SEA PENS AND BURROWING MEGAFAUNA

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

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PREFACE

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

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

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

- Sandbanks which are slightly covered by sea water all the time,
- Estuaries
- Mudflats and sandflats not covered by seawater at low-tide,
- Large shallow inlets and bays
- Lagoons
- Reefs
- Submerged or partly submerged sea caves

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

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

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

- key constituent of several candidate SACs;

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

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

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

Project context and study aims

A number of sites around the UK of high scientific and conservation importance have been designated as marine Special Areas of Conservation (SACs) under the terms of the EU Habitats and Species Directive. As a contribution to the development of management plans for marine SACs, scientific reviews have been commissioned of the dynamics and sensitivity characteristics of selected biotope complexes found at some or all of the sites. These reviews are intended to summarize the available information relevant to conservation management, including the ecological characteristics of each biotope complex, its conservation importance, its sensitivity to natural and human-induced environmental changes, and the monitoring options suitable for use in marine SACs. Attention is focused on 12 candidate SACs selected as ‘demonstration’ sites. This report covers soft-sediment biotopes characterized by sea pens and burrowing megafauna. This biotope complex does not correspond exactly to any category defined in Annex I of the Habitats Directive, but comes closest to the broad heading of ‘Sandbanks covered by sea water at all times’. Particular examples are also located within ‘Large shallow inlets and bays’.

Nature and importance of the biotope complex

The ‘Sea pens and burrowing megafauna’ biotope complex is found on sandy and muddy substrata in sheltered, fully marine conditions. It is characterized by three species of colonial anthozoans (*Virgularia mirabilis, Pennatula phosphorea* and *Funiculina quadrangularis*), and a functionally-defined grouping of animals (‘burrowing megafauna’) which construct large, long-lasting burrows in the bottom sediments. The burrowing megafauna is a taxonomically-diverse assemblage of crustaceans (eg. *Callianassa subterranea*, *Calocaris macandreae*, *Nephrops norvegicus*), worms (eg. *Maxmuelleria lankesteri*) and fish (eg. *Cepola rubescens, Lesueurigobius friesii*). Burrowing megafauna are difficult to sample using traditional ship-borne equipment, and most of our information on their ecology has been obtained in the last two decades using SCUBA diving and underwater video.

Sea pens and burrowing megafauna are considered jointly in this review because they coexist in many sediment biotopes. However, these two groups of organisms are functionally and ecologically dissimilar in most other respects, and they are not invariably associated with each other.

The biotope complex supports a major fishery for one of its characteristic species, *Nephrops norvegicus*, and so is of considerable economic importance. Its scientific importance lies in the potential effects of burrowing and other animal activity on the structure and chemistry of marine sediments. Biological sediment disturbance (‘bioturbation’) can affect the transport and distribution of pollutants such as radionuclides and heavy metals. Shallow coastal sediment areas are useful natural ‘laboratories’ for studying this process, and bioturbation is currently a very active field of research. Examples of the biotope complex in the UK are of conservation importance as the best-studied and most accessible representatives of their kind. Characteristic species with highly localized distributions include the sea pen *Funiculina quadrangularis* and the anemone *Pachycerianthus multiplicatus*. The sediments also support a rich fauna of smaller animals and so form an important reservoir of biodiversity.

Distribution in the UK and elsewhere

Seven biotopes currently recognised in the MNCR classification fall within this complex. Collectively, the biotope complex is found widely around the British Isles. Examples are known from the North Sea, Irish Sea and from many of the Scottish sea lochs. Of the 12 ‘demonstration’ SACs, the biotope complex is represented in seven, and probably absent in the remaining five. Its spatial extent has been mapped in Loch nam Madadh (Loch Maddy), the Sound of Arisaig, Strangford Lough and the Berwickshire/North Northumberland Coast. Burrowing megafauna have also been recorded in Cardigan Bay and Plymouth Sound, while megafauna and sea pens also occur in Portland Harbour, adjoining the Fleet SAC. There is as yet no detailed information on community composition and species abundance in any of the ‘demonstration’ SACs. Considering other candidate or possible SACs, the best examples of the biotope complex occur in Loch Duich, which supports the rare deep mud biotope characterized by *Funiculina quadrangularis* and *Pachycerianthus multiplicatus*.

Outside British and Irish waters, similar biotopes exist in the Adriatic and Aegean Seas, and probably occur in coastal and shelf sediments in many other areas of the world.

Environmental requirements

Biotopes included within this complex exist from the shallow subtidal (< 10 m) to over 100 m in depth in conditions of fully marine salinity. They are always highly sheltered from wave action and subject to weak or negligible tidal streams. Sediment particle size distribution and organic content have a major influence on the abundance and composition of megafaunal burrowing communities. These two environmental parameters are closely interrelated, with finer-grained sediments typically having a higher organic content than coarser-grained substrata. Some megafaunal burrowers are characteristic of muddy, organic-rich substrata, others can inhabit a wider range of sediment types. Megafauna are usually absent from coarse sands, probably because these are unfavourable to burrow maintenance and generally have a low organic content. *Virgularia mirabilis* inhabits a broader range of sediments than the other two sea pen species. The biotopes of the north-eastern Irish Sea have been surveyed using towed video, and demonstrate how sea pen and megafaunal communities change across a gradient of sediment types.

Biology and ecological functioning

The community ecology of subtidal sediment biotopes is quite poorly-understood in comparison with the more accessible and longer-studied intertidal zone. The life cycle and population biology of *Nephrops norvegicus* has been the subject of much attention because of commercial importance of the species, but far less is known about most of the other megafaunal burrowers. Different species can contrast markedly, for example, among the thalassinidean mud-shrimps, *Calocaris macandreae* is known to reproduce slowly, live for up to ten years, and maintain very stable population numbers, whereas *Callianassa subterranea* produces more eggs and has a much shorter life span. Almost nothing is known about the population dynamics of the British sea pens, but data from other species suggest that they are likely to be long-lived and slow-growing, with patchy and intermittent recruitment.

Interconnections between burrows are quite common where several megafaunal species occur in the same habitat. Long-lasting burrows such as those of echiuran worms provide shelter for a variety of small polychaetes and bivalves, but no obligate symbiotic relationships have yet been described. Some unusual sessile animals can be found growing on the bodies of burrowing crustaceans, including one species recently-described from the mouthparts of *Nephrops norvegicus* which appears to represent a hitherto unknown animal phylum. The rarely-recorded deep-water brittlestar *Asteronyx loveni* occurs in association with the sea pen *Funiculina quadrangularis* at one known location (Loch Hourn) on the west coast of Scotland.

Various megafaunal burrowers are preyed upon by fish, but very few specialist predator of sea pens are known from British waters. The importance of predation as a structuring factor in these biotopes is unknown. Sediment disturbance by the larger burrowers can either enhance or reduce the abundance of the small polychaetes, bivalves and other animals that make up the sediment macrofauna. The ‘mosaic’ of disturbance patches created by megafaunal activity may be a factor acting to promote species diversity in the macrofaunal community. However, no single member of this biotope complex is known to be a ‘keystone’ species whose activity is essential to the maintenance of community structure.

Sensitivity to natural events

Subtidal sediment biotopes have not been studied in detail for enough time to assess their sensitivity to naturally-occurring environmental changes. Among the burrowing megafauna there are few studies of population dynamics over extended periods of time, but some contrasting patterns have been found. The mud-shrimp *Calocaris macandreae* has been found to maintain a stable population density over a ten-year period, whereas the echiuran worm *Echiurus echiurus* can experience wide fluctuations in numbers over a scale of 1 - 2 years. Biotopes in this complex are generally highly sheltered from natural physical disturbance (eg. storms). Recruitment rates of shallow-water megafaunal populations may be affected by unusual extremes of temperature, but very few supporting data are available.

The most important known agent of change in soft-sediment communities is organic enrichment and phenomena associated with it such as oxygen depletion. Oxygen depletion can occur naturally as a result of warm summer temperatures combined with prolonged stratification of the water column, but can also be induced by human activities such as sewage disposal or cage aquaculture.

No examples are known of biotopes within this complex undergoing major changes as a result of natural biological factors such as predation, parasitism or disease. However, in the last few years a dinoflagellate parasite has become prevalent in *Nephrops norvegicus* populations around the Scottish coasts, with very high levels of infestation recorded in some stocks. The ecological consequences of this are unknown but so far there appear to be no adverse effects on the *Nephrops* fishery.

Sensitivity to human activities

Observational evidence from towed video and diving surveys suggests that organic pollution and trawling for *Nephrops norvegicus* are the two human activities most likely to affect the biotope complex. Most *Nephrops* stocks around the UK are believed to be fully exploited (the fishery on the Fladen Ground in the North Sea is still expanding). Recent work in the western Irish Sea demonstrates the importance of hydrographic patterns to the maintenance of benthic populations. In this area, *Nephrops* larvae are retained by a seasonal gyre and settle back into the parent population. Largely self-seeding populations such as this may be more vulnerable to over-exploitation, since replenishment by recruits from outside the area may be limited. There is some evidence that trawling can locally deplete *Nephrops* populations in sea lochs. The effects of trawling on other burrowing megafauna are less clear, but one would expect deep-burrowing species to be much less affected by this form of disturbance. Of the three sea pen species *Funiculina quadrangularis* is likely to be the most vulnerable to trawl damage because of its brittle stalk and inability to retract into the sediment. However, experimental studies show that all three species can re-anchor themselves in the sediment if dislodged by fishing gear. The ability of *Virgularia mirabilis* to withdraw rapidly into the sediment provides protection from this form of disturbance, and there is no strong evidence that populations of this species have been damaged by trawling.

Heavy organic pollution excludes large, active megafauna such as *Nephrops norvegicus*, and probably also sea pens. Oxygen depletion is probably the most damaging consequence of organic enrichment. Deep-burrowing megafauna may also be excluded from heavily-impacted areas by hypoxia, physical burial or changes in sediment properties unfavourable to burrow maintenance. The critical thresholds of organic pollution causing changes in megafaunal communities have rarely been identified. Around the Garroch Head sludge dumping ground in the Clyde, burrowing megafauna were common where the sediment organic carbon content was < 4%, but were absent where this exceeded 6%. In semi-enclosed sea lochs, cage aquaculture of Atlantic salmon is the most common source of organic enrichment. The area of sea floor impacted by fish faeces and uneaten food will depend on the size and tonnage of the farm, on water depth, and on the local hydrodynamic conditions.

There are only scattered observations of the effects of other forms of pollution on this biotope complex. In the North Sea, *Callianassa subterranea* appears to be highly sensitive to sediment contamination by oil-based drilling muds. Ivermectin, an anti-parasite chemical now coming into use in the Scottish salmon farming industry, is also toxic to some benthic organisms, and may potentially affect sea loch biotopes. The introduction of non-indigenous species is an increasing cause of concern in coastal ecosystems generally, but so far there are no known examples in the biotope complex under discussion here.

Monitoring options

Several techniques are available for mapping and monitoring subtidal sediment biotopes. The choice of techniques to be used in SAC management will depend on local circumstances and on the type of information sought. Remote sampling by grabs or dredges will not reliably detect large or deep-burrowing animals. Diving provides high-resolution data but can only be employed in relatively shallow water. Video observation using towed cameras or ROVs allows monitoring of bottom topography and faunal distributions over large areas, but analysis of data may be very time-consuming. Acoustic surveying using RoxAnn^{TM} is a highly effective means of mapping the extent of sediment biotopes but provides only limited biological information. Results must be ‘ground-truthed’ using other methods.

For basic mapping of the biotope complex within an SAC, a RoxAnn^{TM} survey backed up by grab-sampling and towed video (or still photography) is recommended. This has already been achieved for several of the ‘demonstration’ SACs (Loch nam Madadh, Sound of Arisaig, Strangford Lough, Berwickshire/North Northumberland). Detailed characterization of burrowing megafauna should involve diving or towed video surveys by experienced observers. For routine biological monitoring, the larger fauna (sea pens, megafaunal surface traces, epifauna) should be used as indicators of the state of the biotope. These are all relatively easy to count first-hand or on videotape. Megafaunal abundance should be assessed from surface features (mounds, burrow openings) grouped into simple morphological categories, as precise estimation of species population density is a complex task with many potential sources of error. Colonies of *Virgularia mirabilis* and *Pennatula phosphorea* can withdraw into the sediment, so that counts of extended colonies will give minimum estimates of population density. Estimates of burrow density from diver observations have been found to agree fairly well with those made from towed video, but divers will tend to record a greater number of small features and care must therefore be taken when comparing data obtained by the two methods.

For SAC monitoring purposes, potential agents of environmental change should be identified. For this biotope complex the most important factors will usually be the intensity of any local *Nephrops* fishery and the volume of organic input to the marine environment (eg. by sewage disposal or from aquaculture).

Gaps in knowledge

There are several gaps in our current understanding of the dynamics and sensitivity of this biotope complex, the addressing of which would contribute greatly to the effective management of examples within SACs. Details of community composition and species abundances are poorly-known for all the relevant SACs, and further surveys using methods appropriate to each site (see below) are highly desirable. Almost nothing is known about the population dynamics of the three sea pen species. Data on growth rate, mortality and recruitment could be obtained by diver monitoring of fixed quadrats. Sea lochs would provide the most appropriate sites for this work. The effects of trawling on sea pen and burrower populations should be determined by quantitative towed video surveys of sites with known levels of trawl disturbance, supplemented by experimental trawling over grounds with pre- and post-disturbance video surveys. The effects of organic enrichment should be quantified by detailed mapping of sea pen and megafaunal densities around pollution sources. Computer models predicting rates of sedimentation around point sources of organic discharge are now available and should be related to observed faunal distribution patterns. The population genetics of some of the characteristic species of the biotope complex should be investigated to determine the degree of interchange between local populations. This would provide infomation on sources of recruitment and the likelihood of recolonization following local depletion or extinction.

