been observed in Loch Creran. Physical removal by divers occurs, although at present levels this seems unlikely to be a problem. Large scale disposal of de-alginated seaweed residue has caused widespread losses but these have recently ceased.

VII MONITORING AND SURVEILLANCE OPTIONS

This chapter discusses the options available for monitoring and surveillance of biogenic reefs, but does not make detailed recommendations for monitoring programmes as these would need to be tailored carefully to the needs of the individual SACs, and will be prepared by the relevant authorities. The information presented here relates mainly to available methods.

There are two types of monitoring which need to be considered by SAC managers: condition monitoring, which is synonymous with surveillance monitoring; and compliance monitoring. These can be defined as follows:

Condition monitoring (**surveillance monitoring**): monitoring designed to determine whether or not the feature is 'maintaining favourable condition status' (Burt, pers. comm.). Essentially this sort of monitoring must attempt to detect unanticipated impacts, including those which may be wide ranging, subtle or which only slowly become obvious (Hartnoll, in prep).

Compliance monitoring: monitoring designed to detect whether particular activities or disturbances are or are not having negative impacts upon the feature (Burt, pers. comm.).

In many instances the methods available for the two types of monitoring are essentially the same, particularly where effects at the level of populations or communities are being investigated (looking for changes in the extent of beds or in population structure, for example). However, the area covered may vary greatly. It may, for example, be possible to limit compliance monitoring for fishing impacts to a small area of biogenic reef in the safe knowledge that fishing does not occur elsewhere, while surveillance monitoring may have to be carried out over a much wider area.

In other cases compliance monitoring can be more focused than surveillance monitoring, for example where levels of contaminants (such as heavy metals in mussels) or physiological changes (such as imposex in gastropods caused by TBT contamination) are being investigated.

Choosing what monitoring methods are most suitable for any given area of SAC requires a more detailed level of knowledge of distribution (of both biotopes and human activities) and other circumstances than can be entered into in this report. However, a range of possible monitoring methods, some quite general and some more specific to the five main biogenic reef species, is given here.

A. INTRODUCTION TO METHODS

Assessment of the reliability and practicalities of a variety of monitoring methods which might be useful for monitoring in SACs is presently underway (Hiscock, 1998a; Hiscock, 1998b). A report summarising two recent workshops on this subject, including interesting field exercises investigating consistency of methods between survey teams, together with a literature survey of methods, is also available (Worsfold & Dyer, 1997).

Details of monitoring options are given for each biogenic reef species in the subsequent sections (B-F). Since subtidal communities will be much more difficult to monitor than intertidal ones, and are more likely to rely on modern technology, a brief overview of some of the available methods is given here.

For many of the subtidal reefs, their distinctive topography and texture renders it likely that modern acoustic monitoring methods such as $RoxAnn^{TM}$ and sidescan sonar may be useful, and these are referred to several times in this chapter. $RoxAnn^{TM}$ interprets the signals from an ordinary shipboard echosounder of the type routinely used for measuring depth, and gives information on the 'hardness/softness' and 'roughness/smoothness' of the bottom, which by calibration against known seabed types can be used to rapidly collect information on seabed type over large areas (for detailed technical information see Chivers et al., 1990). Information is obtained only from the seabed directly below the boat. Sidescan sonar uses a dedicated sonar source towed on a wire behind the boat, relatively near to the seabottom, which 'scans out' a signal to either side many times per second. By interpretation of the signal bounced back from the seabed an image of the seabed, which is based upon both topography and 'hardness/softness' of the bottom, can be produced. This image can typically cover an area of up to a few hundred metres on either side of the boat.

Worsfold & Dyer (1997) contains a useful overview of the use and limitations of RoxAnnTM bottom discrimination, (although for more detailed assessment of the technique's application see Davies et al., 1997). There was no detailed discussion of sidescan, although it was pointed out that no references to its use in the mapping of biological features or biotopes had been found. In fact, use of sidescan for mapping biological features has been successfully used where the features are physically distinct and/or obvious, including for a number of biogenic reef features, particularly *Modiolus* reef areas. Other features such as maerl beds in Scottish sea lochs have also been mapped (Foster-Smith & Davies, in prep). Holt et al. (unpublished) were able to map unusual reef structures formed by *Modiolus* off the north end of the Isle of Man, as well as nearby *Ophiothrix* beds; Magorrian et al. (1995) were able to map *Modiolus* reefs in Strangford Lough. Very large *Modiolus* bioherms have been mapped in Canada using relatively long range sidescan (Wildish et al., in press). Subtidally, areas of semi-infaunal *Mytilus* in the Tay Estuary have recently been mapped by sidescan (Silke Wewetzer, pers. comm.). Rees and co-workers had considerable success in mapping *Modiolus* beds off the Lleyn Peninsula using acoustic methods, particularly RoxAnnTM.

Monitoring of the population structure of the reef forming species and the associated flora and fauna in subtidal communities will be problematical. Options include broadscale surveys using towed video or ROV, although the former might in some cases cause physical damage, hand held diver video, fixed quadrat photography, or diver surveys using Abundance scale Checklist at Exact locations (ACE surveys) or transect/quadrat counts. Video surveys cover larger areas than fixed quadrat photography or diver surveys but only limited conspicuous organisms can confidently be quantified. ACE surveys and transect/quadrat surveys are expensive but more likely to detect change. All of these methods would be limited to macrobiota. Monitoring of infauna and cryptic fauna can only be carried out with destructive sampling techniques which are expensive to process and, given the state of present knowledge of biogenic reef communities, should take a lower priority for now.

Hartnoll (in prep) notes that likely improvements to methodology for work in the sublittoral in the near future will be of great value for survey and monitoring of circalittoral hard substrata, and similar arguments apply in respect of sublittoral biogenic reefs. These improvements relate mainly to increased dive times due, for example, to increasing use of nitrox gas mixtures and rebreathing apparatus, improved location, communication, site marking and recording equipment for divers, and further development and use of non diving technologies including ROV and automatic dataloggers.

B. PROBLEMS ASSOCIATED WITH DETERMINING ACCEPTABLE LIMITS OF CHANGE

Interpretation of results of monitoring programmes is likely many instances to be difficult, because many of the biogenic reef biotopes under consideration (with the probable exception of most *Modiolus* biotopes) undergo natural fluctuations in populations which are either remarkably wide (many *Mytilus*, *Sabellaria alveolata* and probably many annual *S. spinulosa* reefs), so that even almost complete loss of reefs could be regarded as 'normal', or relatively unknown (the more apparently stable *S. spinulosa* reefs at the mouth of the Wash; serpulid reefs). The abundance and diversity of the associated fauna and flora will inevitably have their own sources of variation in recruitment, growth and survival superimposed upon the variations in the 'supporting' reef populations; in general terms one can expect richer and more diverse communities on older and more stable reefs than on younger or less stable ones, but determining acceptable limits of change will again be very difficult in most cases. In the early years the primary benefit of many surveys will be in giving information about typical levels of natural variation, assuming that there are no major human influences.

C. SABELLARIA ALVEOLATA

1. Physico-Chemical Attributes

A number of physical and chemical parameters could usefully be recorded in areas of *Sabellaria alveolata* reef. In particular, these would include coastal water and air temperatures, which may influence growth and fecundity, wave action, and sand distribution/levels, a supply of suspended coarse sand being essential for the formation of the tubes. It would be particularly important to record the latter in areas where coastal developments with the potential to change sediment transport and deposition are likely.

2. Monitoring Distribution and Abundance at Broad Scale

Monitoring and surveillance has to be undertaken at the hierarchy of spatial and temporal scales. At the broadest and longest scale the distribution of *Sabellaria alveolata* should be re-surveyed decadally using Cunningham et al. (1984) as a baseline. Using the broadscale biogeographic approach adopted by Crisp & Southward (1958) and rapid semi-quantitative abundance scales (see Cunningham et al., 1984), the extent of this organism can be rapidly surveyed. Contractions or extensions in range can be mapped and increases in abundance within its range tested using a matched set test (e.g. Friedman's test matching by site over time). For example recent observations at Lyme Regis have shown an increase in the sheet-like reef in recent years which was not detected by Cunningham et al. (1984) in the early 1980s, despite frequent visits by one of the authors (S.J.H.) during this period. The methods to be used are simple and could readily be adopted by County Wildlife Trusts and EN, SNH, CCW regional staff with modest training. Alternatively the resource required would be about 3 months person-time plus travel and subsistence.

3. Monitoring Distribution and Abundance at Intermediate Scales

The extremely broadscale approach described above could be supplemented by more detailed observations using low level aerial photography, (or alternatively fixed viewpoint photography, although this gives more problems in calculating area covered) at low tide. Ideally these should be done annually, because the highly variable nature of *S. alveolata* reefs means that considerable amounts of data would be required to identify trends in abundance. Limited ground truthing would be required and such an approach can be tested using recently acquired aerial photographs of the Cumbrian/Solway coast (Lumb, pers. comm.), since it is not clear

how obvious *Sabellaria* reefs are on aerial photographs. A relatively recent survey (Allen et al., 1991) has also been undertaken on a number of transects on this stretch of coast. Percentage cover estimates were made at 0.5 m vertical intervals in one of two ways: by visual estimates of percentage cover of a 5 m wide band, or by estimates from each of 15 to 25 replicate quadrats. Repeats of these surveys would allow some estimates of change to be measured whilst ground truthing.