Assessment of biodiversity and conservation importance, and recommended actions

Assessment of the biotope complex against a number of criteria for determining conservation importance leads to the conclusion that its importance lies in the rarity and restricted distribution (within the UK) of characteristic species such as *Funiculina quadrangularis* (and its commensal *Asteronyx loveni*) and *Pachycerianthus multiplicatus*, and the fact that the British examples of these biotopes are currently the best-known and best-characterised of their kind. The MNCR biotopes CMU.SpMeg.Fun and IMU.PhiVir are restricted in distribution to a minority of the Scottish sea lochs, with one isolated example of the latter biotope from Portland Harbour in the south of England. The distribution of these uncommon biotopes and species is thus restricted to semi-enclosed water bodies of relatively small spatial extent. These are situations in which local trawling pressure or organic encrichment could be expected to have adverse effects, compounded by the fact that the rare anthozoan species probably have a very limited capacity for larval dispersal and recolonization. The major emphasis in conservation terms should therefore be placed on these semi-enclosed water bodies, in which local management of the potential human impacts is a feasible prospect. Conservation measures may also be taken in open-sea areas supporting the biotope complex, but these are likely to come within the framework of fishery management of *Nephrops* stocks.

Collation of all information on the status of the biotope complex in candidate or possible SACs indicates that the best and most important examples are those in Loch nam Madadh, Loch Duich, Strangford Lough and Portland Harbour (adjoining the Fleet SAC). These are all known to contain species or biotopes of conservation importance. The SACs in the Sound of Arisaig and Berwickshire/North Northumberland may contain good examples of sea pen and megafaunal biotopes, but more detailed information is required for a full assessment of this. There are probably no immediate threats to the integrity of the biotope complex in any of these SACs, although any future expansion of aquaculture in the sea loch sites should be monitored. The conservation importance of the biotope examples in Cardigan Bay and Plymouth Sound is probably low, and no targeted management measures are recommended here.

I. INTRODUCTION

Many coastal sediments around the British Isles support communities of animals whose biology has only recently become accessible to study and whose ecological relationships are still poorly-known. Some members of these communities are rare and restricted in their distribution, while one, the Norway lobster, *Nephrops norvegicus*, is of considerable economic importance. There is reason to believe that some human influences on the coastal environment can adversely affect the integrity of these communities, at least on a local scale, and they are therefore worthy of investigation from a conservation-related perspective.

The objective of this report is to summarize and review the available information on the **'Sea pens and burrowing megafauna'** biotope complex, focusing on the fundamental environmental and biological attributes of the system, its sensitivity to natural and human-induced changes, and options for monitoring such changes that are relevant to the management of candidate SACs.

A. NATURE AND IMPORTANCE OF THE BIOTOPE COMPLEX

1. General description of the biotope complex

The 'Sea pens and burrowing megafauna' biotope complex is a community type found in subtidal particulate substrata, ranging from muddy sands with admixtures of shell and gravel to fine, clay-dominated muds. It is typically found in areas of full salinity, highly or completely sheltered from wave exposure, and with weak or extremely weak tidal currents. These biotopes do not correspond exactly to any category defined in the Habitats Directive Annex I classification. They could be included within the broad category of **'Sandbanks covered by sea water at all times'**, although this Annex I feature is more typically associated with coarser (sandier) sediment habitats. In geographical terms, particular examples of the biotope complex can be found in **'Large shallow inlets and bays'**.

The biotope complex is widespread around the British Isles but is best-known from the north and west of the UK, particularly the north-eastern Irish Sea (Hughes & Atkinson, 1997) and the Scottish sea lochs (Howson et al., 1994). The designation of the biotope complex refers to a taxonomic grouping, 'sea pens' - three species of colonial anthozoan cnidarians - and a functional category, 'burrowing megafauna' - a taxomomically-diverse assemblage of crustaceans, worms and fish whose common feature is their construction of large and conspicuous burrows in the sea bed. Although grouped together for current purposes, and often occurring in the same habitat, it is important to note that sea pens and burrowing megafauna are functionally quite dissimilar and not invariably associated with each other. The focus on large animals which are either highly visible (sea pens) or which produce conspicuous traces on the sea floor (burrowing megafauna) should also not obscure the fact that these habitats typically support a rich fauna of smaller, less conspicuous animals living buried within the sediments, including numerous species of nematodes, polychaete worms, bivalves and crustaceans.

The habitat characteristics and community ecology of the 'Sea pens and burrowing megafauna' biotope complex will be reviewed in detail in Chapters III and IV. The principal species used in the definition of this biotope complex are identified and briefly described below.

2. Major constituent species

a. Sea pens

Sea pens are colonial cnidarians belonging to the Class Anthozoa, which also includes the corals and sea anemones (the Phylum Cnidaria was formerly known as Coelenterata, and the term ‘coelenterates’ is used in much of the older literature). Within the Anthozoa, sea pens form part of the Subclass Octocorallia, distinguished by having polyps with eight pinnate tentacles. The sea pens (Order Pennatulacea) are the only octocoral order adapted for life on soft substrata. Each animal consists of a colony of polyps arising from a central stiffened axis, or rachis. The rachis ends in a basal stalk which anchors the colony in the sea bottom, with the polyp-bearing section held upright above the sediment. The animals are suspension-feeders, living on plankton and organic particles trapped by the polyp tentacles. Three sea pen species are well-known from British coastal waters. A fourth species, *Balticina christii*, has been recorded from the deeper waters of the North Sea. Illustrations and detailed descriptions of all British species can be found in Manuel (1981) and Hayward & Ryland (1990).

Virgularia mirabilis

This is a slender sea pen up to 60 cm long. Polyps occur in small clusters of up to 12, arranged in two opposing lateral rows along the rachis. The living colony is white to creamy-yellow in colour, and is able to withdraw itself into the sediment when disturbed. The species is found in sandy or muddy substrata in sheltered inshore waters, or in deeper waters offshore, in depths of 10 - 400 m. *Virgularia mirabilis* is the most abundant and widespread sea pen in British waters, locally common on all coasts but less frequent in the south. It is often abundant in deep, man-made harbours such as Holyhead Harbour, Anglesey (Hoare & Wilson, 1977), and is also very common in many of the Scottish sea lochs. Howson et al. (1994) recorded the species as present in 83 out of 98 sea lochs listed in their review. Outside British waters, *Virgularia mirabilis* is widespread around western Europe and the Mediterranean, and occurs throughout the North Atlantic possibly as far as North America.

Pennatula phosphorea

This species is much stouter and more fleshy than *Virgularia*, and grows up to 40 cm long (up to 25 cm projecting above the sediment). Fused polyps form large, triangular ‘leaves’ arranged more or less alternately in two opposing lateral rows. The colony is a deep reddish-pink owing to the presence of red sclerites in the tissue. The central axis of the colony is often bent over at the tip like a shepherd’s crook. Both *Pennatula* and, to a lesser extent, *Virgularia*, are bioluminescent, emitting light in brilliant flashes or in rhythmic pulses passing along the colony (Nicol, 1958). *Pennatula phosphorea* occurs in sandy or muddy substrata below about 15 m, probably extending to depths of over 100 m. The species is locally common in the North Sea and around the western British coasts, but appears to be absent from southern Britain. It was recorded as present in 46 of the 98 sea lochs listed by Howson et al. (1994). Other records come from the Mediterranean and North Atlantic, but confusion with other species makes the true geographic range uncertain.

Funiculina quadrangularis

This is the largest of the British sea pens, some colonies extending over 1 m above the sea bed. The polyps are irregularly arranged along the rachis, tending to form oblique rows in places. The flesh is white, yellowish or pale pink, and the central axis has a distinctive quadrangular cross-section. *Funiculina quadrangularis* typically occurs on soft mud substrata and does not extend into water as shallow as the other two species, being usually recorded deeper than 20 m. The lower depth range extends to over 2000 m. Known distribution in British waters is restricted to the north and west coasts of Ireland and Scotland. Howson et al. (1994) recorded it in only 17 out of 98 listed Scottish sea lochs. Outside British waters, *Funiculina quadrangularis* occurs in the North Atlantic and Mediterranean, with other records from as far afield as New Zealand and Japan (Manuel, 1981).

b. Burrowing megafauna

Although the fauna of marine sediments has been studied using ship-borne sampling equipment (grabs, dredges, cores) for well over a century, the abundance and diversity of large burrow structures in many soft substrata was not recognized until it became possible to observe the undisturbed sea bed using underwater photography (still and television), essentially from the early 1960s onwards (Barnes, 1963). The increasing use of SCUBA diving as a research technique from the 1970s onwards allowed direct observation of the behaviour of some of the larger burrowing animals (eg. Chapman & Rice, 1971; Atkinson, 1974; Atkinson et al., 1977). The development of the technique of resin-casting (Shinn, 1968; Atkinson & Chapman, 1984) was also an important advance. This allows the three-dimensional preservation of sub-surface burrow structures in the field, aiding the identification of sea floor features and providing information on the ecology of certain burrowing species which rarely or never show themselves at the sediment surface (eg. Pervesler & Dworschak, 1985; Atkinson & Nash, 1990; Nickell et al., 1995a).

Atkinson (1986) extended the use of McIntyre's (1971) term 'megafauna' to cover the larger, deep-burrowing benthic animals that are difficult to sample using conventional ship-borne methods and are most effectively studied in the field using a combination of SCUBA diving and underwater video. 'Burrowing megafauna' is therefore a loosely-defined, but useful label for a functional category of benthic animals sharing one major ecological trait - the construction of large, and usually long-lasting burrows. Taxonomically, the burrowing megafauna of British coastal seas includes the species belonging to the decapod crustacean infraorder Thalassinidea (lacking common names in most cases, but sometimes collectively termed 'mud-shrimps'), a few larger decapods such as the Norway lobster (*Nephrops novegicus*) and the angular crab (*Goneplax rhomboides*), several large worms belonging to the Phylum Echiura, and a number of fish species. Some other groups such as the holothurians (sea-cucumbers) and enteropneusts (acorn-worms) have representatives which probably fall within the megafaunal burrower category, but these are little-known in British waters.

Atkinson (1986) and Atkinson & Nash (1985) give useful summaries of the ecology of many of the most prominent megafaunal burrowers in British coastal waters, together with descriptions of the burrows they inhabit. This is still a very active field of research, and much additional information has been gained since the mid-1980s. The current state of knowledge of the species concerned is therefore briefly outlined here.

i.Thalassinidean crustaceans

The British members of this group are illustrated in Hayward & Ryland (1990). All are small animals of broadly shrimp-like appearance and all inhabit complex burrows in subtidal sands or muds.

Callianassa subterranea

This species is translucent white in colour and up to 60 mm long. The eyes are tiny, in accord with the burrowing lifestyle. The chelipeds (claws) are asymmetric, with one greatly enlarged. The type of burrow constructed varies depending on the sediment characteristics. In the fine muds of Scottish sea lochs, *C. subterranea* inhabits a complex lattice of galleries usually at a depth of 30 - 40 cm below the sediment surface, but sometimes extending down to over 80 cm (Atkinson & Nash, 1990; Nickell & Atkinson, 1995). The sub-surface lattice is connected to the surface by one or two vertical shafts, one of which usually opens in the centre of a conical mound of ejected sediment. In the coarser sediments of the southern North Sea, burrows extend less deeply below the surface (9 - 23 cm), and have more surface openings (up to eight) than those from sea lochs (Rowden & Jones, 1995). *Callianassa subterranea* is a deposit-feeder, 'mining' organic material from the sub-surface sediment or possibly feeding on surface detritus trapped in the burrow openings.

Callianassa subterranea is widespread and common around the British coasts, and has been recorded in large numbers in the southern North Sea (Witbaard & Duineveld, 1989; Rowden & Jones, 1994) and the north-eastern Irish Sea (Swift, 1993; Hughes & Atkinson, 1997). The species is also a prominent member of the megafaunal burrowing communities of the Scottish sea lochs (Howson et al., 1994, and personal observations). Total geographic range extends from Norway to the Mediterranean. A second *Callianassa* species, *C. tyrrhena* also occurs in southern British waters but there is no detailed information on its behaviour.

Calocaris macandreae

This mud-shrimp is more squat in form than *Callianassa subterranea*, and has relatively small chelipeds. It constructs a system of U-shaped tunnels with distinctive three-way junctions where tunnels connect (Nash et al., 1984). The burrow system is usually built at two interconnected levels in the sediment, with a total depth of up to 21 cm. The openings to the sediment surface also typically occur in groups of three, although this pattern may be obscured by the collapse or blocking of some of the openings. *Calocaris macandreae* is found in muddy sediments with high silt-clay fractions and does not occur in sandy substrata (Buchanan, 1963). The species occurs throughout the eastern Atlantic and Mediterranean at depths of 30 - 1100 m. In British waters it is best-known from the Northumberland coast (Buchanan, 1963), the Clyde Sea area and Firth of Lorne (Nash et al., 1984), and the Irish Sea (Calderon-Perez, 1981).

Jaxea nocturna

In appearance this species resembles a miniature lobster, with very long, slender chelae. Overall body length is 4 - 6 cm, colour a drab greyish-yellow, often obscured by clinging sediment. The animal inhabits a very deep (up to 90 cm) burrow of obliquely-descending tunnels, sometimes with one or more vertical shafts (Pervesler & Dworschak, 1985; Nickell et al., 1995b; Nickell & Atkinson, 1995). Up to 14 surface openings may be present, although at any one time only a few of these may be in use, the rest blocked by plugs of sediment. Active openings are often surrounded by a distinctive 'collar' of sediment resembling a pie-crust, formed as the animal 'bulldozes' small piles of material out of its burrow. The animal deposit-feeds from the walls of its burrow and may also scavenge organic material from the sediment surface. *Jaxea nocturna* occurs in muddy sediments at water depths below about 10 m. The species is probably widespread and relatively common in suitable habitats around the British coasts, but is under-recorded owing to its deep-burrowing, cryptic lifestyle. It is certainly present in the Scottish sea lochs (Nickell et al., 1995b), the north-eastern Irish Sea (Swift, 1993) and the English Channel (Marine Biological Association, 1957). Underwater video surveys show that burrows of *Jaxea nocturna* are abundant in the deeper waters of the Clyde Sea area, especially in Loch Fyne and to the east of Arran (R.J.A. Atkinson, personal communication). Outside British waters, the species occurs south to the Mediterranean and Adriatic Seas (Pervesler & Dworschak, 1985).

Upogebia spp.

Three species of this genus occur in British waters, *U. delatura, U. pusilla* and *U. stellata.* All have a similar ecology. Burrows are relatively simple, consisting of one or two connected U- or Y-shaped components penetrating the sediment to depths of up to 25 cm (Dworschak, 1983; Nickell & Atkinson, 1995; Astall et al., 1997b). Shafts decending from the main U-component may penetrate much more deeply into the sediment. Surface openings are usually inconspicuous holes without associated mounds. *Upogebia* species differ from the mud-shrimps discussed previously in being primarily suspension-feeders, actively pumping water through their burrows and filtering out particulate matter (Dworschak, 1981). They are usually found in sands or muddy sands with mixtures of stones or shell gravel, rather than in the finer muds associated with *Calocaris macandreae* or *Jaxea nocturna*. In Stravanan Bay, on the south-west coast of the Isle of Bute, *U. deltaura* inhabits the sediment underlying an extensive maerl bed (J. Hall-Spencer & R.J.A. Atkinson, unpublished observations), an unusual habitat record for a megafaunal burrower. All three British *Upogebia* species range from Norway to the Mediterranean. *Upogebia pusilla* is the least common in British waters. *Upogebia deltaura* and *U. stellata* are more widespread, occurring off all coasts, sometimes in mixed populations.

<u>ii. Other decapod crustaceans</u>

Norway lobster, *Nephrops norvegicus*

The Norway lobster (sometimes referred to as 'Dublin Bay Prawn' or 'Scampi') is one of the more familiar megafaunal burrowers. The burrowing habit of this large (total body length may be over 25 cm) crustacean was first confirmed in the field by sea bed photography. Burrows may be very large, with tunnels over a metre in length and up to 10 cm in diameter. Simple burrows consist of a straight or T-shaped tunnel descending at a shallow angle and penetrating the sediment to a depth of 20 - 30 cm (Rice & Chapman, 1971). Large piles of excavated sediment are often seen around the burrow entrances. More complex systems are created when juvenile animals construct burrows leading off from those of the adults (Tuck et al., 1994). A comprehensive analysis of burrow form is given by Marrs et al. (1996). In shallow water, the animals spend most of the day inside their burrows and emerge at night to forage (Chapman & Rice, 1971). *Nephrops* is carnivorous, feeding on sediment-dwelling polychaetes, bivalves and crustaceans, and also on carrion. The species is found on soft mud substrata all around the British and Irish coasts, from as little as 5 m depth in shallow sea lochs to several hundred metres offshore. Total range extends from Norway and Iceland to the Mediterranean. *Nephrops norvegicus* is the subject of a major fishery and its ecology and population biology have therefore been intensively studied (eg. Chapman, 1980; Bailey et al., 1986; Tuck et al., 1997a).

Angular crab, *Goneplax rhomboides*

This crab has a distinctive rectangular carapace with prominent spines at the front corners. The chelipeds are highly elongated, particularly those of the male. Burrows are quite similar to those of *Nephrops norvegicus* but are smaller, descending only 10 - 15 cm into the sediment, with 1 - 6 surface openings (Rice & Chapman, 1971; Atkinson, 1974a). Semi-circular ‘runs’ at the burrow entrances, formed as the crab carries out excavated mud and sweeps it aside with its chelipeds, are a useful identifying feature. *Goneplax* can be found on muddy sands from 8 - 80 m deep on all British coasts. Distribution extends south to the Mediterranean.

iii. Echiuran worms

The Echiura is a small phylum of marine worms (sometimes referred to as ‘spoon-worms’) distinguished by possession of an unsegmented, sac-like body and, in almost all species, a highly extensible strap-like or ribbon-like proboscis. Most echiurans are burrowing deposit-feeders, using the proboscis to graze detritus from the sediment surface. Only a few species occur in British coastal waters but these can be locally common, and owing to their large size can be an important component of the burrowing megafauna.

Maxmuelleria lankesteri

This is a large echiuran, with a body length in the contracted state of up to 18 cm. It has the long proboscis characteristic of the phylum and is a vivid dark green colour in life. The animal inhabits a narrow, sinuous burrow in the shape of an elongate U, with a surface opening at each end (Hughes et al., 1996a). One end opens at the apex of a volcano-like mound of ejected sediment up to 30 cm high and 40 cm across (Hughes et al., 1996b). The burrow may extend over 80 cm deep into the sediment (Nickell et al., 1995b), with up to 2 m between the surface openings. *Maxmuelleria lankesteri* is highly averse to light and, at least in shallow water, extends its proboscis to feed only at night (Hughes et al., 1993). The species is found in fine muds and muddy sands in water depths of 10 - 80 m. Previously thought to be rare and localized, *M. lankesteri* is now known to be common in the Irish Sea, Clyde Sea, and in many of the Scottish sea lochs (Hughes et al., 1996b). There are also records from south-west Ireland and the English Channel, but so far none from the North Sea. The species is also known from the Kattegat and Skagerrak, and from north-west Spain.

Amalosoma eddystonense

This is a large echiuran worm (body length up to 14 cm) originally described from near Plymouth but now known also from a number of the Scottish sea lochs (Connor, 1990; Howson et al., 1994). The species has been recorded from muddy sand substrata and inhabits a burrow up to 25 cm deep (Connor, 1990). The animal has a long, ribbon-like proboscis with a strongly bifurcated tip, which it uses to pick up detritus particles from the sediment surface. *Amalosoma* appears to be locally common in some areas but its ecology has not yet been studied in detail.

Echiurus echiurus

This echiuran is smaller than *Maxmuelleria lankesteri* (body length up to 11 cm) and greyish-yellow rather than green in colour. Burrows have not been described in detail, but appear to be U-shaped and perhaps up to 15 cm deep (Reineck et al., 1967). The ecology of *Echiurus* has not been studied in British waters but it is known to occur off the east coast of Scotland from Peterhead to St Andrews, and in the Firth of Forth (Stephen, 1934). It is also found further south in the North Sea (Rachor & Bartel, 1981), and in the Kattegat and Skaggerak, sometimes in very dense populations.

iv. Burrowing fish

Many fish species, belonging to a number of different families, have adopted a burrowing lifestyle (Atkinson & Taylor, 1991). In British waters there are three species known to excavate sizeable burrows in shallow coastal sediments.

Red band-fish, *Cepola rubescens*

This is a fish of striking and distinctive appearance, with a slender, elongate body up to 70 cm long, dorsal and anal fins continuous with the tail fin, and large eyes. The body colouration is orange-red with yellowish fins. The fish excavates a large burrow consisting of a wide (up to 20 cm) shaft descending vertically into the sediment, ending in an expanded terminal chamber (Atkinson et al., 1977). A narrow side shaft is often present (Atkinson & Pullin, 1996). Most burrows are 30 - 70 cm deep, but some extend down to over 1 m. The fish feeds on planktonic crustaceans caught during short excursions from the burrow. *Cepola* occurs on muddy sands from 12 - 200 m water depth off the southern and western British coasts, and ranges south to the Mediterranean and north-west Africa. In British waters it is best-known from around the isle of Lundy and from Irvine Bay off the Ayrshire coast (Atkinson et al., 1977).

Fries' goby, *Lesueurigobius friesii*

A stout-bodied goby up to 13 cm long with a fawn or grey background colouration and conspicuous golden-yellow spots, this species was shown to construct burrows in muddy sediments by Rice & Johnstone (1972). The burrow is a shallow, U-shaped tunnel up to 20 cm long but rarely extending more than 10 cm into the substratum. The burrow openings are narrow and circular, but the tunnel is expanded in the centre and used for the deposition of eggs (Gibson & Ezzi, 1978). The diet consists mainly of small polychaetes. Fries' goby occurs from the Irish Sea northwards to the Clyde and western Scotland, around the Irish coast, and in the Kattegat and Skagerrak. Known depth range is 10 - 350 m.

Snake-blenny, *Lumpenus lampraetiformis*

The snake-blenny has a very slender, almost eel-like body up to 40 cm in length. Body colouration is pale brown-yellow with irregular darker brown spots. Burrows are shallow, horizontal tunnels of circular cross-section with distinctive, Y-shaped junctions (Nash, 1980; Atkinson et al., 1987). Individual burrow systems may be over 70 cm long, though most are 20 - 35 cm. The species occurs on soft mud bottoms at depths of 20 - 200 m, being more abundant below 50 m. Distribution ranges from the northern and western British coasts, the North Sea, Scandinavia and the Baltic north to Spitzbergen, and from Iceland to north-eastern North America.

v. Other megafaunal burrowers

The species described above are those which have been most frequently recorded in megafaunal burrowing communities and which have received the most detailed study. However, these studies are biased to some extent by geography, with much of our information coming from a few of the more easily-accessible Scottish sea lochs. The British marine fauna includes a number of other species that can be regarded as megafaunal burrowers, but whose distribution and ecology are still very poorly-known owing to their cryptic lifestyle, occurrence in deep water, or in regions not yet subjected to detailed study. It is likely that future studies will find some of these species to be locally common and ecologically important.

Axius stirhynchus is a thalassinidean crustacean sporadically recorded from the shallow subtidal off southern and western Britain (Marine Biological Association, 1957; Allen, 1967). Little is known of its ecology, but it has been recorded burrowing under stones on sandy and muddy estuarine shores. The related *Axius serratus* has been recorded burrowing to depths of over 3 m in Nova Scotia (Pemberton & Risk, 1976), the deepest megafaunal burrows known. It is therefore likely that *A. stirhynchus* has been under-recorded, and may be more common than the few records suggest.

The amphipod crustacean *Maera loveni* has a northern Atlantic distribution and reaches its southern geographic limit in Scotland, where it occurs on both east and west coasts. In Loch Riddon in the Firth of Clyde, the species constructs a complex burrow system of interconnected U-shaped tunnels. The tunnels are narrowly elliptical in cross-section and reach the sediment surface in a cluster of up to 70 slit-like openings (Atkinson et al., 1982). Uniquely among the species discussed here, the larger burrows appear to be constructed by a colony of animals, but this cooperative social behaviour has not been studied in detail.

Labidoplax digitata, a large, worm-like holothurian (sea-cucumber) up to 30 cm long, is known from western British coasts to a depth of 70 m. The animal burrows in clean or muddy sand and feeds on surface detritus collected with its oral tentacles. Burrow form and ecology have not so far been studied.

The hagfish, *Myxine glutinosa* occurs on muddy substrata and is known to inhabit burrows with conspicuous, volcano-like mounds (Foss, 1962, 1968). Burrows seem to be a simple U- or J-shape, and to be lined with mucus (Hardisty, 1979). The hagfish is mostly found at depths well beyond the range of air diving and so is difficult to study in the field. Among fish species, another likely burrower is the four-bearded rockling, *Enchelyopus cimbrius*, which has been observed in association with burrows in the deep waters of the Clyde Sea (R.J.A. Atkinson, personal communication).

In addition to those fish and invertebrates that are specialist or obligate burrowers, there are others that do not normally excavate their own burrows but will opportunistically inhabit those constructed by other species. Of these, the most frequently observed is the black goby, *Gobius niger*. In Scottish sea lochs, this fish will take up residence in burrows belonging to *Maxmuelleria lankesteri* and other species, frequently enlarging or modifying the shape of the burrow opening (Nickell et al., 1995a; Marrs et al., 1996). The squat lobster, *Munida rugosa*, is frequently found inhabiting burrows on the periphery of megafaunally-burrowed muds, where these merge with coarser substrata (C.J. Chapman, personal communication). It is uncertain whether *Munida* excavate their own burrows or take over those made by other animals.

Much still remains to be discovered about the basic biology of even the best-known species of burrowing megafauna, and the makers of some distinctive burrow types still remain unidentified. Paired sediment mounds, each surrounded by a ring of holes, have been seen using towed underwater video in the Clyde Sea (Tuck & Atkinson, 1995) and elsewhere. These may be the work of enteropneusts (acorn-worms), but this has still to be confirmed. Observations such as these suggest that the list of large burrowing animals in British waters will expand as work continues.

3. Importance of the biotope complex

a. Economic importance

The 'Sea pens and burrowing megafauna' biotope complex is of considerable economic importance because of the fishery targeted on one of its principal constituent species, *Nephrops norvegicus* (Howard, 1989). *Nephrops* was almost unexploited prior to the 1950s, but since then has grown rapidly in importance to the UK fishing fleet, with Scottish landings in 1995 totalling 22476 tonnes, with a market value of £47.6 million (Marine Laboratory, Aberdeen). In 1995 the most important fishing areas around the UK were the western Irish Sea (about 8000 tonnes), the Fladen Grounds in the North Sea (7087 tonnes), the North and South Minches (3656 and 4678 tonnes respectively) and the Clyde (3989 tonnes), with important fisheries also in the Firth of Forth, Moray Firth and eastern Irish Sea. Bottom trawling is the main technique used, but inshore creel fishing is also locally important, particularly on the west coast of Scotland.