4. Monitoring Distribution and Abundance at a Local Scale

The next level of detail would be to choose groups of adjacent sites within a region (e.g. three shores at each of Galloway, Cumbria, Cardigan Bay, S. Wales, N. Cornwall, S. Devon) and undertake quantitative work at each site. This would enable separation of local effects (beach movements, trampling, failure of local recruitment) from more widespread effects (e.g. the effects of climate on reproductive output). On each shore three sub-areas of *Sabellaria* habitat would need to be selected. The abundance of *Sabellaria* could be assessed quantitatively by stretching 25m long tapes parallel to the shore line and scoring the number of times *Sabellaria* is found under every half metre (50 intersection points). An hierarchical analysis of variance could be used to separate regional, local (between shores) and within shore variation. This approach could be coupled with biotope mapping on stretches of shore, whole shore photographs, photographs of areas, plus qualitative descriptions of types of colony. Using a video recorder would be an excellent way of retaining these records.

5. Monitoring Individual Reefs

More detailed studies could focus at the individual reef level at selected key sites within cSACs. This level of detail would be particularly good for looking at the growth, development and senescence of reefs and their associated flora and fauna. Much useful background exists in the work of Wilson (1971) and Gruet (Gruet, 1977; Gruet, 1981; Gruet, 1982; Gruet, 1985; Gruet, 1986; Gruet, 1989) but this was largely autecological and not very quantitative. There is a need to measure rates of colony growth and decay. The approach to be adopted would be to mark out replicated reefs in various stages of growth or senescence (after Wilson, 1971). These would be measured and mapped. The associated flora and fauna could be qualified non-destructively using replicated small 0.25 x 0.25 quadrats thrown on the reef. Wilson (1971) also reported that the use of a skewer inserted between adjacent tubes in order to measure the thickness of a colony resulted in no apparent harm. This simple method could be used in order to compare growth rates.

For detailed studies of intertidal growth rates, Bamber & Irvine (1997) successfully attached substantial pieces of *S. alveolata* reef (c. 1.5 l volume) to plywood bases using epoxy resin. These were cured overnight in seawater and then screwed to larger plywood sheets which were themselves screwed onto the bedrock on the shore. This system appears to have been used successfully for over a year. The reefs were periodically removed and the volume measured by the displacement of water. Calculation of the volume using measurements obtained by photography gave a consistently larger estimate compared to the displacement volume.

D. SABELLARIA SPINULOSA

1. Distribution

Given the lack of knowledge about true *Sabellaria spinulosa* reefs (as opposed to annually forming thin crusts) one pressing priority is for detection of their whereabouts and extent. In this regard, therefore, it is necessary to concentrate on those beds found recently in the mouth of the Wash, in order to gain experience in identifying and mapping them, as well as to satisfy monitoring requirements. Traditional destructive sampling methods are of little use, and remote methods will need to be used. However, recent experience has suggested that neither RoxAnnTM nor sidescan survey alone is as useful for mapping the extent of beds as might be expected (Foster-Smith, pers. comm.). Sidescan was particularly disappointing as it failed to distinguish clearly between *Sabellaria spinulosa* reef and nearby patchy hard bottoms. RoxAnnTM showed some potential for identifying likely areas of *Sabellaria spinulosa* and for confirming suspected boundaries, but groundtruthing, probably by a combination of video and diving, would be essential. ROV is to be preferred over towed video, which will probably be negligible. The latter is likely either if it can be demonstrated that recovery is rapid, or that the reef area is very extensive and the areas damaged very small.

2. Recruitment

Information on recruitment to the beds would be important. Unfortunately, given the strong stimulation to settle by adult *S. spinulosa*, and the lack of settlement in its absence, settlement plates may be of little use. Unless settlement plates can be shown to be worthwhile, recruitment would best be monitored by investigating samples of reef. George & Warwick (1985) had little difficulty in distinguishing early year classes in grab samples. Grab samples, unfortunately, are likely to be very unreliable and damaging in the true reef areas and diverobtained samples may be required. A programme would need to be devised which would identify inter-annual variation in recruitment.

3. Associated Communities

Detailed methods for monitoring of the associated epifaunal community can only be prepared once we have a clearer idea of what it is and how it functions. However, much useful information on the large epifauna can probably be gained using diver recording surveys for detailed areas and video recordings to study distribution of the more conspicuous species over wider areas.

4. Existing Monitoring Programmes

The majority of licenses awarded for aggregate extraction contain conditions. These include monitoring requirements although until recently these were restricted to physical parameters. It is anticipated that biological monitoring associated with a number of dredging operations will contribute to an understanding of the ecology and monitoring of *Sabellaria spinulosa* (P. Gilliland, pers. comm.). Inclusion of analysis of recruitment and population structure on a seasonal and interannual basis could substantially increase the knowledge gained from such work.

E. MODIOLUS MODIOLUS

As part of the UK Marine SACs project, development of appropriate survey and monitoring methods for *Modiolus* beds/reefs is already underway. CCW is the lead organisation in this work and one of the authors (E I Rees) is involved. For this reason this section is more detailed than other sections in this chapter.

Those beds of the horse mussel *Modiolus modiolus* that build up bioherms are likely to be persistent features in the long term. Evidence for this comes mainly from the scale of build up, the ages of the older animals (30 - 40+ years), the wide range of size individuals usually present and anecdotal history. As a working hypothesis, *Modiolus* beds are considered to be more naturally persistent than beds of *Mytilus* and less likely to be renewed following catastrophic events. In the absence of more specific information, sometimes inferences here have to be drawn from *Mytilus* monitoring for commercial stock assessment purposes. Monitoring strategies do however need to be related to anticipated types of change that might befall bioherm forming *Modiolus* beds, though with some capability to detect unexpected types of event.

Changes to the favourable conservation status of any particular *Modiolus* biogenic reef, whether brought about by natural or anthropogenic causes, are most likely to happen in the following types of ways:-

1. change to the overall extent of the designated bed, through destruction, fragmentation or spread at the margins

2. integrity of the bed and change to the percentage cover, through breaks in the bed, cuts across it, division into discrete patches and ultimately even into a scatter of isolated clumps

3. major change to the vertical relief of the bed

4. physico-chemical changes to the sedimentary matrix of the bed, including the organic content and redox potential of the faecal deposits

5. recruitment failure over a very long period so that ultimately the bed comprises just a sparse relict population of very old animals

6. major changes in the rates of mortality through predation or diseases

7. significant changes to the associated fauna:

a) changes to the biodiversity, species mix and abundance of associated sessile epifauna, including any species of special functional or conservation interest, and the associated motile epifauna

b) changes to the biodiversity and abundance of the associated infauna

Recommendations for monitoring are made here for each of the above attributes which might change. Some are relatively straightforward, some will rely on standard techniques for marine environmental measurements and some will require more evaluation and refinement.

1. Extent of a Designated Bed

Since beds of horse mussels have acoustic reflectivity characteristics that often differ markedly from the surrounding seabed, it is possible to locate and map the broad areas occupied by the beds remotely. This has been done in Strangford Lough and off the Lleyn Peninsula using RoxAnn[™] acoustic seabed discrimination equipment and off the northern tip

of the Isle of Man using side-scan sonar. We would recommend that a combination of RoxAnnTM and side-scan be used. It is essential that Differential GPS is used for position fixing and would recommend the use of a side-scan system that automatically logs the positions and makes allowance for the lay back of the sonar fish. The best practice for post-survey processing of such data is still evolving, but it is likely to involve the use of Geographic Information Systems for bringing displays to common scales, formats and displays.

Ground-truthing is probably best carried out by drop-down video. Since the absolute values given by acoustic systems are seldom 100% stable over time and under different circumstances, we would recommend that ground truthing is carried out each time a monitoring survey of a particular bed is done. Special attention will need to be made to determining an agreed standard or standards for what is to be regarded as the edge of the bed. This will particularly be a problem if there is fragmentation at the edge of the bed or if it continues as a wider spread of isolated clumps. If there is adequate standardisation, and using facilities either within the GIS software or using an area measurement package such as Sigma-Scan, it should be possible to compare areas determined on different surveys over time.

With RoxAnn[™] the precise extent of the footprint of each recorded reading is at present not known so it is impossible to indicate the minimum patch size detectable. Indeed, even if there is a pronounced difference in the acoustic properties of the horse mussel bed and the underlying stony seabed, it will not be clear whether intermediate acoustic readings come from footprints that fall partly on the two types of ground or whether they come from deposits of dead shell that give intermediate acoustic readings. Because of these complications, special efforts should be made to make ground truth video observations at the margins of the bed. Consideration should be given to undertaking video transects across the edge of the bed along tracks that are in repeatable directions. Special attention might also need to be given to the boundaries of the bed where they coincide with local inshore fishery, ie the 6 mile limit of the jurisdiction of a Sea Fisheries Committee where byelaws limit the size of vessels or types of gear.

RoxAnnTM makes measurements just along the track taken by the survey vessel, so interpolation is needed between survey lines. Surfer and DGM3 are amongst the interpolation packages routinely used with RoxAnnTM data. Particularly where the beds are somewhat patchy, there are currently concerns about the extent to which the interpolated outputs really represent the spread of the patches. More work is needed to see how differences in the spacing of survey lines and or their orientation affects the displayed output from the interpolations. However, if side-scan is used in conjunction with RoxAnnTM it should be possible within the GIS to make more intelligent adjustments to the end result.

On side-scan sonar displays horse mussel beds show up both as having a different texture from the surrounding seabed and, particularly where mounds or waves form, in a different pattern of relief. From acoustic shadows it is possible to measure the height of features in the bed. Some modern side-scan sonar systems have built in software to do this.