The squat lobster, *Munida rugosa*, also supports a small commercial fishery. Reported annual landings are currently only about 10 tonnes, mostly from the Clyde area (C.J. Chapman, personal communication), but this has the potential to increase if the market expands.

b. Scientific importance

No other megafaunal burrower, or any sea pen species, has any economic importance in the UK. However, the activities of burrowing megafauna can impinge on human usage of the sea in other respects. It has become generally recognized over the past two decades that disturbance of the sea bed by animal activity can have major effects on the structure, movement and chemistry of marine sediments (McCall & Tevesz, 1982). These disturbance processes, collectively termed ‘bioturbation’ include the construction of burrows, the transport of material from deep sediment layers to the surface (or vice versa), and the sorting of sediment particles for feeding purposes. By circulating water through their burrows, benthic animals transport oxygen to deep, otherwise anoxic layers of sediment. In heavily-burrowed expanses of sea floor, burrow walls can collectively greatly increase the surface area of sediment in contact with the water column. Both factors can profoundly affect the types and rates of chemical reactions taking place at the sediment-water interface, in particular the recycling of nutrients such as nitrate and phosphate, and metals such as manganese. The burrowing megafauna are likely to be particularly important in these processes as a result of their large body size and the depth of their activity in the sediment (Nickell et al., 1995b).

The effects of burrowing animals on sediment-water chemistry take on a practical significance with respect to the fate of man-made pollutants discharged into the sea. Contaminants such as toxic metals, pesticides or radionuclides often become bound to sediment particles and accumulate in the sea bed. Bioturbation is one means by which sedimentary pollutants can be redistributed, and potentially returned to the human environment (Lee & Swartz, 1980), and for this reason the process has become a major area for research in recent years. In the UK, the possibility that benthic animals might significantly affect the distribution of radionuclides such as plutonium and caesium in the sediments of the Irish Sea was recognized in the early 1980s (Kershaw et al., 1983; Swift, 1993). This discovery greatly stimulated research into the ecology of species such as *Maxmuelleria lankesteri*, about which very little was previously known (Hughes et al., 1996b).

The increasing interest in bioturbation and its effects has led to a significant use of shallow coastal sediment areas as natural ‘laboratories’ where the ecology of burrowing animals can be studied under natural conditions. In this respect, several of the Scottish sea lochs (notably Loch Sween in mid-Argyll) have been especially important, as their organically-enriched sediments typically support a diverse burrowing megafauna in shallow, highly sheltered waters suitable for diving fieldwork (Nickell et al., 1995b). Data collected in sea lochs has been used to assess the relative importance of different species in the redistribution of radionuclide particles in the bottom sediments of the north-eastern Irish Sea (Hughes & Atkinson, 1997). Observations made in coastal environments can also help to interpret the behaviour of burrowing animals in the deep sea (eg. Ohta, 1984; Hughes et al., 1994). The ‘Sea pens and burrowing megafauna’ biotope complex is therefore of considerable scientific value as a model for studying processes of general importance in marine benthic ecology, and this value is likely to increase as further sites are investigated and additional species become available for study.

c. Biodiversity and conservation importance

As outlined earlier, the three shallow-water sea pens all have wide distributions around the north-eastern Atlantic and Mediterranean, some extending further afield. *Funiculina quadrangularis* has a more restricted distribution in British coastal waters than the other two species and is considered to be of greater national conservation importance. Another nationally rare species found in the deep mud biotope is the large anemone *Pachycerianthus multiplicatus*, known in the British Isles only from some of the Scottish and Irish sea lochs/loughs (Howson et al., 1994).

The major megafaunal burrowers are also widely distributed. Species that currently appear to be rare or localized in distribution are in many cases probably merely overlooked or under-recorded. This situation is inevitable given the cryptic habits of these animals, the comparatively recent advent of techniques such as SCUBA and underwater video, and the small number of localities that have been surveyed in detail using these methods. The echiuran *Maxmuelleria lankesteri* remained in obscurity for decades after its formal description, known only from a handful of specimens, but recent work has shown it to be widespread and locally common where it occurs. The same will probably turn out to be true of other species about which little is currently known. It is therefore not possible at present to identify any burrowing megafauna likely to be confined to British waters, or truly rare on a national or international scale.

The soft-sediment biotopes with sea pens and burrowing megafauna known from the UK are, however, of conservation importance as the best-characterized and most intensively-studied examples of their kind. Comparable animal communities are known from elsewhere (see below), but work in British waters has progressed much further in identifying the principal species present (Atkinson & Nash, 1985; Atkinson, 1986), determining the structure of their burrows (eg. Atkinson & Chapman, 1984; Nash et al., 1984; Atkinson & Nash, 1990; Nickell et al., 1995a; Nickell & Atkinson, 1995; Rowden & Jones, 1995), and quantifying their effects on the sediment (Nickell et al., 1995b; Hughes et al., 1996a). This is particularly true of the communities found in the Scottish sea lochs, which provide favourable conditions for detailed study matched in few other places. Since the best-known examples of this biotope complex occur in shallow, semi-enclosed bodies of water, where they are potentially vulnerable to disturbance by a variety of natural and human-induced environmental changes (see Chapters V and VI), they could be used as indicators of the ‘health’ of the local coastal environment.

In terms of species number, the sediment-dwelling meio- and macrofauna of sedimentary habitats far exceed the larger, more conspicuous animals around which this biotope complex is defined. This component of the biological community is therefore also of potential conservation importance, although not usually discussed in this context. The interaction between the burrowing megafauna and these smaller organisms will be discussed in Chapter IV.

The conservation importance of this biotope complex will be assessed more fully in Chapter IX, after its ecological functioning and sensitivity to environmental change have been reviewed.

B. KEY POINTS FROM CHAPTER I

- The ‘Sea pens and burrowing megafauna’ biotope complex is found on sandy and muddy substrata in sheltered, fully marine conditions.
- The biotope complex is characterized by three species of colonial anthozoans (a taxonomically-defined grouping) and a functionally-defined grouping of animals which construct large, long-lasting burrows in the bottom sediments.
- The burrowing megafauna is a taxonomically-diverse assemblage of crustaceans, worms and fish which are difficult to sample using traditional ship-borne equipment. Most information on their ecology has been obtained in the last two decades using SCUBA and underwater television.
- The biotope complex supports a major fishery for one of its characteristic species, *Nephrops norvegicus*, and hence is of considerable economic importance.

- The disturbance of marine sediments by animal activity (bioturbation) is a subject of major scientific interest, partly because of its potential effects on the movement of pollutants. Shallow coastal sediment areas are useful natural ‘laboratories’ for studying this process, so adding to the scientific value of the biotope complex.

- Examples of the biotope complex in the UK are of conservation importance as the best-studied and most accessible representatives of their kind. Characteristic species such as *Funiculina quadrangularis* and *Pachycerianthus multiplicatus* are nationally rare and localised in distribution. Sediments support a rich fauna of smaller animals and so form an important reservoir of biodiversity.

II. STATUS AND DISTRIBUTION

This chapter will clarify the status of the biotope complex within the classification system developed by the Marine Nature Conservation Review, and summarise what is known of its geographic distribution in the UK (with particular reference to SACs) and elsewhere.

A. STATUS WITHIN THE MNCR BIOTOPE CLASSIFICATION

The Marine Nature Conservation Review (MNCR) biotope classification provides a hierarchical framework for differentiating and classifying the shallow-water benthic habitats and biological communities of the British Isles (Connor et al., 1997). The basic unit of classification is the **Biotope**, a recognizeable **Community** of conspicuous species occurring in a **Habitat**, defined according to parameters of the physical environment such as substratum type or degree of wave exposure. Groups of biotopes with similar overall character, suitable for local mapping where biotopes consistently occur together and are relatively restricted in their extent, are termed **Biotope complexes**. For the purposes of this report, the ‘Sea pens and burrowing megafauna’ biotope complex is taken to include all biotopes containing either sea pens **or** burrowing megafauna as characterizing species (as opposed to considering only those biotopes in which both groups are present). This inclusive definition has the advantage of including situations where, for example, biotopes occur along a gradient of water depth or sediment type, with biological communities changing as a result of the differing environmental requirements of the characterizing species. The relevant biotopes from the MNCR classification are summarised below. Full descriptions are given in Connor et al. (1997).

*1. MNCR Code **CMU.SpMeg***	Sea pens and burrowing megafauna in circalittoral soft mud
*2. MNCR Code **CMU.SpMeg.Fun***	Sea pens, including *Funiculina quadrangularis*, and burrowing megafauna in undisturbed circalittoral mud

These are the typical deep mud biotopes of the Scottish sea lochs, characterized by the sea pens *Virgularia mirabilis* and *Pennatula phosphorea*, and the megafaunal burrowers *Nephrops norvegicus, Callianassa subterranea, Calocaris macandreae, Maxmuelleria lankesteri* and *Lesueurigobius friesii*. The biotope coded as CMU.SpMeg has been recorded in most of the Scottish sea lochs (Howson et al., 1994) and in the Shetland voes (Howson, 1988). It has also been observed by towed camera surveys in the north-eastern Irish Sea (Hughes & Atkinson, 1997) and in the deep offshore waters of the North Sea (Dyer et al., 1982). These offshore examples of the biotope cover extensive areas and form the major *Nephrops* fishing grounds. The biotope coded CMU.SpMeg.Fun is a variant recorded in the deeper basins of some of the Scottish sea lochs, characterised by forests of the larger sea pen *Funiculina quadrangularis*.

3. MNCR Code ***CMU.BriAchi***

Brissopsis lyrifera and *Amphiura chiajei* in circalittoral mud

This deep, offshore mud biotope is characterized by the urchin *Brissopsis lyrifera* and the brittlestar *Amphiura chiajei.* The megafaunal burrowers *Nephrops norvegicus* and *Calocaris macandreae* may also be present. Connor et al. (1997) recognize this biotope from the northern Irish Sea off the coast of Cumbria. Its status requires clarification, and it may turn out to be identical with CMU.SpMeg, with the apparent differences resulting from contrasting survey techniques (D. W. Connor, personal communication).

4. MNCR Code ***CMS.AfilEcor***

Amphiura filiformis and *Echinocardium cordatum* in circalittoral clean or slightly muddy sand

This biotope exists in conditions of slightly greater wave exposure, and consequently coarser-grained sediments than are typical of CMU.BriAchi. An infaunal brittlestar and urchin are again the main characterizing species, but the community also includes *Callianassa subterranea*. The sea pen *Virgularia mirabilis* may also occur, but not in large numbers. The biotope is widespread around the British Isles, being recorded from a number of Scottish sea lochs, from the northern Irish Sea, the central and southern North Sea and the Isles of Scilly (references given in Connor et al., 1997).

5. MNCR Code ***CMS.VirOph***

Virgularia mirabilis and *Ophiura* spp. on circalittoral sandy or shelly mud

6. MNCR Code ***CMS.VirOph.HAs***

Virgularia mirabilis and *Ophiura* spp. with hydroids and ascidians on circalittoral sandy or shelly mud with shells or stones

The sea pen *Virgularia mirabilis* may occur in moderate numbers on sandy or shelly substrata such as occur in many sea lochs, usually at shallower depths than the finer muds supporting the CMU.SpMeg biotope. The brittlestars *Ophiura* spp. are the other major characterizing species. The variant CMS.VirOph.HAs is distinguished by the greater numbers of small stones and shells on the sediment surface, which provide a substratum for attached hydroids, ascidians and other epifauna. Both biotopes are recognized in the Scottish sea lochs (Connor et al., 1997).

7. MNCR Code ***IMU.PhiVir***

Philine aperta and *Virgularia mirabilis* in soft stable infralittoral mud

Virgularia mirabilis may also occur at high densities on fine-grained and physically very stable muds, typically in shallow water (to 12 - 15 m). The opisthobranch gastropod *Philine aperta* is usually very common. Burrowing megafauna are generally rare or absent. In the UK this biotope is almost confined to the most sheltered basins of certain sea lochs, with one example known from Portland Harbour in southern England. Further south it can be recognized in the Gulf of Gascony and the Mediterranean (Connor et al., 1997).

B. OCCURRENCE WITHIN CANDIDATE SACs

The ‘Sea pens and burrowing megafauna’ biotope complex is represented to varying degrees in several of the candidate SACs around the UK. The quality of information available also varies from area to area, extending in some cases only to a record of sedimentary habitats in which a biotope can be inferred to exist. The 12 ‘demonstration’ SACs with which the UK Marine SACs Project is mainly concerned will be discussed first in detail, followed by a summary of known or likely occurrence in other proposed SACs. It should be borne in mind that the practicalities of surveying benthic environments, especially over large areas, mean that a statement of non-occurrence of a particular biotope usually represents only an assessment based on the currently available information, an assessment which will always be subject to revision in the light of future observations. However, the hydrodynamic or topographic characteristics of a site often preclude the occurrence of a particular biotope (eg. soft mud biotopes are unlikely to exist at an open-coast site subject to strong tidal currents or heavy wave exposure).

1. ‘Demonstration’ SACs

The occurrence or non-occurrence of the biotope complex is summarized in the table below.

Biotope complex definitely present	**Biotope complex probably absent**
Loch nam Madadh	Papa Stour
Sound of Arisaig	Solway Firth
Strangford Lough	Morecambe Bay
Cardigan Bay	Llyn Peninsula & the Sarnau
Plymouth Sound & Estuaries	The Wash & North Norfolk Coast
Chesil & the Fleet (Portland Harbour)*	
Berwickshire & North Northumberland Coast	

* Portland Harbour adjoins the Fleet SAC but falls outside its currently-defined boundaries.

a. SACs probably lacking the biotope complex

Papa Stour in Shetland has a broken, rocky, and in places very exposed coastline. There are no soft-sediment biotopes around the island, although these do exist in the sheltered voes elsewhere in Shetland (Howson, 1988).

The Solway Firth is notable for its estuarine intertidal mudflats. Recent surveys of sublittoral biotopes found no evidence of sea pens or burrowing megafauna (Covey, 1992; Cutts & Hemingway, 1996), although both are well-represented further south in the Irish Sea proper. The biotopes in question have also not been recorded in Morecambe Bay (Emblow, 1992; Rostron, 1992). Mills (1997) notes that benthic sampling undertaken in the Irish Sea off Blackpool, about 30 km from the mouth of the bay, found muddy sands at depths of 25 - 30 m with *Virgularia mirabilis, Calocaris macandreae* and *Goneplax rhomboides*. Rostron (1992) found *Upogebia deltaura* in a dredge sample off the coast of Walney Island. However, this community has not been recorded within Morecambe Bay itself. The Llyn Peninsula is bordered by the Irish Sea to the north and Cardigan Bay to the south. Megafaunally-burrowed sediments occur in both sea areas but have not so far been recorded close inshore to the peninsula, except for one record of *Upogebia* sp. burrows in the anchorage at St Tudwal’s Road (Hiscock, 1984). To some extent, the presence or absence of the biotope complex in these three SACs on the Irish Sea periphery is a matter of boundary placement, but any representation within them is likely to be marginal.

The Wash in North Norfolk contains large expanses of intertidal and shallow subtidal sediment, but is not known to support either sea pens or burrowing megafauna (Covey, 1991; Hill et al., 1996).

b. SACs containing the biotope complex

The locations of those candidate SACs believed to contain extensive examples of the ‘Sea pens and burrowing megafauna’ biotope complex are shown in Fig. 1. The sites themselves are discussed individually below. Where there is sufficient information, biotopes are assigned to one of the MNCR categories described above.

Fig. 1. Location of the ‘Sea pens and burrowing megafauna’ biotope complex around the British Isles. ‘Demonstration’ candidate SACs in which these biotopes can be found are indicated by solid circles. Non - ‘demonstration’ candidate or possible SACs are marked by open squares. Non-SAC areas supporting the biotope complex are shown by vertical hatching. The distributions of *Pennatula phosphorea* and *Nephrops norvegicus* in the North Sea are adapted from Dyer et al. (1982), and *Callianassa subterranea* from Künitzer et al. (1992).

i. Loch nam Madadh

Entec (1996) carried out an acoustic (RoxAnn^{TM}) survey of Loch nam Madadh, supplemented by towed video and grab sampling. The outer reaches of this complex loch system, south of the island of Flodday, was found to contain an extensive sediment plain, ranging from shelly mud near Lochmaddy village and Charles Harbour, to finer mud near the mouth of the loch. All three sea pen species were recorded, with *Virgularia mirabilis* having the most extensive distribution. This occurred commonly on the shallower, shelly mud (6 - 24 m depth), while *Pennatula phosphorea* and *Funiculina quadrangularis* were confined to the deeper muds in the outer loch. *Nephrops norvegicus* and *Pachycerianthus multiplicatus* were also recorded. These findings are supported by the diving observations of Howson (1991). She found the fine muds at 27 - 40 m depth to be heavily burrowed by *Calocaris macandreae* and *Nephrops norvegicus*. Burrowing megafauna were not mentioned in the shallower, shelly mud characterized by *Virgularia mirabilis*. These observations, summarized in Fig. 2, suggest that the biotopes CMU.SpMeg, CMU.SpMeg.Fun and CMS.VirOph can be recognized here.

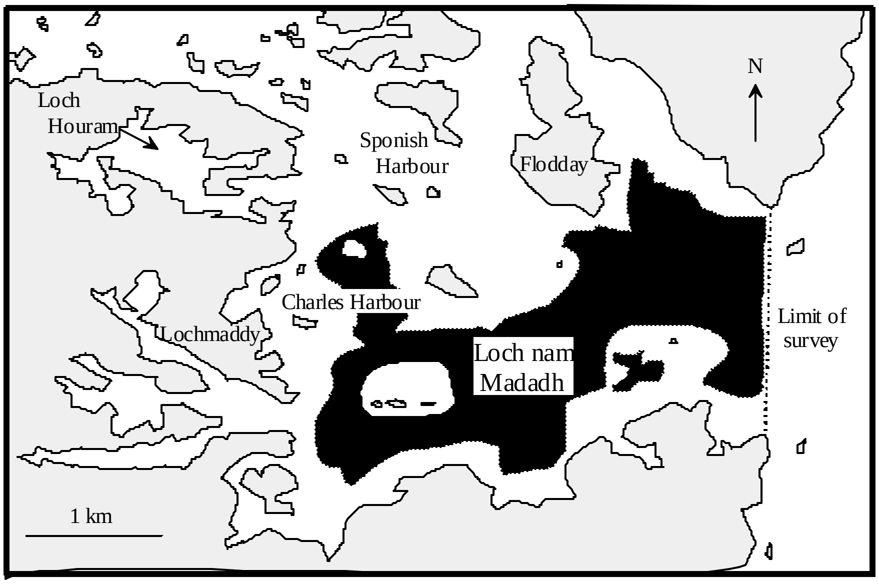

Fig. 2. Distribution of fine sand/mud substrata supporting sea pens and burrowing megafauna in Loch nam Madadh. Modified from Entec (1996).

ii. Sound of Arisaig

Davies & Hall-Spencer (1996) used the same set of techniques (RoxAnn^{TM}, ground-truthed by towed video and SCUBA) to survey the benthic biotopes of the Sound of Arisaig SAC. Extensive areas of fine mud in the 30 - 60 m depth range were found in the Sound of Arisaig itself and in Loch Ceann Traigh (Fig. 3). These sediments were heavily burrowed by megafauna, although only *Nephrops norvegicus* was specifically mentioned. Howson (1990) recorded *Maxmuelleria lankesteri* from a site near the mouth of Loch Ailort, with *Virgularia mirabilis* 'in moderate numbers'. This may represent biotope CMU.SpMeg, although more detailed information on species composition is clearly needed. Both Davies & Hall-Spencer (1996) and Howson (1990) recorded circalittoral sandy muds with *Virgularia mirabilis* in shallower water (10 - 37 m), particularly in areas where hard substrata gave way to sediment. The presence of *Ophiura* spp. and scarcity of attached epifauna (Howson, 1990) indicate that this association represents biotope CMS.VirOph.

Fig. 3. Distribution of deep-water muds with sea pens and burrowing megafauna (vertical hatching) and shallower circalittoral sandy mud with *Virgularia mirabilis* (Stippled) in the Sound of Arisaig candidate SAC. Modified from Davies & Hall-Spencer (1996).

iii. Strangford Lough

This large, virtually land-locked marine inlet contains a diverse range of benthic biotopes, including megafaunally-burrowed fine muds. Species present include *Nephrops norvegicus* and *Goneplax rhomboides* (Erwin, 1977). Magorrian et al. (1995) mapped the substrata of the lough using acoustic methods (RoxAnn^{TM}), supplemented by video and still photography. Areas of very soft, featureless sediment with few burrows occupied large areas in the north of the lough. Firmer muds towards the lough centre supported high densities of *Nephrops* burrows (Fig. 4). The *Nephrops* grounds were estimated to cover 12 km^2 of the 22.9 km^2 surveyed.

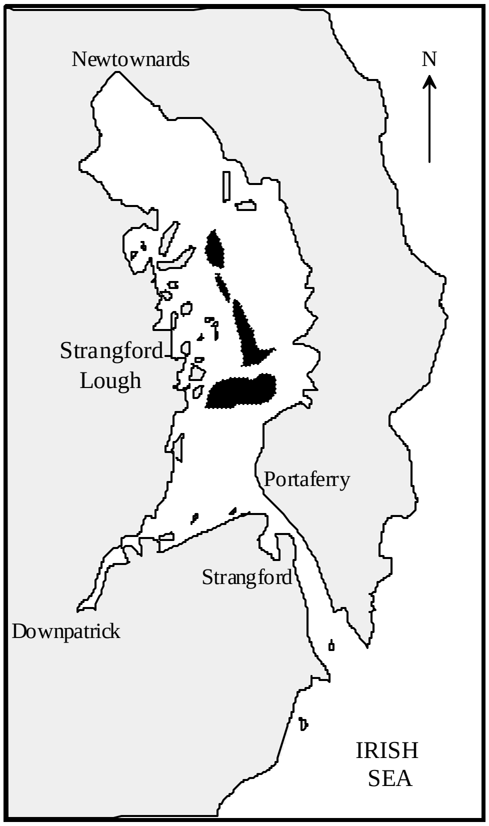

Fig. 4. Distribution of soft mud habitats with *Nephrops norvegicus* in Strangford Lough. Modified from Magorrian et al. (1995).

iv. Cardigan Bay

The subtidal sediment fauna of this large bay is relatively poorly known. However, several species of burrowing megafauna have been recorded from areas of muddy sand inshore near Aberystwyth, and further north near Pwllheli, the latter area bordering on the Llyn Peninsula SAC (Fig. 5). Species present include the crustaceans *Upogebia deltaura* and *Callianassa* sp., and the holothurian *Labidoplax digitata* (Mackie et al., 1995).

v. Plymouth Sound and Estuaries

Plymouth Sound contains a wide range of both hard and soft substrata (Davies, 1997). Burrowed sediments occur in the sound, and species records indicate that the megafauna may be quite diverse (Marine Biological Association, 1957). *Callianassa subterranea*, *Upogebia deltaura* and *U. stellata* have been collected from muds just north of the breakwater in the middle of the sound, and the rarely-recorded *Axius stirhynchus* occurs in the low intertidal on muddy shores. Hiscock & Moore (1986) found burrows of *Goneplax rhomboides* near Plymouth Hoe. Larvae of *Jaxea nocturna* are not uncommon in summer in the Plymouth area (Marine Biological Association, 1957), suggesting that this species may occur within the sound. Records of the echiuran *Maxmuelleria lankesteri* from the south coast of England (Hughes et al., 1996b) suggest that this species might also conceivably be present. There are a few records of the sea pen *Virgularia mirabilis* from Plymouth Sound (Hiscock & Moore, 1986), but the species does not appear to be common here.

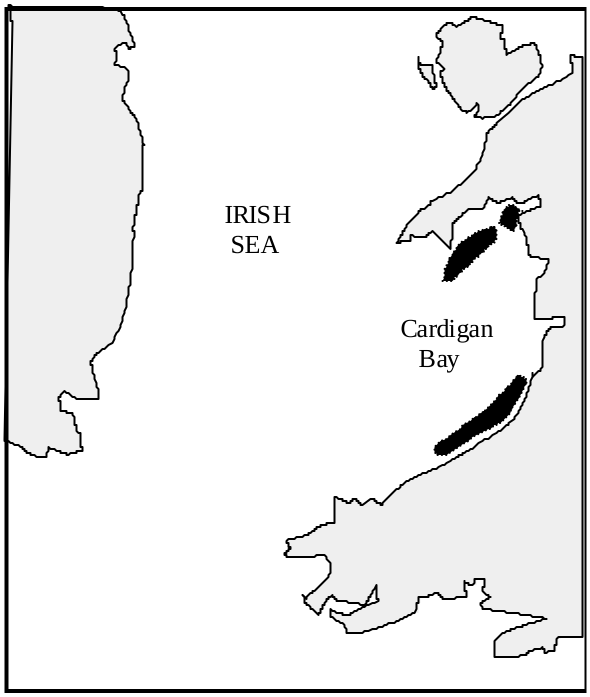

Fig. 5. Distribution of muddy sand substrata with thalassinidean crustaceans in Cardigan Bay. Modified from Mackie et al. (1995).

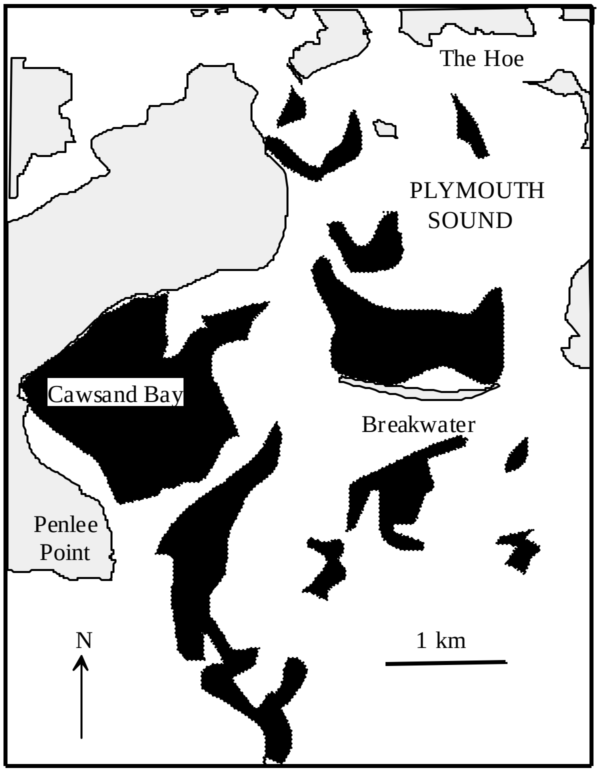

Fig. 6. Distribution of mud and muddy sand substrata in Plymouth Sound. Modified from Devon Wildlife Trust (1993).

vi. Chesil & the Fleet

The shallow tidal inlet of the Fleet contains soft mud substrata in its western embayment, but there are no records of the biotopes under consideration here (Dyrynda, 1984). However, the Fleet is connected to the sea via Portland Harbour, which supports the sole known example of the biotope IMU.PhiVir (*Philine aperta* and *Virgularia mirabilis* in soft stable infralittoral mud) in southern Britain (Portland Harbour falls outside the currently-defined boundaries of the Fleet SAC, but the community found there will be briefly described because of its regional importance). Dyrynda recorded burrows of *Cepola rubescens* and *Goneplax rhomboides* at about 10m depth in the harbour, with *Virgularia mirabilis* abundant in patches. The anemone *Scolanthus callimorphus*, otherwise known in the British Isles only from western Ireland, was also recorded here. Sediments were found to consist of 54% silt-clay and 5% organic matter.

vii. Berwickshire and North Northumberland Coast

Foster-Smith et al. (1996) carried out an acoustic survey of the benthic biotopes of this candidate SAC. Towed video was used to ground-truth the RoxAnn^{TM} results. A site at the southern edge of the surveyed area was found to have a fine silty sand substratum with beds of *Virgularia mirabilis*. The acoustic survey indicated that an extensive belt of this biotope runs parallel to the coastline in fairly deep water (50 - 70 m) (Fig. 7). The sea bed in the observed area was worked into burrows and mounds. Species responsible were not identified, but *Calocaris macandreae* and *Nephrops norvegicus* are likely candidates in this area. The echiuran worm *Echiurus echiurus* is common further offshore at the St Abbs sewage sludge disposal ground (I. Jack, Scottish Environmental Protection Agency, personal communication), so might also be expected to occur here. The offshore sediment fauna of the Northumberland coast belongs to the classical '*Brissopsis-chiajei*' community of Petersen (Buchanan, 1963). This corresponds to CMU.BriAchi in the MNCR biotope classification.