2. Integrity of the Bed

Indications of this should be gained from the acoustic surveys of the bed with $RoxAnn^{TM}$ and side-scan sonar. However the level of detail really needed will probably require the running of video and or photographic transects across the bed. If the bed is sufficiently shallow this could be done by diver held cameras, but it is more likely that remote cameras will be used.

Using Differential GPS it should be possible to position the start of video transects with a measure of replicability. Undertaking tows across the bed always in the same direction will be much more difficult as in some cases it will be difficult to achieve much more than a drift transect as influenced by tide and wind conditions. With a sledge mounted camera system, in good weather, working over slack water on a neap tide and with a vessel equipped for slow running and with an acoustic doppler system to measure speed over the ground, it should be possible to run along transits that a repeatable within about 30 metres.

At present there is no information about the level of damage done to a horse mussel bed by towing a camera sledge over it. It is inevitable that some of the epifauna will be damaged or dislodged, but whether a trail of broken large mussels is left is not known. Intuitively it is suggested that camera sledge tows done at intervals of several years would not cause unacceptable damage, but it would be unwise to undertake replicated tows several times a year.

For the purposes of measuring exactly the amount of ground covered by mussels it is likely that still camera images will be more suitable. In this case the camera should be pointing directly downwards and the light should be at an angle of around 60°. This arrangement provides a constant known size quadrat field of view and the minimum amount of back-scatter from particles in the water. If as sometimes happens, the front of the sledge lifts as it is being towed, the pattern of lighting will usually allow the change in orientation to be detected. Some experimentation will be needed to achieve the optimum length of towing cable and speed over the ground. As a first approximation we suggest that the towing cable needs to be about twice the water depth. On vessels where towing is off a trawl winch it is recommended that a braided nylon or other synthetic rope about 20- 30 metres long is used as a leader to minimise the risk of the heavier wire touching the bottom ahead of the sledge. Use of a wire, rather than relying solely on a rope has advantages as the sag of the wire in the water helps to keep the gear down, particularly for deeper deployments. Ball swivels are recommended both where the rope is attached to the bridles on the sledge and between the leader rope and the towing wire. A float is needed to counteract the weight of the swivel and shackles. Normally a tail rope is attached at the back of the sledge, with a surface float. This serves as a safety recovery mechanism, it helps indicate where the sledge is relative to the boat and it's drag helps to stabilise the direction of travel of the sledge. It is best to arrange to the sledge against the tide. This has the advantage of allowing the towing vessel to maintain steerage at speeds of less than 1 knot over the ground and it means that any turbid material stirred up by the sledge runners does not form a cloud in the field of view.

Where conditions permit, consideration might be given to establishing permanent dive transects across part of a bed. How relocatable marks can be established in an offshore mussel bed has yet to be addressed, though in some cases there may be identifiable large boulders protruding from the bed which could have marks attached to them.

3. Bed Relief Changes

This should be detectable first from the acoustic surveys. However, it is not known how fast beds build up or whether any meso-scale relief on them like a wave form is constant. There is scope here for long-term investigations of the thickness of the deposits both by shallow subbottom acoustic profiling and perhaps by diver operated probes or even fixed marks. The rate at which mussel deposits erode away after the living mussels have gone may need to be investigated.

4. Physico-Chemical Attributes

A suite of measurements will be needed such as grain size distributions, carbonate content in various size fractions, redox potential and a range of measures of organic content. Chemical measures may be needed of carbon, nitrogen and phosphorus contents of the sediment. Consideration needs to be given to finding ways of determining how much of the sediment is faecal deposits and how much is suspended material carried in over the bed during spring tides or storms.

Tidal flows may need to be measured at the designated beds as it may be difficult to extrapolate from Tidal Stream Atlas data. It would be of fundamental interest to know more about the details of the turbulent flows across horse mussel beds and hence the water mass available for filtration. Measurements of seston on the upstream and downstream sides of the bed could be compared.

5. Recruitment

Recruitment of spat to horse mussel populations is usually erratic (Brown, 1984). Clues to this may be obtained from studies of the age distribution of the populations. However, the animals do need to be aged as modality in size distributions is not a good guide to the ages. An initial study of age distribution in each of the designated beds is recommended. In contrast to *Mytilus*, simple counting of annual growth rings after gentle cleaning with bleach solution seems to be a reliable method in most cases. In cases where difficulty is encountered the shell sectioning - acetate peel technique, as often used for *Mytilus*, can successfully be used (Anwar et al., 1990). After this, ways need to be considered for monitoring recruitment on an annual basis and possibly on a seasonal basis. Methods need to be found to do this that are not too destructive. In beds of *Mytilus*, spat recruitment has been recorded by putting out spat collectors. Plastic pan scourers have been used as a standardised item for this. As an initial trial, it would be possible to attach pan scourers to moored weights to see if *Modiolus* spat would settle on them.

6. Predation and Disease

Abnormal levels of predation should be detectable from the video and camera sledge monitoring. Diseases and parasitism in *Mytilus* are quite well known but very much less so in *Modiolus*. Studies of these would mainly be justifiable if abnormal mortality was detected. Parasitic castration due to trematode parasites may warrant investigation.

7. Associated Fauna

Preliminary indications are that there are a range of variations in the mix of associated species associated with the mound forming types of *Modiolus* beds. Thus the appearance of samples dredged from off the south of the Isle of Man, before that bed declined, was rather different from samples taken at the same time from beds only less than 30 miles away in apparently similar situations NW of Anglesey. The most obvious difference was that the Manx one had substantial numbers of the very large barnacle *Balanus hameri* growing on the mussels, while off Anglesey they were absent.

Temporal changes are to be expected that are in no way related to the long-term structural integrity of the persistent *Modiolus* beds. *Ophiothrix fragilis* is often abundant in *Modiolus* beds at present, but examining long-term records from the English Channel, Holme (1983)

showed that there had been major changes to brittle star beds off Plymouth apparently linked to changes in the population of the predatory starfish *Luidia ciliaris*.

a. Epifaunal biodiversity

An initial inventory of the associated epifauna of each bed will be needed. Published and anecdotal evidence suggests that different beds have differences in the degree of dominance by different epifaunal organisms. The reasons for such differences are not clear. Some are dominated by turfs of hydroids and bryozoans, others have a predominance of *Alcyonium*, others have more sponges, while in others there are more barnacle and calcareous worm tube crusts on the mussels.

After the initial inventory, any major changes to the dominant epifauna should be detectable using the video or camera sledge transects made to assess cover by mussels. Sufficient images should be available to satisfy statistical criteria for the reliability of detecting changes. Larger mobile epifauna such as whelks and starfish should be detectable by the same means, but consideration might be given to deploying appropriate traps for some of the smaller epifauna.

b. Infaunal biodiversity

It is impossible to sample the infauna without destructive sampling. The techniques for infaunal sampling are well reviewed elsewhere, though there are complications in doing this quantitatively in mussel beds because of the abundance of solid items liable to block the jaws of grabs. The infauna associated with beds where much faecal matter accumulates will be rather different from the gravel binding type of bed. In the former type there will be obvious parallels with the fauna known to be associated with enrichment by anthropogenic organic wastes. It is reasonable to extrapolate from the literature on Mytilus to suggest that in summer the faecal matter deposited by the horse mussels will have a higher content of labile organic matter than sediments depositing without the agency of mussel filtration. Responses to the organic enrichment can be seen both at a gross scale and on the scale of a crevice fauna. Thus although horse mussel beds may be in areas with moderately strong tidal currents, part of the associated fauna is made up of a suite of organisms more often found in more sheltered conditions. For example in the Lleyn Modiolus bed miniature versions of the Abra community are to be found between the shells of very large dead horse mussels that have remained in the life position but which have nearly filled with sediment. As far as is known there have been no studies of the small scale heterogeneity likely to be found amongst the infauna associated with the crests and troughs of horse mussel beds. It will not be possible without further study to extrapolate directly from soft sediment sampling protocols to determine how many replicates are needed to detect prescribed levels of change.

F. MYTILUS EDULIS

1. Extent of Beds

Aerial photography with image processing and combined with ground estimates of biomass has been found suitable for extensive surveys of the Wash (Walker et al., 1990). The method compares favourably with transect based survey methods. Aerial surveys in Denmark calibrated by ground transects were reported by Munch-Petersen & Kristensen (1989). Ideally surveys should be conducted annually within cSACs with good examples of *Mytilus* reefs.

Where the mussels form a shore belt in land-locked fjords Olafsson & Hoisaeter (1988) used a two stage stratified sampling design to estimate populations per length of shore. This involved initial mapping of 86 km of steep rocky shoreline into short lengths of shore, each described according to four subjectively chosen categories of mussel density. Representative samples of these smaller shorelines were then subsampled by removing and weighing strips of mussels (using divers due to the inaccessibility of the shores) and the results extrapolated to produce biomass figures. Full details of the method, which is claimed to give reliable results from minimal sampling, are given in Olafsson & Hoisaeter (1988). Similar methods might be useful where, for any reason, aerial surveys are impracticable.

2. Patch Dynamics

Although monitoring may indicate beds as a whole may be stable, patches within it are much more dynamic (Svane & Ompi, 1993).

3. Ageing Mussels

Mussels are more reliably aged by the annual growth bands in shell sections using acetate peels than by external marks (Richardson & Seed, 1990; Seed & Richardson, 1990). Furthermore, samples of *M. edulis* taken from offshore platforms exposed for known periods suggested that year classes found from sections do not coincide with apparent size-class frequency nodes (Richardson et al., 1990).