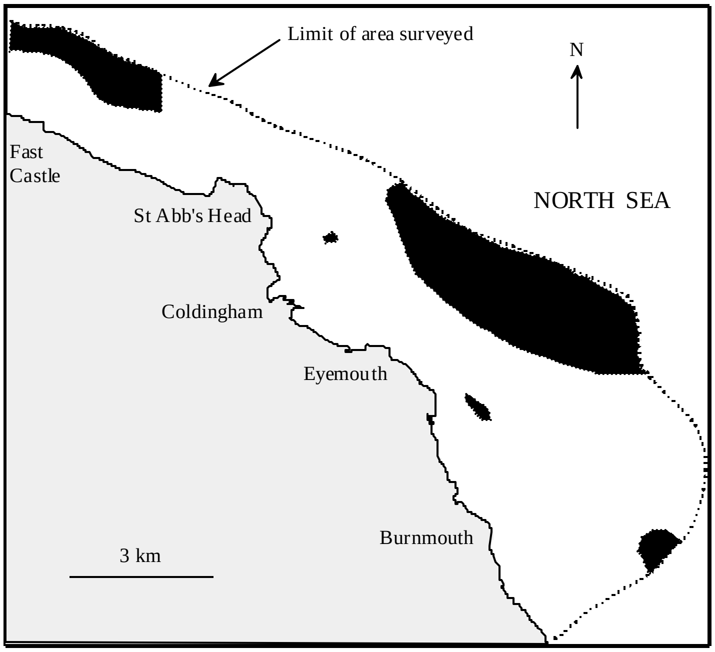

Fig. 7. Distribution of fine silty sand with *Virgularia mirabilis* and burrowing megafauna off the Berwickshire/North Northumberland Coast. Modified from Foster-Smith et al. (1996).

2. Other SACs

Several other candidate or possible SACs are known to support examples of the 'Sea pens and burrowing megafauna' biotope complex. The Moray Firth (designated as an SAC because of its bottlenose dolphin population) is an important fishing ground for *Nephrops norvegicus*, with 1279 tonnes landed in 1995 (Marine Laboratory, Aberdeen). It is likely therefore that other megafaunal burrowers will also occur here. The Loch Alsh/Duich/Long system contains extensive mud and muddy sand plains with *Virgularia mirabilis* (Connor, 1989). Loch Duich supports particularly good examples of the CMU.SpMeg and CMU.SpMeg.Fun biotopes, with forests of *Funiculina quadrangularis* and burrows of *Nephrops norvegicus, Callianassa subterranea* and *Lesueurigobius friesii*. The head of Loch Duich has one of the largest known populations of the rare anemone *Pachycerianthus multiplicatus* (Fig. 8).

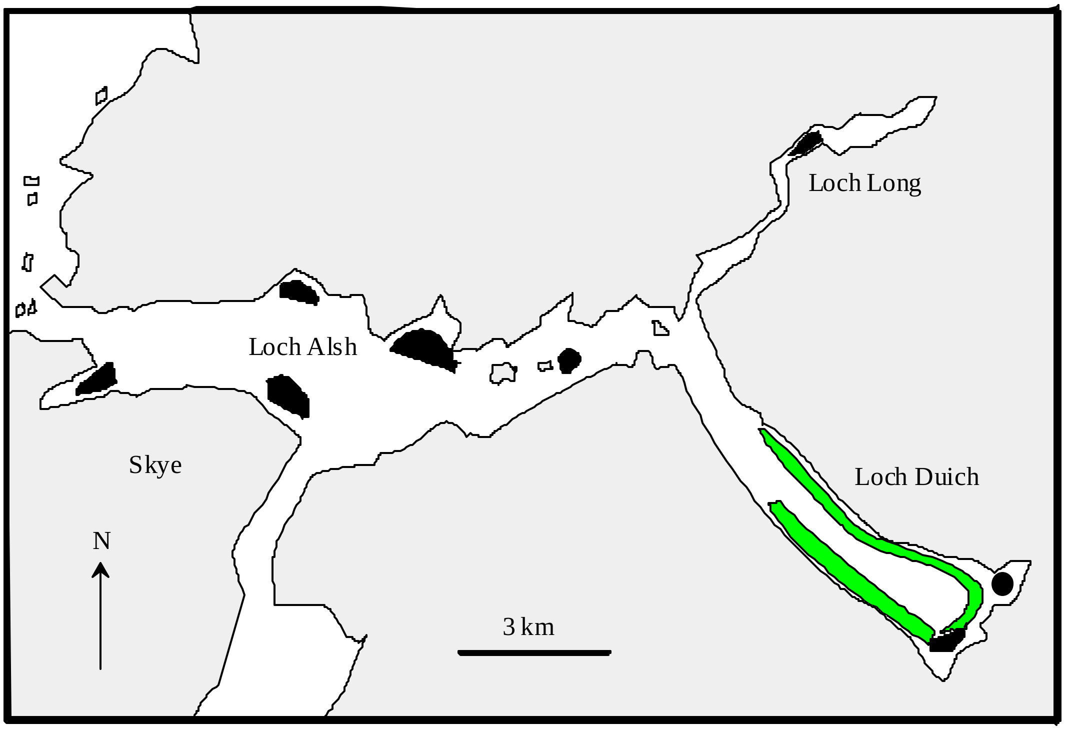

Fig. 8. Distribution of the 'Sea pens and burrowing megafauna' biotope complex in the Loch Alsh/Duich/Long possible SAC. Occurrences of *Virgularia mirabilis* are shown by black patches. The deep mud biotope with *Funiculina quadrangularis* is shown by dark grey patches. The solid circle at the head of Loch Duich indicates the location of a dense population of the anemone *Pachycerianthus multiplicatus*. Modified from Connor (1989).

None of the other proposed SACs are known to contain examples of this biotope complex, and the habitat criteria underlying their selection (eg. lagoons, estuaries, reefs) suggest that its occurrence is unlikely.

3. Assessment of the biotope complex within SACs

The ‘demonstration’ SACs discussed in (i)-(vi) above all contain examples of the ‘Sea pens and burrowing megafauna’ biotope complex extending over wide areas of sea bed. In the cases of Loch nam Madadh, Sound of Arisaig, Strangford Lough and Berwickshire/North Northumberland, the geographic extent of the biotope complex has been mapped, whereas in Cardigan Bay and Plymouth Sound its spatial distribution is less accurately known. In none of these SACs has there been a detailed study of sea pen density, the species composition of the burrowing megafauna or their relative abundances. This information can only be gained by field observation using SCUBA, or by detailed analysis of towed camera recordings (see Chapter VII). So far, this has been achieved only in the north-eastern Irish Sea (Hughes & Atkinson, 1997) and in Lochs Sween and Fyne, Argyll (Atkinson, 1989; Howson & Davies, 1991; Nickell et al., 1995b), none of which are located within proposed SACs.

In the absence of data on community composition and species abundance, it is difficult to say at present which of the candidate SACs possess the ‘best’ examples of the biotope complex, ie. those which are most important from a scientific or conservation-related perspective. However, some general assessments based on geographic distribution can be made. Loch nam Madadh and Loch Duich contain the biotope variant characterised by *Funiculina quadrangularis*, which is unlikely to be found in any of the other SACs. The red band-fish *Cepola rubescens* is known from Portland Harbour, adjoining the Fleet SAC, and is not known to be present in any other candidate SACs. More detailed information on the megafaunal communities of southern and eastern Britain (ie. Plymouth Sound and Berwickshire/North Northumberland SACs) would be interesting, as our present concept of the biotope complex is derived largely from sites in north-west Britain (sea lochs, Irish Sea), and different combinations of species may be expected to occur elsewhere.

C. DISTRIBUTION OUTSIDE THE BRITISH ISLES

As noted in Chapter I, all of the sea pen species and the major megafaunal burrowers have distributions which extend beyond British and Irish waters. Aspects of the ecology of several megafaunal burrowers have been studied elsewhere, notably in the Mediterranean (eg. Dworschak, 1982; Pervesler & Dworschak, 1985; Ziebis et al., 1996), but there have been fewer community-level studies using SCUBA or underwater video. However, recent towed camera surveys have shown that heavily-burrowed muds exist in several areas of the Adriatic and Aegean Seas (Marrs et al., 1996), indicating the presence of megafaunal communities comparable to those known from British waters. In the Adriatic, crustacean burrowers include *Nephrops norvegicus*, *Jaxea nocturna*, *Upogebia* spp. and the mantis shrimp *Squilla mantis* (Atkinson et al., 1997). The fauna also includes a large echiuran worm, *Maxmuelleria gigas* (Atkinson et al., in press). In much deeper water (> 400m) in the Evoikos Gulf, Aegean Sea, the mud bottom is burrowed by *Nephrops norvegicus, Calocaris macandreae, Callianassa subterranea* and (probably) *Maxmuelleria gigas* (Marrs et al., 1996). Unusually, the burrowing community here also includes large numbers of another echiuran worm, *Bonellia viridis*, a species previously recorded only from hard substrata (Hughes et al., in press). These observations suggest that analogues to the ‘Sea pens and burrowing megafauna’ biotope complex will eventually be found to be widespread on suitable substrata in the Mediterranean area.

Thalassinidean mud-shrimps are common and diverse in coastal and continental shelf sediments throughout the world. They have been found to be important agents of bioturbation in tropical lagoons (Suchanek & Colin, 1986; Suchanek et al., 1986). Other groups of burrowing megafauna have been barely studied outside north-west Europe, but there is no reason to doubt that future work will result in the identification of new species (eg. Rogers & Nash, 1996) and confirm the importance of these animals within sediment biotopes worldwide.

Various species of sea pen are common elements of the benthic fauna throughout the world's oceans, from shallow coastal waters to the deep sea (eg. Langton et al., 1990). The few detailed studies of their ecology refer to species found on the Pacific coast of North America (Birkeland, 1974; Kastendiek, 1976; Davis & Van Blaricom, 1978). Where relevant to the British species, these will be discussed in Chapters IV and V.

D. KEY POINTS FROM CHAPTER II

- The ‘Sea pens and burrowing megafauna’ biotope complex includes seven biotopes currently recognised in the MNCR classification.

- The biotope complex occurs widely around the British Isles, with examples known from the Irish Sea, North Sea and many Scottish sea lochs.

- The biotope complex is definitely present in seven of the ‘demonstration’ SACs and probably absent in five others. Its distribution has been mapped in Loch nam Madadh, Sound of Arisaig, Strangford Lough and Berwickshire/North Northumberland. Its spatial extent is less well-known in Cardigan Bay and Plymouth Sound. Sea pens and burrowing megafauna are also known to occur in Portland Harbour, adjoining the Fleet SAC.

- There is no detailed information on community composition and species abundance in any of the proposed SACs, and consequently it is not possible yet to evaluate their relative scientific or conservation importance. Important characterizing species (*Funiculina quadrangularis, Pachycerianthus multiplicatus, Cepola rubescens*) appear to be present in only one or two of the SACs.

- Outside British and Irish waters, analogous biotopes exist in the Adriatic and Aegean Seas, and probably occur in coastal and shelf sediments in many other areas of the world.

III. ENVIRONMENTAL REQUIREMENTS AND PHYSICAL ATTRIBUTES

Like all biological communities, those included within the ‘Sea pens and burrowing megafauna’ biotope complex exist under a particular set of environmental conditions, and are absent where their requirements are not met. This chapter will summarize the nature of the physical environment in which these biotopes exist, and outline the most important parameters influencing the composition of the biological community.