4. Condition of Mussels

Because they are widely available sessile filter feeders, mussels of the genus *Mytilus* are routinely used in biomonitoring and as model organisms for toxicological investigations (see reviews in Gosling ed., 1992). Duration of survival out of water, provides a simple measure that integrates stress effects caused by accumulations of contaminants (Smaal, et al., 1990). Various measures of condition index were compared by Davenport & Chen (1987).

5. Embryo Assay

In bivalves, embryonic development is very sensitive to reduced water quality. The D larva stage in *Mytilus edulis* is reached in 48 hours and comparisons between numbers reaching this stage between artificial fertilisations done in control and test waters provide useful indications of environmental quality (Quiniou & Toularastel, 1992).

Laser diffraction techniques could prove useful in measuring the short-term effects of various environmental conditions, such as episodes of high sediment loads from resulting dredging projects, which can affect growth (Sushko & Freeman, 1991).

6. Associated Fauna

The use of meiobenthos in pollution monitoring studies was reviewed by Vincx & Heip (1991). Since there are similarities between the biodeposition of faecal matter from mussels with organic loads higher than the surrounding sediment there are obvious parallels to be drawn between enrichment due to sewage and that due to the deposits from high concentrations of filter feeding invertebrates. Techniques for monitoring the infaunal macrobenthos should also broadly follow the protocols laid down for pollution monitoring. It is however essential that there is much more precision in the placing of the samples than when ordinary soft

sediment locations are monitored. Sampling needs to be carefully stratified so that replicates truly come from biogenic reef communities.

G. SERPULA VERMICULARIS

Monitoring requirements of serpulid reefs at present need to be tailored specifically towards Loch Creran, the only UK location where good examples are known to occur with certainty, and where a good baseline knowledge of extent, number and size of reefs exists for the whole loch (Moore, 1996).

1. Distribution and Extent of Reefs

In view of the rapid loss of reefs reported from Loch Sween in recent years, it is recommended that a broad indication of the extent and integrity of the reefs over the whole loch is carried out at least every 5 years, to include any changes in depth limits. A number of options would seem to be available for monitoring of the extent and integrity of serpulid reefs. Since they are clearly well developed structures they are likely to be visualised well with acoustic methods such as sidescan sonar and RoxAnn[™], though there are sometimes limitations with RoxAnn[™] in very shallow waters. There is presently no experience with these methods for serpulid reefs, however. As always with acoustic methods, ground truthing would be required, although perhaps less extensively than with some other communities given the distinctiveness of the serpulid reefs. Diver surveys and video surveys (either diver-operated or ROV) both have potential for this.

ROV surveys have been successfully carried out on serpulid reefs in Loch Creran recently (Donnan, pers. comm.). Again, the large size and obviousness of the reefs makes them ideal for study by this method. Mapping of the distribution and integrity of reef areas could be carried out using ROV, perhaps in combination with acoustic methods. Towed video would, of course be far too damaging to be of use.

2. Detailed Monitoring of Reefs and Associated Communities

More detailed studies of one or more limited areas should be carried out more regularly, perhaps annually, including measurements of reef dimensions to give annual accretion rates, ratio of living / dead worms and observations on the general state of the reefs (siltation, epiphyte cover). The method of attaching portions of *S. alveolata* reef to plywood bases and subsequent measurement of volume (Bamber& Irvine, 1997; see section C above) may be adaptable to *S. vermicularis* for more detailed growth studies. Associated fauna should also be monitored. Study of associated fauna has so far been limited to diver surveys (e.g. Howson et al., 1996; Bosence, 1973; 1979), which work well only for those animals and plants visible at the surface of the colonies. Given the relatively open structure of the reefs, it is likely that many more species and organisms would be found by destructive sampling. However, this should be limited to very small amounts until the potential for regeneration of areas, either naturally or with provision of suitable substrata, has been established.

3. Recruitment

Unusually intense larval recruitment seems to be a crucial factor in serpulid reef development. Regular monitoring of recruitment using settlement plates would seem to be sensible in order to help to identify causes of any population changes.

4. Physical and Chemical Parameters

It is difficult to make precise recommendations for monitoring of physical and chemical parameters, including water quality, since there is little knowledge of the requirements of the organism. However, suspended sediment levels, particularly in the settlement period, may be worth measuring in relation to larval settlement, since the presence of too much silt on the substratum may be inhibitory. Likewise, low oxygen levels are thought to limit downward extension of the reefs. In the typical enclosed loch situation in which the reefs occur low oxygen levels are likely to occur in the deeper waters; they should therefore be measured routinely.

5. Fishing

Fishing operations in the loch should be monitored, primarily so that any potential damage might be more easily forestalled but also so that, in the event of any sudden damage, the likelihood that fishing was the cause can be determined.

H. KEY POINTS FROM CHAPTER VII

- Monitoring suggestions for each biogenic reef type have been given. It seems likely that aerial photographs backed up by groundtruthing would provide a useful way of monitoring changes in the extent and integrity of intertidal reef areas, as has been well demonstrated for *Mytilus* reefs. The method is as yet unproven for *S. alveolata* reef areas, although it seems likely to be successful. There are a variety of standard techniques available for monitoring changes in community structure, including the richness and diversity of associated fauna.
- Monitoring of changes in the extent of sublittoral biogenic reef communities will require acoustic methods in many cases, particularly where they are deep and extensive. Acoustic methods always require some groundtruthing, whether by video/ROV, and in some circumstances perhaps diver surveys. Present experience of both is limited but very promising. Moreover, at present advances in technology for acquiring and processing data are rapid and cost is generally falling. Recommended frequency of monitoring depends on stability of the community. *Modiolus* reefs would require monitoring far less frequently than other communities, and *Mytilus, Sabellaria alveolata* and *S. spinulosa* reefs should preferably be monitored annually. Serpulid reefs are probably of intermediate or longer stability, but the whole of Loch Creran should be surveyed at least every five years (and more frequently if recruitment studies or annual surveys of smaller areas indicate potential problems) because of the apparent rapid loss of reefs in Loch Sween for unknown reasons.
- Techniques for monitoring the richness and diversity of associated communities subtidally are more problematical than intertidally and likely in many cases to be limited to surveys of large epifauna by video/ROV in deeper areas, or diver recording surveys and fixed photographic surveys in shallow areas. These methods have limitations but are likely to be of use in detecting gross changes (Worsfold & Dyer, 1997).
- Recruitment processes are important in all biogenic reef communities and it is suggested that efforts are made to monitor settlement patterns both spatially and temporally (preferably annually) in all these communities. Such monitoring would be essential to identify the cause of any change in status of the reefs.

VIII GAPS AND REQUIREMENTS FOR FURTHER RESEARCH

A. SABELLARIA ALVEOLATA

1. Methods for Monitoring Distribution

It is anticipated that in many cases monitoring of the extent of *Sabellaria alveolata* reefs would probably be best carried out using aerial photography plus groundtruthing, but it has not yet been demonstrated conclusively that reefs can clearly be picked out by this method. However, it is anticipated that work by English Nature on the Cumbrian / Solway coast area will clarify this in the near future (Lumb, pers. comm.) (see previous chapter).

2. Range of Recruitment

It is also essential to know the range over which *Sabellaria* recruits. This question can be addressed using molecular markers of populations to measure the degree of interchange between them. At the simplest level allozyme based methods could be used to compare the gene flow between populations, although this may not have the discriminating power of such methods as microsatellite analysis or RAPDs (Random Amplified Polymorphic DNA). Wilson (1971) proposed that larval swarms occurred. If this is the case there could be evidence of genetic variation between reefs of different ages in a locality. The failure of *Sabellaria alveolata* to colonise the Isle of Man also points to quite localised recruitment cells. It would be useful to be able allocate reefs in particular SACs to a grouping.

3. Interspecific Interactions

Other gaps in our knowledge of Sabellaria include interactions with other species. We do not know what positive and negative interactions occur between Sabellaria and other species. In many instances both mussels and Sabellaria alveolata are common, presumably as similar factors influence the larval supply of both. The degree of interaction of mussels and Sabellaria needs to be investigated by controlled experimental manipulations (i.e. removals and additions of mussels). Mussels may hasten the decline of older colonies. There is also the need to investigate the increase of diversity of fauna and flora associated with Sabellaria, and in particular what happens when reefs are formed, grow and decline. It is apparent that S. alveolata reefs do enhance diversity but further work is necessary to clarify certain issues: comparisons need to be made between the various physical forms of Sabellaria (sheets / hummocks / reefs) to see if there are differences in the associated communities they support; the effects of size and age of the reefs needs to be further investigated; and regional differences should be investigated. We suspect that interference with foraging by limpets, and possibly winkles and trochids, may be involved, in turn leading to proliferation of algae. Again manipulative field experiments (grazer removals, additions) need to be undertaken. Seaweed growth may ultimately lead to the decline of older colonies. There is a need to investigate this by manipulating algal growth - particularly fucoids on top of Sabellaria. Such studies would require detailed work on a large number of individual reef areas, with multivariate statistical analysis. Finally, the reasons why there are only limited reports of S. alveolata extending subtidally are unknown; it seems possible from known distributions that the ability to extend subtidally depends at least partially on a high level of turbidity preventing algae from outcompeting the *Sabellaria*, but this idea has not been investigated.