A. PHYSICAL ENVIRONMENT

1. Hydrographic conditions

In British and Irish waters, the ‘Sea pens and burrowing megafauna’ biotope complex extends from the shallow subtidal (< 10 m depth) to over 100 m in the northern North Sea (Dyer et al., 1982), the western Irish Sea (Hensley, 1996), and the deepest sea lochs (Howson & Davies, 1991). Thalassinidean mud-shrimps occur in the low intertidal zone in many parts of the world but are not known to do so here, with the exception of the rarely-recorded *Axius stirhynchus*. The biotope characterized by *Virgularia mirabilis* and *Philine aperta* (IMU.PhiVir) can be found in water less than 10 m deep in the sheltered inner basins of some sea lochs (Howson et al., 1994). In the Caol Scotnish basin, Loch Sween, *Maxmuelleria lankesteri*, *Callianassa subterranea* and *Jaxea nocturna* occur in very fine, stable muds in as little as 8 m depth (Nickell et al., 1995b), but sea pens are absent here. The burrowing megafauna is typically more abundant in slightly deeper water (> 15 m), while the large sea pen *Funiculina quadrangularis* occurs at depths > 20 m.

Low-energy conditions are a prerequisite for the existence of fine sedimentary substrata. Areas supporting this biotope complex are usually highly sheltered from wave exposure and with weak or negligible tidal streams. The most extremely sheltered conditions occur in the almost landlocked inner basins of many sea lochs. The biotope coded CMS.AfilEcor, which includes *Callianassa subterranea* and *Virgularia mirabilis*, exists in slightly more energetic conditions, with consequently coarser sediments than are found in the inner sea lochs.

Biotopes within this complex occur in conditions of fully marine salinity and do not extend into estuaries (the sole exception seems again to be *Axius stirhynchus*, which has been recorded on estuarine shores). Shallow coastal habitats in the British Isles clearly experience wide seasonal temperature changes. Species characteristic of these biotopes may respond with seasonal patterns of behaviour (see Chapter IV), but within the British Isles most do not appear to be temperature-limited in their distribution.

2. Sediment particle size and organic enrichment

The size distribution of particles in a marine sediment is an extremely important ecological parameter and can have a major influence on the composition of the biological community. Grain size distribution can be expressed in a number of ways, but a simple three-way division can be made between sand (particles 62 - 2000 µm in diameter), silt (4 - 62 µm) and clay (< 4 µm) fractions (Buchanan, 1984). A further simplification is often made by pooling the two smaller size fractions into a silt-clay category. Sediments with silt-clay fractions > 80% are generally classified as 'muds', those with fractions in the range 30 - 80% as 'sandy muds', and those with 10 - 30% silt-clay as 'muddy sands'. The finest sediments at the heads of sheltered sea lochs may have a silt-clay content exceeding 95% (of sediment dry weight). Generally, finer sediments (higher silt-clay component) are found in conditions of lower exposure to waves and currents, and have a higher organic content than sandier substrata. This is because low-energy conditions favour the accumulation of settling plankton and detritus from the water column, and because the smaller sediment grains provide a larger total surface area for the growth of bacteria and other microorganisms. Organic content of unpolluted coastal sediments can range from < 1% in clean sands to 7 - 8% in sea loch muds (much higher figures can exist in situations of gross organic pollution by sewage, alginate waste or fish farm effluent)

Sea pens are anchored within the sediment but do not depend upon it for food. Of the three British species, *Virgularia mirabilis* has the broadest environmental tolerances, occurring both in extremely fine inner sea loch muds (biotope IMU.PhiVir) and in much sandier substrata containing large numbers of small stones and shell fragments (biotope CMS.VirOph.HAs).

Megafauna which burrow within the sediments, and in many cases feed from it, have a more obvious interaction with the substratum, and some species are characteristically found in a particular set of conditions. Buchanan (1963) found *Calocaris macandreae* only in areas where silt-clay formed more than 20% of the sediment. Highest densities occurred where the silt-clay content exceeded 60%. *Jaxea nocturna* is also associated with fine, organic-rich sediments. *Callianassa subterranea* is able to inhabit a wider range of sediment types, including fine sea loch muds and the much sandier sediments of the central North Sea. The animal constructs a distinctively different burrow in each of these two environments (Atkinson & Nash, 1990; Rowden & Jones 1995).

The burrowing megafauna are generally absent from very coarse sands. The limiting factors may be the low organic content (inadequate food supply) and low cohesion (burrows will tend to collapse easily) of sandier sediments. In coarser sediments *Callianassa subterranea* will line its burrow with mucus to prevent collapse, a precaution unnecessary in highly cohesive muds (Atkinson & Nash, 1990). To date, most studies of burrowing megafauna have been carried out in sea lochs with very fine muddy substrata, and the communities in coarser sedments have received less attention. At Lundy, *Cepola rubsecens*, *Callianassa subterranea* and *Upogebia* spp. are found burrowing in muddy gravel (Hoare & Wilson, 1976). In the Clyde Sea, *Cepola* is also commonest on relatively coarse sediments (R.J.A. Atkinson, personal communication).

The larger burrowers also appear to be excluded from areas of very high organic enrichment, for example the centres of sewage sludge disposal grounds (Pearson & Rosenberg, 1978; Smith 1988). This phenomenon will be discussed further in the section of this report dealing with the impact of human activities on the biotope complex (Chapter VI).

a. Case study: the north-eastern Irish Sea

There have been very few surveys of the distribution of biotopes within this complex over large areas of sea floor with a gradient of sediment types. The most detailed is that of Hughes & Atkinson (1997), who used towed underwater video to plot the distribution of megafaunal burrowers in the north-eastern Irish Sea off the Cumbrian coast. Visual estimates of population densities were supplemented by data from box-core samples. Sediments were distributed in broad bands running roughly parallel to the coastline (Fig. 9), extending from an offshore muddy sand (10 - 30% silt-clay content) onto progressively finer muds (up to 75 - 85% silt-clay), before coarsening again close inshore (muddy sand, 20 - 30% silt-clay, underlain by a layer of shell gravel). The sea floor was heavily burrowed by megafauna, but community composition changed markedly over the gradient of sediment types. The offshore muddy sand was dominated by *Callianassa subterranea* (estimated density 88 individuals m^{-2}), occupying multi-opening burrows of the type previously described from the North Sea (Witbaard & Duineveld, 1989; Rowden & Jones, 1995). The large thalassinoidean *Upogebia deltaura* was also common (estimated 22 individuals m^{-2}). The crab *Goneplax rhomboides* was present at low density. No sea pens were seen here.

The central finer muds supported a more diverse megafaunal community, with sea floor topography dominated by burrow openings of *Nephrops norvegicus* and the large ejecta mounds of *Maxmuelleria lankesteri*. The visual survey gave an estimate of 0.6 - 1.3 *Nephrops* burrow systems m^{-2}, while box-core samples indicated a density of up to 10 *Maxmuelleria* individuals m^{-2}. The burrowing community also included *Callianassa subterranea*, *Calocaris macandreae*, *Jaxea nocturna* and *Goneplax rhomboides*. The sea pen *Virgularia mirabilis* was present but rare.

The inshore muddy sand had a much lower burrow density than the other two zones, with no large ejecta mounds or *Nephrops* burrows. The most common burrower was again *Callianassa subterranea* (estimated 23 individuals m^{-2}), with *Upogebia deltaura* present at much lower density. *Goneplax rhomboides* was fairly common (estimated 2 individuals m^{-2}). *Virgularia mirabilis* also occurred most commonly in this biotope (10 individuals m^{-2}). Although its characteristic ‘volcano’ mounds were not seen on the video recordings, box-coring showed that *Maxmuelleria lankesteri* was also sparsely present in this relatively coarse sediment.

The sediment characteristics and faunal composition of the biotopes observed are summarised in the table below. An assessment of their position in the MNCR biotope classification is also given.

	Offshore muddy sand	**Central mud/sandy mud**	**Inshore muddy sand**
Sampling location*	54° 25.07’N 03° 50.22’W	54° 19.83’N 03° 41.64’W	54° 24.00’N 03° 33.30’W
Depth (m)	~30	~35	~20
% Silt-clay	~20	~85	~25
Major megafaunal burrowers	Callianassa subterranea Upogebia deltaura	Maxmuelleria lankesteri, Nephrops norvegicus	C. subterranea U. deltaura G. rhomboides
Other megafaunal burrowers present	Goneplax rhomboides	C. subterranea Calocaris macandreae Jaxea nocturna G. rhomboides	M. lankesteri
Virgularia mirabilis	Absent	Rare	Common
MNCR Biotope code	Most similar to CMS.AfilEcor	CMU.SpMeg	Most similar to CMS.VirOph

* The locations of each station sampled by box-coring in June 1995 are given. These stations corresponded closely with areas surveyed by towed camera in September 1993.

A significant finding, obtained by comparing the results of towed camera and box-core surveys in the same area, was that visual estimates of megafaunal densities (derived from counts of burrow openings) consistently underestimated the number of animals present in the sediment. This issue will be discussed further in the section dealing with monitoring and surveillance options (Chapter VII).

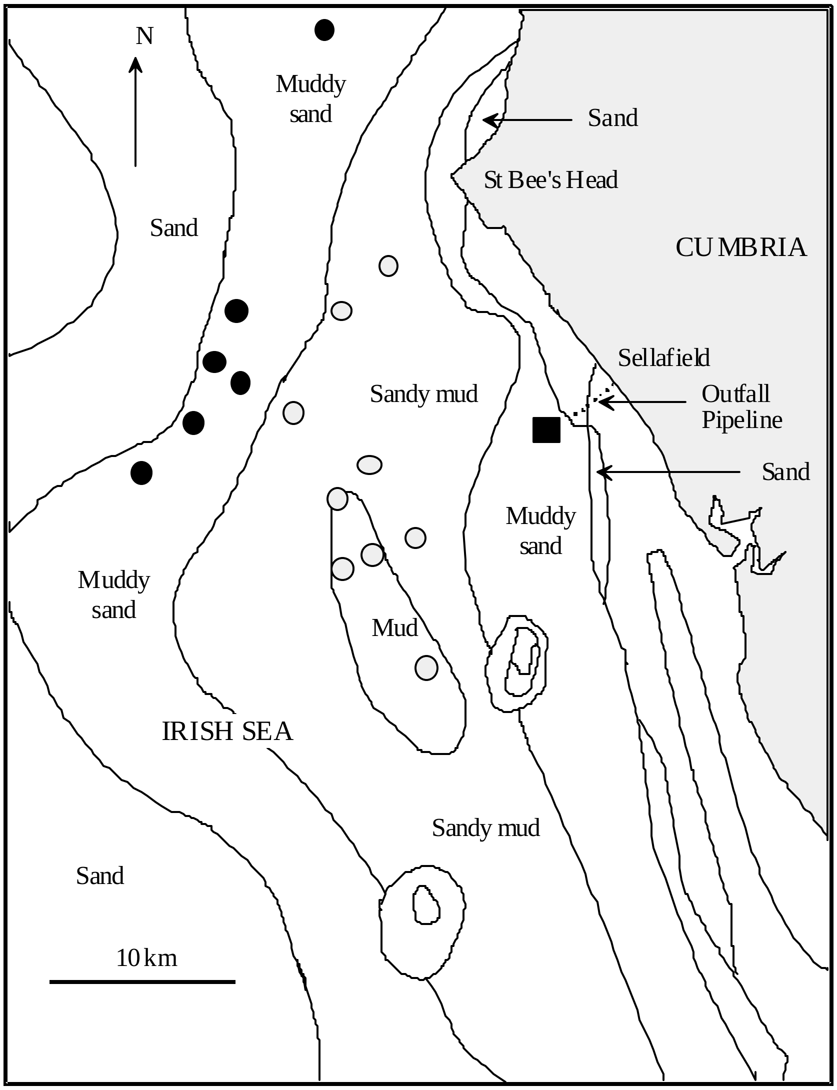

Fig. 9. Distribution of sediment types in the north-eastern Irish Sea near Sellafield, Cumbria. Solid black circles: Offshore muddy sand with *Callianassa subterranea* and *Upogebia deltaura*. Solid grey circles: Central mud/sandy mud with *Maxmuelleria lankesteri, Nephrops norvegicus* and other burrowing megafauna. Solid square: Inshore muddy sand with *Virgularia mirabilis, Callianassa subterranea* and *Upogebia deltaura.*

B. KEY POINTS FROM CHAPTER III

- Biotopes within the ‘Sea pens and burrowing megafauna’ complex exist from the shallow subtidal (< 10m) to over 100m depth in conditions of fully marine salinity, highly sheltered from wave action and subject to weak or negligible tidal streams.

- Of the three common sea pens, *Virgularia mirabilis* has the broadest habitat tolerances and occurs on the widest range of substrata.

- Sediment particle size distribution and organic content have a major influence on the abundance and composition of megafaunal burrowing communities. Finer-grained sediments typically have a higher organic content than coarser substrata.

- Some megafaunal burrowers (eg. *Calocaris macandreae*) are confined to muddy, organic-rich sediments. *Callianassa subterranea* can inhabit a wider range of sediments, varying its burrow form accordingly.

- Burrowing megafauna are usually absent from coarse sands and from conditions of very high organic enrichment.

- The biotopes of the north-eastern Irish Sea demonstrate how megafaunal burrowing communities change along a gradient of sediment types.

IV. BIOLOGY AND ECOLOGICAL FUNCTIONING

The relatively recent advent of SCUBA diving and underwater video as research techniques means that our understanding of the ecology of subtidal communities lags far behind that gained in the far more accessible intertidal zone. This is especially true for the biotopes considered here, in which many of the principal species live a cryptic existence within the bottom sediments. There are still many gaps in our knowledge of the basic biology of many of the most important megafaunal burrowers, while the British sea pens have hardly been studied at all in the field. The community ecology of subtidal sediment biotopes - the interactions between the different species, and between the animals and their environment - is still barely known, and there is no body of data comparable to those relating to intensively-studied environments such as rocky shores. This chapter will review and summarize what is known of the ecological functioning of this biotope complex. The burrow form and basic feeding biology of the megafauna have been described briefly in Chapter I.