4. Geographical Variations in Reproduction, Growth and Longevity

Persistence of *Sabellaria alveolata* depends on continued recruitment. Therefore basic work on the reproductive seasonality throughout its UK range needs to be undertaken to see if successful spawning occurs at the edges of its range. Increases in the abundance and extent of *Sabellaria alveolata* at the edge of its range in recent years may be a response to warmer weather, and this hypothesis needs to be tested.

Growth rates and longevity of colonies may also vary geographically. There is a considerable amount of information on this subject from the work of Wilson in Cornwall (eg Wilson, 1971a,b) and Gruet in France (eg Gruet, 1981; Gruet, 1982; Gruet, 1985; Gruet, 1986; Gruet, 1989). However, growth rates and longevity/stability of colonies in the Cumbrian area might be expected to be different since the species is here at its northerly limit of distribution. Moreover, Wilson worked only on colonies on bedrock and large boulders; colonies on less stable substrata such as cobble and smaller boulders, as frequently occur, might be expected to be less stable and composed of younger individuals on average.

5. Recovery of Damaged Reefs

Recovery of damaged reefs has not been studied in detail. Experiments could be carried out simulating heavier damage and on a wider range of reef morphologies than the preliminary work carried out by Cunningham et al. (1984). Comparisons could also be made of reefs in acessible and heavily used tourist areas and less accessible / protected sites. SACs could play a useful role in such comparisons. Care would be needed to ensure that the scale of damage simulated was realistic in relation to levels actually observed, since it is presently not very clear what levels of damage are commonly sustained in heavily used areas.

6. Role in Stabilisation of Boulder / Cobble Shores

The role of *S. alveolata* in conferring stability to boulders and cobble shores by cementing together potentially mobile boulders/cobbles needs to be evaluated. They could play an important role - along with mussels - in maintaining the integrity of the coastline.

7. Predators

At present we do not know what the main predators of *S. alveolata* are, nor do we have any knowledge of their effects. Predation by birds has never been mentioned in any reports we have seen, so it seems likely that the main predators, if any, are marine organisms such as crabs. This might be tackled initially by fixed underwater video cameras to record predatory activity, with gut analysis of suspected predators.

B. SABELLARIA SPINULOSA

A number of requirements for further study of *S. spinulosa* reefs were outlined by Holt et al. (1997) (Holt et al., 1997a). As part of that study Holt et al. identified gaps in knowledge relating to the requirements for the identification of 'Critical Natural Capital' (or Critical Environmental Capital) (CNC or CEC) in the maritime zone, as proposed by Masters & Gee (1995). The summary table from Holt et al. (1997) (Holt et al., 1997a) giving the information requirements identified by Masters & Gee and the present state of knowledge identified by Holt et al. is given here in Appendix 1. This work highlighted the lack of knowledge on recruitment and regeneration processes for *S. spinulosa* reefs.

1. Geographical Distribution

The geographical distribution of *Sabellaria spinulosa* aggregations, particularly the stable, well developed reefs described in the mouth of the Wash, is not known.

2. Recruitment, Longevity and Stability

There is a need for information on recruitment, longevity and stability on a variety of *S. spinulosa* reefs from areas where they appear to be mainly annual and areas where they may be more stable and long lived. Settlement surfaces, bearing varying amounts of existing *Sabellaria spinulosa*, could be placed in a variety of suitable locations and subsequently monitored monthly. A minimum three year programme was suggested. This would be a relatively expensive programme, requiring considerable boat time, and probably diving studies, in more than one site. It should ideally be carried out in conjunction with an aggregate dredging monitoring programme such as that outlined in chapter VII.

3. Recovery Potential

Clearly one of the most informative programmes which can be envisaged would be observations on recovery in an area where fishing activities have previously had effects but have ceased. Within Britain this would probably be limited to the Morecambe Bay area, about which we presently have very little information. Fishery exclusion areas are politically and practically difficult to obtain, and notoriously difficult to police even when close inshore and highly visible. The apparent cessation of the commercial pink shrimp fishery in Morecambe bay is therefore very promising in this regard, though of course if the reefs are no longer present then bottom fishing for other species (*Crangon*, flatfish) may have become possible in the same area. Sankey (1987) implies that these areas may remain rough and as such may not be fished. Recent LIFE funded surveys of some appropriate parts of Morecambe Bay have confirmed that the bottom remains rough but have so far failed to find any S. spinulosa. If possible this work should be continued to cover remaining areas known to have supported S. spinulosa reefs. If these also fail to find S. spinulosa this would be strong evidence for a lack of larval supply following widespread loss of the reefs, although other factors such as changes in bottom characteristics can not be completely ruled out.

4. Interspecific Competition

Interactions with other filter feeders need to be investigated. Very low recruitment, growth and (probably) fecundity in an area of the Bristol Channel in 1976 were all attributed to dense populations of the brittle star *Ophiothrix fragilis* preventing adequate feeding (chapter V). In one area of the Waddensee *S. spinulosa* reefs were permanently replaced by communities often dominated by *Mytilus edulis* (chapter VI) but it seems likely that differential sensitivities to the physical impacts of fishing are more important in this regard. Effects of varying densities of *Ophiothrix* on *S. spinulosa* communities need to be investigated, including rates of removal of the *Sabellaria* larvae themselves from the water, as well as settlement, recruitment, feeding rates, growth, and fecundity. Unfortunately investigations of this nature are likely to prove extremely difficult.

5. Nature of Associated Communities

There is presently little information upon the associated community on reefs. The newly discovered areas within and adjacent to the Wash and North Norfolk cSAC present an ideal opportunity to gain initial ideas of the richness and diversity of associated communities, including seasonal variations. Initial information requires sampling for investigation of both large epifauna and flora and cryptic biota, plus observational methods such as video, photographic or diver surveys in order to look at broader spatial variations.

C. MODIOLUS MODIOLUS

1. Monitoring Methods

Although several studies show that horse mussel beds can be mapped using acoustic methods, the protocols for doing this for monitoring in the long-term need more refinement and testing. The sensitivity of the method for determining replicable boundaries needs more testing especially where the beds become patchy. With techniques that rely on measures of the acoustic reflectivity of the seabed special attention needs to be given to the optimum spacing of survey lines and the effects of this on results from computer generated interpolations.

Protocols need to be developed for diver transects across horse mussel beds, particularly if the same lines are to be repeatable.

Some experimentation is needed to see whether the towing of camera sledges across a horse mussel bed causes too much incidental damage for this method to be used in the long-term.

2. Recovery Potential

That horse mussel beds can be destroyed by repeated scallop dredging is well established. However, the recovery potential of the beds to relatively small impacts needs to be investigated. For example if a cut is made through a bed through a scallop dredge being towed through it how long does the scar persist? Do the clumps of mussels spread into the gap? Indeed, how long do gaps in the bed made by scientific sampling persist? This is important in relation to long-term monitoring of populations where some destructive sampling is almost unavoidable.

Although it seems inconceivable that large areas could be artificially regenerated, it has been suggested in the Draft UK Biodiversity Action Plan for *Modiolus* beds there may be potential for mitigation of small scale damage by moving *Modiolus* from non-reef areas. This would inevitably have negative impacts on the areas from which the *Modiolus* were collected. The true potential, including negative aspects, of attempts to recreate *Modiolus* reef areas need to be investigated.

3. Sensitivity to Pot Fishing

Tests are also needed to establish whether any significant damage is caused by whelk pots or other types of traps. High concentrations of whelk fishing activity is sometimes directed specifically to parts of the seabed where horse mussel beds enhance the whelk population.

4. Distribution of Modiolus Reef Biotopes

A biodiversity action plan is in preparation for *Modiolus* biotopes. It is therefore becoming increasingly important that more information is available on their wider distribution throughout UK shelf seas and away from the locations known from earlier studies. Searches of unpublished data in research vessel log books, combined with acoustic searches and drop down video makes this a practical proposition. This will provide a chance for the variations in the associated fauna, which distinguish different versions of the *Modiolus* biotopes, to be clarified. Special attention needs to be paid to the distribution of the gravel bound form of the *Modiolus* dominated biotopes. This seems to be much scarcer than the mud mound type and is presently not known from any cSACs or pSACs. Genetic checks should also be made that the *Modiolus* living infaunally in gravel are identical with those forming mud mounds.

5. Recruitment Processes

More work is needed on the patterns of spat recruitment to *Modiolus* beds. This might be achieved by deploying spat collectors of the plastic pan scourer type that have been successfully used with *Mytilus* (Gee & Warwick, 1996; King et al., 1990). Other artificial substrata with a complex geometry might also be tried (Jacobi & Langevin, 1996). With *Mytilus*, Gosling & Wilkins (1985) were able to demonstrate that cohorts settling at different times of the year were genetically different.

Genetic studies would be a useful way of measuring the degree of interchange between *Modiolus* populations. Traditional allozyme based methods could be used but greater discrimination would result from DNA-based probes such as RAPDS.

D. MYTILUS EDULIS

1. Associated Communities

The fauna associated on mussel clumps on soft sediment is far less well studied than in rocky shore mussel beds which have frequently been used as models for ecological hypotheses. There is thus room for more fundamental work on the way the infauna exploits the abundance of quite labile organic matter deposited within the matrix of a mussel mound. Because this is often a soft environment, ingenious ways will have to be found to gain access to the mussel mounds without trampling on and destroying the key features.

2. Comparison of Natural and Disturbed Reefs

The ecological consequences of mussel seed transplantation need to be studied further and comparisons made between the ecology of natural mussel beds and cultured plots.

Comparison is needed between the ecology and spat recruitment into an entirely undisturbed mussel bed and one which is quite intensively fished by hand.

3. Stock Recruitment Processes

Opportunities should be taken to maximise collaboration between fisheries agencies and conservation bodies over the monitoring of recruitment in mussels around the country. In particular there is an urgent need for understanding of the stock recruitment relationships

within the entire catchments of large embayments and the conditions that favour larval retention or survival in these locations.

E. SERPULA VERMICULARIS

1. Status in Loch Sween

Recent dive surveys within Loch Sween have reported only dead reefs, but unfortunately detailed information such as the areas covered but the dives, is not available (D. Donnan, pers. comm.). It would be worth carrying out further surveys using remote methods, particularly ROV and perhaps sidescan, and backed up by dives, in order to determine the true status of the reefs over the whole area.

2. Growth Rates

We have presently no direct knowledge of the rate of development of reefs over time, and relatively little knowledge of growth rates of individual worms. A diving survey to monitor a limited number of small known reefs initiated on settlement substrata such as shells would be simple and relatively inexpensive. Simple in situ measurements such as reef height and lateral dimensions plus photographs and a description would be valuable. Measuring individual worms in the early stages would give information on growth rates. Counting, or estimating, the number of worms in the early stages where practical might give information on recruitment to reefs which could supplement simple settlement plate experiments. Photographic monitoring of groups of worms within the reefs might yield information on growth rates, longevity and mortality rates of individual worms but this would depend to some extent upon the rate of accretion of additional worms to the reefs. The actual programme could be amended during progress but presently it would seem sensible to suggest visits very two months or so for the first year, biannually for the next year, and annually thereafter. For completeness a series of such observations at a number of depths and locations would be best, but even monitoring a small number of reefs at medium-depths in an area where reef development is known to be good would be valuable.

3. Associated Communities

There is presently no knowledge of associated fauna other than macrofauna easily visible on the surface of colonies. Research on this would be relatively easily if destructive sampling techniques were allowed and impossible otherwise. It is suspected that growth rates are such that a sensible destructive sampling programme could easily be supported, but for prudence this should be demonstrated first. This could be done by introducing suitable surfaces as part of the programme described above. Simple monitoring of the percentage of such surfaces which develop 'minireefs', perhaps categorised using some sort of simple scale (none; scattered worms; aggregations to up to x worms etc) would be a simple way of gaining useful information.

4. Potential for Artificial Regeneration

The possibility of transplantation within Loch Creran to supplement areas damaged for any reason should be investigated. There are two main potential methods which should be investigated: breaking off sections of existing reefs and moving them; and creating new 'minireefs' by placing suitable settlement tiles / shells / stones in suitable areas for subsequent movement. This latter option might be valuable if it is found that recruitment is better in

certain parts of the loch than others. This in turn could be investigated by the use of settlement plates.

Reintroduction of reefs to areas such as Loch Sween seems infeasible on present knowledge given the apparent need for dense retention of large numbers of larvae within the system. However, depending on the success of artificial settlement surfaces plus transplantation it may be worth reconsidering in the future.

5. Methods for Ageing Worms

Artificial settlement surfaces would also provide a source of worms of known ages. Simple investigations could then be carried out to find out whether shell morphology, or shell sectioning techniques, can be used to age individual worms.

6. Predators

There is presently little knowledge of the likely effects of predators upon the serpulid reefs. Static cameras left in situ would help to determine the likely main predators in Loch Creran and give some information on predation rates and methods.

F. KEY POINTS FROM CHAPTER VIII

Broad gaps in knowledge which have been identified include the lack of descriptions and data suitable for making judgements about the nature of many recorded communities and biotopes regarding their possible categorisation (or otherwise) as biogenic reefs, and the need for refinement of methods, particularly acoustic, for monitoring of the distribution of subtidal reefs, particularly *Modiolus* and *Sabellaria spinulosa*, but also *S. alveolata* and perhaps even *Mytilus*.

Areas requiring further study in relation to particular communities follow, with a rough prioritisation:

Sabellaria alveolata

High priority:

- suitability of aerial photographs for monitoring changes in distribution of reefs
- dispersal range
- interactions with other species including *Mytilus* and grazers, and biodiversity of associated communities

Medium priority:

- basic biology at extremes of range (reproductive seasonality, growth rates and longevity)
- growth rates and longevity/stability of reefs on different substrata
- recovery of heavily damaged reefs
- role in stabilisation of boulder / cobble shores

Low priority:

• what, if any, are the important predators

S. spinulosa

High priority:

- true distribution of reefs
- recruitment, longevity and stability in a variety of populations but especially the more long-lived ones
- composition of associated communities

Medium priority:

- potential for recovery after extensive damage (given medium priority only because there is already evidence that recovery is poor).
- interactions with other filter feeders such as *Ophiothrix* which may have the potential to reduce growth, recruitment and fecundity

Modiolus modiolus

High priority:

- true distribution of reef communities, especially the infaunal gravel bound type
- Survey methods (already under way)

Medium priority:

• between reef variation in associated fauna

Low priority:

- potential recovery from damage on a variety of scales
- recruitment patterns / dispersal of larvae

Mytilus edulis

High priority:

- ecological consequences of transplantation of mussel seed, including comparisons of the ecology with that of natural reefs
- comparison of spat recruitment in undisturbed and intensively fished reefs
- stock recruitment processes within the entire catchments of large embayments

Low priority:

• structure and dynamics of communities associated with highly organic rich mussel mud

Serpula vermicularis

High priority:

- true status of reefs in Loch Sween
- potential for mitigation such as by transplanting to regenerate areas of reef loss or damage

Medium priority:

- rate of growth and development of worms and reefs
- information on associated communities especially cryptic fauna
- major predators in Loch Creran and their likely importance

IX SYNTHESIS AND APPLICATION OF INFORMATION FOR CONSERVATION MANAGEMENT RELEVANT TO MARINE SACS.

A. DEFINING AND CATEGORISING BIOGENIC REEFS

There was difficulty in defining and categorising biogenic reef communities at the outset of this study. Much of the existing data and descriptions (including some MNCR biotopes) was not obtained with the category 'biogenic reefs' in mind and interpretation is therefore often difficult or ambiguous. This might indicate that further refinement of the definition of 'biogenic reefs' is required. During preparation of this work strong consideration was given to the idea of defining communities as reefs if they formed a layer two or more animals thick (so that the top animals were not living on the original substratum). It was felt that this was maybe realistic for mussels but less so for worms, especially *Sabellaria spinulosa* which can be quite small, and this idea has not been taken any further at this stage.

There are many cases where a community meets the two criteria suggested in chapter I (the unit should be substantial in size and should create a substratum which is reasonably discrete and substantially different to the underlying or surrounding substratum), <u>except</u> that it is not somewhat raised (i.e. it does not 'rise from the seabed' as in the JNCC definition of 'reefs'). Although in many cases it is probably more realistic to refer to these as beds, the ecology, biology, and sensitivity of these areas are nevertheless likely to be very similar to those of protruding reefs, and they have therefore been discussed here alongside true biogenic reef communities. There are also cases, particularly with *Mytilus*, where non-raised aggregations are formed on hard substrata. In general, these have not been interpreted as biogenic reefs for the purposes of this report.

B. CONSIDERATION OF BIOGENIC REEFS AS A GROUP

There is, perhaps surprisingly, little consistency in the biology, ecology and sensitivity within the grouping 'biogenic reefs', which is to some degree an artificial conglomerate of biotopes with differing characteristics. This is emphasised in Table 4, which summarises a number of important biological and ecological features of the five biogenic reef types. In addition to these points, the physical structure, size and shape of the reefs varies enormously both between, and to a lesser extent within, each species. It is clear that management issues must be considered separately for each type. Table 4 A summary of some of the major biological, ecological and sensitivity features of biogenic reefs according to presently available knowledge.

	S. alveolata	S. spinulosa	M. modiolus	M. edulis	S. vermicularis
Usual habitat	Rocks, boulders, cobble in intertidal & shallow subtidal with a good supply of suspended coarse sand	Turbid circalittoral mixed sediments	Circalittoral mixed sediments in a variety of current / wave exposures, varying from open coasts to enclosed sealochs	Firm mixed sediments in enclosed bays and estuaries	Very enclosed sheltered sea lochs, mixed sediments
Geographical distribution of reefs in Britain	South and west of Britain only	Fewer in Scottish waters (all 'reefs' including crusts)	Rare south of Severn & Humber Estuaries	Widespread	Loch Creran only
Rarity as a species	Moderate	Widespread and common	Widespread and common	Extremely widespread and common	Widespread and common
Rarity as a reef biotope	Fairly unusual	True reefs appear to be rare but less stable 'crusts' probably common, less so in Scotland	Scattered clumps much more widespread and common than very dense reefs or gravel embedded reefs	Common	Extremely rare
Natural variations in abundance over periods of a few years	Very high	Crusts annual & probably variable, others probably more stable	Low	Some extremely variable, others quite stable	Probably low
Reproduction & recruitment	Sexually mature in 1st year. Recruitment very variable. Settlement strongly induced by contact with adult tubes (living or dead)	Sexually mature in 1st year. Recruitment often seems variable. Settlement induced by contact with adult tubes (living or dead)	Sexually mature after 3-6 years. Recruitment often variable Juveniles survive best within byssus threads of adults	Sexually mature in 1 st year. Settlement often a two stage process. Recruitment highly variable	Sexually mature in 1st year. Preferential settlement on calcareous structures
Richness of associated communities	Varies from extremely low when colonies are young to moderate when colonies are older	Probably high or very high on stable reefs, less so on crusts	Very high	Usually low or moderate but higher than surrounding areas	Probably very high
Importance of predation	Not thought to be very important overall although crab predation was important in transplanted reefs	Not known.	Predation by invertebrates very important in first 3 or 4 years, low thereafter	Invertebrate and fish predation can be very high on small animals. Bird predation very high on adults	Not known.
Importance as food for other species	Probably low overall	May be moderately important for prawns?	Probably low overall	Extremely important for some birds, especially eiders and oystercatchers	Probably low overall
Known major sensitivities to human impacts	Possibly major changes to sediment regime (could be positive as well as negative effects)	Prawn trawling and probably aggregate extraction	Towed bottom gear (eg scallop and queen scallop dredges and trawls)	Overexploitation	Mooring of cages, organic waste disposal. Potentially queen scallop trawling & diver collection
Physical fragility	Moderate	Moderate?	Moderate (low if very recessed?)	Moderate	High
Recovery after damage	Probably generally good but possibly not after large scale losses or at extremes of range	Probably generally good but not if fishing impacts continue or if damage is over very wide areas	Likely to be very slow, and possibly not at all if completely lost, especially in enclosed areas	Generally very good but evidence of poor recovery after widespread losses	Probably slow, and not at all after large scale loss

C. CONSERVATION IMPORTANCE OF BIOGENIC REEFS

All five biogenic reef types are regarded as of high conservation importance for the reasons outlined in Table 5. This may not be apparent to many coastal users, particularly those involved in fishing, since many of these species are common and widespread. Conservation importance of biogenic reefs may need to be the subject of educational campaigns in order to secure support for their conservation. The use of the emotive term 'reef' could, of course, be of value in this regard. However, it conjures up images in the general public which are often far removed from the reality of the biotopes under discussion here. There is a danger both with the general public and conservation bodies that overemphasis of the term 'reef' could lead to an inflated opinion of the importance of some areas. A realistic approach needs to be adopted.

	Table 5 A summary of information relating to the conservation importance of biogenic reef biotopes according to criteria given in Hiscock (in prep).						
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	S. alveolata	S. spinulosa	M. modiolus	M. edulis	S. vermicularis
Rare or very restricted in distribution	Somewhat	Yes (true stable reefs as opposed to annual crusts)	Somewhat, especially some forms	No	Very
In decline or has been	Some suggestion of a decline in range	Yes	Yes	Overexploited in places but not really 'in decline'	Yes
High proportion of the regional or world extent	Yes world?	Yes regional?	Yes regional?	No	Yes world?
Particularly good or extensive examples of their type	Yes	Yes	Yes	Yes?	Yes
Keystone species providing a habitat for other species	Possiblyy more important subtidally than intertidally?	Yes	Yes	Yes	Yes
Biotopes with a particularly high species richness	No	Probably	Yes	No	Probably
Biotopes important for efficient functioning of regional ecosystems	No, though some role in stabilisation of some shores possible.	Probably not	? Possible nursery grounds ?	Yes	No
Of high aesthetic, symbolic or recreational importance	Arguably aesthetic?	No	No	Indirectly because of associated bird populations	Arguably aesthetic?

D. REPRESENTATION OF BIOGENIC REEFS WITHIN cSACs

Mytilus reef biotopes are well represented in presently designated cSACs and pSACs. Good quality intertidal and subtidal *Sabellaria alveolata* reef biotopes appear to be included within a number of cSACs, although it is unclear whether the extensive intertidal and subtidal reefs around Dubmill Point are included within the Solway Firth cSAC. *Modiolus* reef biotopes seem to come in a wider variety than other biogenic reefs, some of which presently fall within cSACs or pSACs. The apparently rarer type, infaunal reefs in areas of very strong tidal currents, are only known presently from nearby non-UK waters but seem likely to exist in UK waters. *Sabellaria spinulosa* stable reefs, as opposed to thin crusts, are known for certain from only one or two locations, but almost certainly one of these falls partially within the Wash and North Norfolk Coast cSAC. Within the UK, serpulid reefs are known only from Loch Creran (which also has *Modiolus* beds which probably qualify as reefs) so that they are not covered at all by any cSACs or pSACs.

E. LEVEL OF AVAILABLE INFORMATION

1. General

The level of available knowledge for *Mytilus* is very high, although much is directed at its ecology and biology in relation to rocky shores which is of little relevance to biogenic reefs (at least as they are considered here). The level of available knowledge of the other biotopes under consideration is moderate, with significant gaps which have been identified in chapter VIII. Some synthesis is presented in the bullet points below:

• There are still significant gaps in our knowledge of distribution of marine benthic biotopes, particularly in the subtidal. The JNCCs MNCR data base, upon which much of our knowledge is based, has significant gaps on the northern and eastern coasts of Scotland and open coasts of eastern England. As an example, around 6 km² of seabed supporting *Modiolus* reef communities (infaunal gravel bed type) were found to the north of the Isle of Man as recently as 1996, despite the continuous presence of a marine research laboratory within fifty km for over 100 years.

Similar arguments can be made in respect of stable, well developed *S. spinulosa* reefs, existence of which has been a contentious issue for many years, and which has only recently been confirmed in the mouth of the Wash.

• Lack of knowledge on rates of recovery after damage is a recurring theme. In *Mytilus* the pressing need is only for information on recovery after very large scale damage, while recovery from more modest scales of damage should be studied for the other biogenic reef communities. *Modiolus* communities in particular are thought to be likely to have extremely slow rates of recovery, potentially decades or more. *Sabellaria spinulosa* reefs have apparently been lost from several large areas due to fishing for prawns using bottom gear, and in at least some cases deliberate breaking up of the reefs using heavy fishing gear to improve the fishing To our knowledge none of these areas have recovered. It seems likely that this is largely because bottom fishing activities have continued, but we do not know whether, or how fast, reefs might return if bottom fishing ceased or reduced. Lack of recruitment may be a problem given the wide areas involved. This could be aggravated where fishing has resulted in the development of *Mytilus* dominated communities which might continue to dominate in the absence of heavy *Sabellaria* recruitment. Long-term fishing is thought to be able to alter sediment structure which conceivably might further influence the likelihood of recolonisation.

- Sensitivity to direct physical impacts in general is another recurring theme. Sensitivity is linked to some extent to structure of the reefs, to vulnerability in terms of position, and strongly to recoverability, which in general we know little about.
- Lack of knowledge of associated communities is a further recurring theme. This is less important for the intertidal (*Mytilus*, *S. alveolata*) than for the subtidal where communities are likely to be both richer and more diverse, and less well known.
- We know almost nothing about predators and their effects on the worm reefs (*Sabellaria, Serpula*) whereas there is a great deal of literature on the effects of predators on *Mytilus* and to a lesser degree *Modiolus*.
- There are a number of potentially important species interactions which need to be studied, including *Mytilus* and *S. alveolata* on scar grounds; *S. alveolata* and algae on rocky and shallow sublittoral shores. The possibility that *Ophiothrix* communities might spread over subtidal biogenic reef communities and prevent them from feeding and perhaps settling has been noted several times. This is rather speculative but is based on a number of known facts; dense beds of *Ophiothrix* are thought to have greatly reduced recruitment to at least one year class of *Sabellaria spinulosa*, and to have reduced feeding and fecundity, on reefs in the Bristol Channel; *Ophiothrix* populations have been known to fluctuate greatly in some situations; *Ophiothrix* beds can be present on and near to *Modiolus* reef areas; *Ophiothrix* is a very efficient and relatively un-selective filter feeder which can take a wide range of food particles, and can feed well on *Artemia* larvae in laboratory conditions, for example (J. Allen, pers. comm.).

2. Prioritising Gaps in Knowledge

It is important to try to prioritise the gaps in knowledge. The following are thought to be of particularly high priority:

- Serpulid reefs are of national importance and are not found in any presently proposed cSACs. It would be extremely useful to know the true status in Loch Sween. This probably requires the preparation of as detailed a report as possible on the recent diving surveys (not presently available) followed if necessary by further surveys.
- Information on the potential for recovery of reefs of *Sabellaria spinulosa* and *Modiolus modiolus* damaged by physical impacts and especially by fishing is of high importance, but at present, given the political sensitivities of closure of fishing grounds, it is not likely that a realistic programme could be devised to investigate recovery from fishing impacts. In the absence of such a programme, studies on recruitment processes aimed at improving our knowledge of the major influences on them should take a high priority.
- Further information on distribution of *S. spinulosa* reefs and certain types of *Modiolus* communities is of high importance. Allied to this is the need for development of better, and standardised, survey and monitoring methods for subtidal biogenic reefs.
- Recruitment range and sources for *S. alveolata*, *S. spinulosa*, *Mytilus edulis* and *Modiolus modiolus* reefs need to be identified.
- A better understanding of the 'Added Value' of the biodiversity of reef areas versus adjacent areas, and in particular a better understanding of the role of reef builders as ecosystem engineers, would help in promoting the conservation of biogenic reefs.

• A better knowledge of the natural variation in extent, density and population structure of reefs, especially serpulid and *Sabellaria spinulosa* reefs, is required.

F. SOME IMPORTANT MANAGEMENT CONSIDERATIONS

Only the most important potentially damaging activities or other management considerations are mentioned here and the reader should refer to the relevant chapter for more details.

Limits of acceptable change for monitoring and management purposes are going to be very difficult to determine, except for *Modiolus* which appear to be relatively stable communities in which any detectable changes over periods of a few years are likely to be regarded as unacceptable. Intertidal *Sabellaria alveolata* populations are generally highly variable and it seems likely that large scale losses over wide areas can be attributable to natural causes such as cold winters or lack of recruitment. Even in areas where *S. alveolata* is always found, there may be very large scale fluctuations in populations over periods of years due to variations in recruitment. There is some evidence that recruitment cells are moderately localised, as with *Mytilus*, but considerably more information on the geographical scale over which recruitment occurs is essential with all species to be able to decide whether local action or more widespread action would be required to prevent, or mitigate, loss of communities in an SAC. For example, would the maintenance of the extensive populations at the Dubmill Point area of the Solway Firth SAC ensure future recruitment elsewhere in that SAC, or elsewhere along the Cumbrian Coast north of St Bees Head? It is presently not possible to answer such questions.

Some impacts are too widespread for local management decisions to be effective, but need to be recognised so that changes resulting from them may be distinguished from those where local action may be effective. These include general eutrophication; global warming; and diffuse pollutants. Apart from the obvious potential problems from anoxia and clogging of gills caused by dense phytoplankton blooms, one possible problem associated with eutrophication is that enrichment often appears to be associated with changes in the species composition of phytoplankton, often favouring smaller groups at the expense of diatoms (Smayda, 1990) and this could have unknown consequences for all filter feeding organisms including biogenic reef species.

In early guidance from the Scottish Office on proposed SACs (Anon., 1996) it is stated that "By their nature, reefs are protected from trawling and dredging and so this is not at present an issue for this habitat." While this is clearly true for the vast majority of rocky reefs it certainly does not apply to biogenic reefs. Extensive areas of Modiolus reef have been lost or damaged by trawling or dredging for scallops and queen scallops, including notably in Strangford Lough cSAC. Potential exists for similar fishing damage elsewhere, and there is a possibility that widespread damage has already occurred, for example, to Modiolus reefs in the Shetland Voes. The experience gained during the designation of Strangford Lough as an MNR in 1993 will be invaluable (Leekley, pers. comm.; Weyl, pers. comm.): Fisheries regulations preventing the use of mobile fishing gear in areas which include some relatively undisturbed beds of *Modiolus* were introduced in 1993. This was prior to designation but as a direct consequence of the MNR consultation procedure. There was some conflict with fishermen during this process and lessons may be learned from the experience. The opportunity now exists to study the recovery process in damaged areas (Service, pers. comm.).

Similarly, *Sabellaria spinulosa* reefs are widely been reported to have been lost in areas subject to fishing for pink shrimp, *Pandalus montagui*. Recovery after widespread loss appears to be extremely poor even in the absence of pink shrimp fishing, reasons for which are unknown. *Serpula vermicularis* reefs are not known to be heavily impacted by dredges and trawls, but would undoubtedly be very badly damaged by them.

In the case of all three of these species (*Modiolus modiolus*, *Sabellaria spinulosa* and *Serpula vermicularis*), where important reefs occur within cSACs in areas where trawling or dredging can occur they can only be protected from damage by prohibiting such bottom fishing.

Serpulid reefs are susceptible to physical damage and it seems likely that they would also be damaged by potting, and are known to be susceptible to damage by mooring systems for salmons cages. Likewise, *Modiolus* reefs and *Sabellaria spinulosa* reefs would doubtless be badly impacted by physical activities such as cable trenching and pipelaying. The latter is particularly likely to be directly affected by sand and gravel extraction since it tends to inhabit areas that are suitable for commercial exploitation of aggregates. Such activities should be prevented over areas of good quality reefs both within and, preferably, outside cSACs.

Mytilus alone of the biogenic reef species is of importance as a fishery. This may lead to conflict with fishermen and re-layers and those, such as SFCs, charged with managing the fishery. It must be taken into account that legislation frequently requires that the fishery is managed so as to actively develop the fishery. However, Mytilus is a resilient species, even in reef communities, which tends to regenerate quickly from natural losses except where these are on the scale of entire large embayments such as the Wash, when recruitment failure can occur. In the most productive and exploitable biogenic reef communities the associated fauna and flora is relatively unremarkable, and ecologically speaking its importance as a food source for birds (particularly oystercatchers and eiders, but also others) is likely to be of overriding importance in many areas. It should therefore be possible to find compromises which allow active developments of fisheries without detriment to bird populations, which are likely mainly when mussels have been overexploited (which is of course also undesirable from the fishery point of view). Guidance will need to be sought from those responsible for management of SPAs, who will have a greater knowledge of the requirements of birds in such There should be opportunities for sharing resources between conservation instances. managers and fisheries scientists or managers in monitoring certain important aspects of biogenic reef communities such as recruitment, growth rates and size/age structure of populations, and this may in some cases include access to detailed unpublished historical data.

Where more stable *Mytilus* reefs exist within cSACs, greater importance should be attached to the associated fauna and flora (which are likely to be richer and more diverse) by carefully limiting, and if necessary preventing, exploitation.

Caution is required regarding *Modiolus* since there may be potential for a fishery. It is large, edible, and may turn out to be more accessible than has hitherto been known. Potential for cultivation has been commented on in the past (Comely, 1978) but seems unlikely. It certainly has a rapid growth rate in early years but obtaining seed mussels would be very difficult. Direct effects of aquaculture as a commercial venture would probably not be great but if it created a demand fishing on some grounds could conceivably become an issue. It is worth noting that fisheries legislation often refers only to shellfish in general terms, so that theoretically the requirement for fisheries managers to actively promote fisheries within an area could also include *Modiolus*. The authors are not aware of any significant areas where this is presently likely to be a problem, however.

There are a number of localised factors in enclosed sea lochs, such as organic enrichment from salmon farms, which could potentially be a problem for biogenic reefs found there. There is no evidence of any special sensitivity of any of the biogenic reefs under study to such enrichment, and sensible location of farms should be able to prevent widespread damage.

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APPENDIX 1

Assessing the extent to which present knowledge of sensitivity allows assessment of criteria for identifying Critical Natural Capital (CNC). Taken from Holt et al. (1997)

The following questions are those which need to be asked in order to identify CNC in the maritime zone, according to Masters and Gee (1995, Appendix 1b) who used the term Critical Environmental Capital (CEC). CEC is considered as a parallel to Critical Natural Capital (CNC) Gillespie & Shepherd (1995). Comments on the present state of knowledge regarding sensitivity are made where relevant. Some of the questions can only be effectively answered in relation to specific sites. The questions are from flow charts which are not given here.

a) Species Reproduction These questions test the ability of key species to regenerate and reproduce themselves.

What key species are present on site?	<i>Sabellaria spinulosa</i> can be regarded as a key species when it forms long lasting reefs, but might not if the population is strongly annual.
Are any key species longlived (25+ years)?	Not long-lived as individual animals but possibly so as reefs. Insufficient information on longevity/stability of reefs.
Do these [long lived] species have reproductional rates such that generational turnover is 25+ years?	No.
Is the populational trend of any key species declining?	Some areas of reef have been lost in Morecambe Bay and the Wash, and in the southern North Sea.
Can this decline be halted and reversed by human intervention?	Insufficient knowledge for longer lived, more stable reefs, which are likely to be the ones most at risk.

b) Species Physical Sensitivity This section addresses the sensitivity of key species to physical disturbance, and the effect this may have on their fitness.

Are these species habitat specific?	Generally yes, though we do not know in detail how much hard bottom is needed. High sediment loadings are required in the water. Presence of other <i>Sabellaria spinulosa</i> is likely to be very important.
Are any of key species particularly sensitive to physical damage, disturbance or pollution?	Can be very sensitive to fishing and possibly other physical disturbance, probably not particularly sensitive to pollution in general.
If the site is threatened by these impacts, could human intervention make good the resulting damage?	Insufficient experience or knowledge to answer this properly, but seems unlikely.

c) Island Biogeography These criteria relate to the ability of key species to (re)colonise a site.

Are any key species at the site isolated by physical space or barriers from the nearest neighbouring colony?	Not relevant to this study.
Are these barriers impenetrable? Or Is the nearest neighbouring source of recolonisation beyond the normal dispersal range of these key species?	Not relevant to this study. No direct knowledge of dispersal range though larvae reported to be in the water for 2-3 months before settling so likely to be considerable.
Could recolonisation of key species be achieved by human intervention (technically and financially)?	No knowledge therefore seems unlikely.

d) **Natural Processes** These criteria relate to the role a site may play in coastal processes, in earth science interest, or coastal defence.

Does the site contain features that potentially make a significant contribution to coast protection / sea defence?	Not relevant to this study. <i>S. spinulosa</i> reefs seem unlikely to perform this role alone.
Would it be technically and financially feasible to replace these natural features with engineered coastal protection/sea defence?	Not relevant to this study.
Does the site play a significant role in natural coastal processes?	Not known but seems unlikely.
Would it be technically and financially feasible to maintain these processes at the site artificially?	See above.

e) **Technological Factors: Ecological Restoration** These criteria consider whether it is technically and financially possible to restore a natural habitat/community artificially.

Should the site be destroyed, could the conditions that existed previously be reinstated/recreated at the same site and or another available location within the natural area?	Not relevant to this study.
Would key species be able to recolonise site naturally? (refer to biogeography criteria).	Where <i>S. spinulosa</i> acts as an annual we may often be able to answer yes quite confidently to this question. However, where there are apparently more long-lived stable reefs, we will not be able to answer the question confidently.
Would it be technically and financially feasible to restore these key species to the site artificially?	No knowledge therefore seems unlikely.

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