A. BIOLOGY OF THE MAJOR CHARACTERIZING SPECIES

1. Life cycle and population dynamics

a. Sea pens

The sexes are separate in sea pens (ie. each colony of polyps is either male or female). The reproductive biology of the British sea pens has not been studied, but in other species the eggs and sperm are released from the polyps and fertilization takes place externally. In Puget Sound, Washington State, USA, the sea pen *Ptilosarcus guerneyi* spawns in late March, with up to 200,000 eggs produced per female colony. The free-swimming larvae do not feed and will settle within seven days if a suitable substratum is encountered (Chia & Crawford, 1973). This species may live for up to 15 years, and takes five or six years to reach sexual maturity (Birkeland, 1974). Larval settlement was patchy in space and highly episodic in time, with no recruitment to the studied population taking place in some years. This pattern gave rise to a discontinuous population size structure, made up of overlapping patches of colonies differing in age and size (Birkeland, 1974). Large year-to-year differences in recruitment rates were also seen in the 'sea pansy' *Renilla kollikeri*, a sea pen from the coast of California (Davis & Van Blaricom, 1978).

There have been no studies of population structure or life cycle in any of the British sea pens, but the limited data available from other species would lead one to predict a similar pattern of patchy recruitment, slow growth and long life-span.

b. Burrowing megafauna

i. Thalassinidean crustaceans

In typical decapod crustacean fashion, the fertilised eggs are carried on the abdomen of the female before hatching into planktonic larvae. The mating process is something of a mystery in this group, since in laboratory observations mud-shrimps have been found to be highly aggressive to members of their own species, regardless of sex, and intolerant of intruders into the burrow (Tunberg, 1986; Rowden & Jones, 1994; Dr L.A. Nickell, personal communication). *Callianassa subterranea* is sexually dimorphic, the major chela of the mature male being massively-enlarged (Rowden & Jones, 1994). However, the situation in this species is complicated by the occurrence of intersexes with both male and female reproductive organs (Dr L.A. Nickell, personal communication), suggesting that at least some individuals may change sex during their lifetime.

In the North Sea, *Callianassa subterranea* females carrying eggs were found from April to September (Rowden & Jones, 1994). Abundance of planktonic larvae was highest in August, indicating a summer breeding season with about four weeks spent in the plankton before settlement. There was some evidence that large females might have a second reproductive period in late winter. Life-span appeared to be 2 - 3 years. Less is known about reproduction in other species and localities. In the north-eastern Irish Sea, egg-bearing females of *C. subterranea*, *Jaxea nocturna* and *Upogebia deltaura* were found in June (personal observation). In Sweden, *U. deltaura* females also carried eggs from May to August, with one breeding season per year (Tunberg, 1986).

A rather different life history pattern was found in *Calocaris macandreae* off the coast of Northumberland (Buchanan, 1963, 1974). Animals were protandrous hermaphrodites (initially male, becoming female later in life) producing eggs in January-February which hatched in September-October. Only about 100 eggs were produced in each batch and the large larvae had no free-swimming phase before settling. In contrast to the short-lived *Callianassa subterranea*, individual *Calocaris macandreae* were very long-lived (9 - 10 years) and slow-growing, did not become sexually mature until five years of age, and produced only two or three batches of eggs in their lifetime. Partly as a consequence of this life history pattern, the studied population was very stable in numbers over a 10-year period.

ii. *Nephrops norvegicus*

Female *Nephrops* attain sexual maturity at 2.5 - 3 years of age at a carapace length of 21 - 22 mm (Howard, 1989; Bailey et al., 1986). Males become mature after three years at a carapace length of 25 mm. In Scottish waters the eggs are spawned and fertilized between August and November and carried by the females until the larvae hatch (April-August). The larval stages spend about 50 days in the plankton before settlement. The juveniles appear to preferentially take up residence in existing adult burrows, constructing their own burrows as an extension of these (Tuck et al., 1994).

The economic importance of *Nephrops norvegicus* means that far more attention has been devoted to its population biology than is the case for any other megafaunal burrower (eg. Bailey et al., 1986; Chapman & Howard, 1988; Tully & Hillis, 1995), and only the briefest outline of this subject can be included here. Local populations may vary considerably in density, individual size composition and growth rate (Tuck et al., 1997a). Individual growth rate may be reduced in high density conditions as a result of increased competition for food. Chapman & Bailey (1987) suggested that high population densities were usually found on coarser muds with a relatively high sand content, whereas lower burrow densities (and animals of larger size) were associated with finer muddy substrata. More recent work suggests that the peak in density occurs on mixed sediments of sand, silt and clay, with lower densities on very coarse or fine substrata (Tuck et al., 1997a), and that the main cause of local variation in population density may be the intensity of juvenile settlement rather than any direct effect of sediment type.

iii. *Maxmuelleria lankesteri*

Very little is known about the life cycle of this species (Hughes et al., 1996b). All individuals examined have proved to be female. Related echiuran species show extreme sexual dimorphism, with tiny parasitic males living on or in the female body, but so far these have not been found in *M. lankesteri*. In Loch Sween, Argyll, females containing eggs can be found almost year-round, with some slight evidence for a winter spawning. The larval form is completely unknown, but the large, yolky eggs suggest that the planktonic stage is brief or absent. Small juvenile worms are also very rarely recorded. The adults appear to be sedentary, never leaving or relocating their burrows (Nickell et al., 1995a). The individual life-span is not known, but a period of at least several years is likely. Diving observations at several sites in Loch Sween over a period of roughly ten years have provided no evidence of any major fluctuations in population size, and it seems likely that *M. lankesteri* is long-lived, with stable populations and low recuitment rates.

iv. Burrowing fish

The red band-fish *Cepola rubescens*, is sexually dimorphic, the males being larger and heavier than the females. Spawning takes place in late summer (Atkinson et al., 1977). Fish spawn just above the bottom, where fertilization takes place. The eggs are pelagic.

On the Scottish west coast, Fries' goby, *Lesueurigobius friesii*, lives for up to 11 years (Gibson & Ezzi, 1978). Growth is rapid in the first three years, slow thereafter. the females are larger than the males. Breeding occurs from late May to August. In contrast to *Cepola*, the eggs are laid on the roof and sides of the burrow, and presumably guarded by one parent.

The snake-blenny *Lumpenus lampraetiformis* is known to live for up to nine years, but little else is known of its life cycle (Gordon & Duncan, 1979).

2. Seasonal and diel activity patterns

Field observational data are available for a few of the principal species in this biotope complex. Hoare & Wilson (1977) found that colonies of *Virgularia mirabilis* in Holyhead Harbour were not synchronized in their behaviour. Some colonies were retracted into the sediment while others were extended. The sea pens were insensitive to light, but extension was possibly influenced by tidal conditions.

The activity patterns of thalassinidean crustaceans are difficult to identify since most species rarely (*Jaxea nocturna*) or never (*Callianassa subterranea*, *Calocaris macandreae, Upogebia* spp.) leave their burrows. Tunberg (1986) found that *Upogebia deltaura* remained inactive in the deepest parts of its burrow during the winter. Measurement of the quantities of sediment expelled from burrows can be used as an index of activity rate. Rowden & Jones (1997) found that sediment ejection by *Callianassa subterranea* from the North Sea was negligible during the period January-April, then increased steadily to a maximum in September before declining again over the autumn and early winter. Sea bed photographs supported this picture of seasonal activity, with a marked contrast between a smooth, inactive sea bed in January, and one covered with numerous ejecta mounds and burrow openings in September.

In shallow water, *Nephrops norvegicus* usually remain within their burrows by day and emerge at sunset to forage during the night (Chapman & Rice, 1971). The animals return to their burrows around sunrise. In deeper water (~100 m) this activity rhythm is reversed, and the animals are more active by day. Emergence occurs around dawn and dusk at intermediate depths. These patterns suggest that *Nephrops* is preferentially active at a particular optimum light intensity, and the period of emergence at different depths corresponds to the occurrence of this light level at the sea bed (Chapman et al., 1975). Individual *Nephrops* do not always return to their original burrow, and fighting for burrows has been observed (Chapman & Rice, 1971). In Loch Sween, burrows were aggregated in groups during the late summer, with the aggregations breaking up into a random distribution during the winter (Tuck et al., 1994). Aggregations may arise from the burrow complexes formed when juvenile *Nephrops* settle in pre-existing adult systems, then break up as the juveniles gradually extend their own burrows and lose contact with those of the adults.

In the shallow waters of Loch Sween, the echiuran *Maxmuelleria lankesteri* extends its proboscis to collect surface sediment only at night (Hughes et al., 1993) (a different activity pattern might be expected in deeper water where less light penetrates to the sea bed). The proboscis is only extended for short periods of about ten minutes, and only a small number of extensions (< 10) is made per night. The proboscis is therefore above the sediment surface for only a very small proportion of the total time. The worms are active all year round but seem to show peaks of activity in December and April when the proportion of easily-degradable organic matter at the sediment surface is at its highest (Hughes et al., unpublished data).

Red band-fish feed most actively at dawn and dusk, and enlarge or maintain their burrows by day. At night they remain inactive within their burrows (Atkinson & Pullin, 1996).

B. COMMUNITY ECOLOGY: INTERACTIONS BETWEEN SPECIES

1. Interactions between megafaunal burrowers

Where several species of burrowing megafauna occur together in the same habitat it is not uncommon for burrows to interconnect, and some quite complex multi-species systems have been revealed by resin-casting. Examples include burrow complexes of *Cepola rubescens* with *Goneplax rhomboides* and *Callianassa subterranea* (Atkinson et al., 1977), *Nephrops norvegicus* with *Goneplax rhomboides* and *Lesueurigobius friesii* (Atkinson, 1974b), and *Nephrops norvegicus* with *Maera loveni* (Atkinson et al., 1982). Interspecific connections are very common in some localities. Tuck et al. (1994) found that 34% of *Nephrops* burrows at a site in Loch Sween showed evidence of interactions with other species, including *Maxmuelleria lankesteri*, *Jaxea nocturna* and *Lesueurigobius friesii*, while 22% of the *Maxmuelleria* burrows examined by Nickell et al. (1995a) were connected with those of *Jaxea nocturna*. In some of the latter cases the *Maxmuelleria* and *Jaxea* shared the same burrow opening.

These interconnections are likely to be accidental in most cases and not indicative of any close symbiotic relationship between the different burrowers. However, once made, it is likely that connections will be maintained for their nutritional and ventilatory advantages. For example, a species such as *Jaxea nocturna* may benefit from association with *Maxmuelleria lankesteri* by taking advantage of the organic-rich surface sediment pulled into the burrow by the worm.

The interactions within megafaunal burrowing communities are still too poorly-known to say whether the presence of particular species has any positive or negative effects on the abundance of others. *Nephrops norvegicus* has been observed to prey on *Calocaris macandreae* (Smith, 1988), and will probably eat any of the other thalassinidean species if encountered. However, high densities of *Nephrops* and *Calocaris* coexist in many localities (Chapman, 1979). It is possible that the digging activities of *Nephrops norvegicus* may very occasionally unearth specimens of *Maxmuelleria lankesteri* (personal observations), leading to the demise of the worm, which is probably unable to re-burrow when exposed.

It is conceivable that sea pens might be adversely affected by high levels of megafaunal bioturbation, perhaps by an inhibitory effect on the survival of small, newly-settled colonies. Sea pens and various species of burrowing megafauna certainly coexist in many localities, but so far there has been no investigation of the interaction between them.

2. *Commensals*

A variety of small benthic animals will take advantage of the shelter offered by megafaunal burrows, especially when these are long-lasting or permanent structures. Echiuran burrows in particular have been found to harbour a rich associated fauna (Fisher & MacGinitie, 1928; Ditadi, 1982). Nickell et al. (1995a) found that numerous small bivalves and polychaete worms colonized the walls of *Maxmuelleria lankesteri* burrows. Mobile polychaetes such as *Ophiodromus flexuosus*, which normally live out on the sediment surface were also seen to enter burrows. A similar commensal fauna has been recorded in burrows of *Echiurus echiurus* in the German Bight (North Sea) (Rachor & Bartel, 1981). In most cases the commensal organisms also occur as part of the ‘background’ sediment fauna and are not obligate burrow residents. Within burrows they probably benefit from the echiurans’ irrigation activities which supply both oxygenated water and food, and may additionally gain some refuge from predators.

Thalassinidean burrow walls are probably a less suitable habitat for commensals because of the continual reworking and sediment grazing activities of the crustacean occupant. However, the body of the mud-shrimp itself may offer a substratum for colonization. The ctenostome bryozoan *Triticella flava* grows as a dense ‘furry’ covering on the antennae, mouthparts and legs of burrowing crustaceans. It occurs most commonly on *Calocaris macandreae*, but has also been found on *Nephrops norvegicus*, *Goneplax rhomboides*, *Jaxea nocturna* and *Upogebia* spp. On *Calocaris macandreae*, the bryozoan coverage is densest in late summer, but is shed when the crustacean moults its exoskeleton in September-October (Buchanan, 1963). However, the reproductive cycle of *Triticella* is synchronized with the moult cycle of its host and larvae are available to recolonize the crustacean body after the moult (Eggleston, 1971).

A truly remarkable commensal organism was described in 1995 from the mouthparts of *Nephrops* collected in the Kattegat, Denmark (Conway Morris, 1995). This organism, named *Symbion pandora*, is a tiny sessile animal less than 1 mm long with a basal attachment disc and an anterior ciliated food-gathering organ. It has a complex life-cycle involving both sexual and asexual stages. In the details of its structure, *Symbion* is so different from anything described previously that its discoverers created an entirely new phylum (Cycliophora) to contain it (Funch & Kristensen, 1995). Since the animal kingdom includes only about 35 phyla (each representing a major basic body plan), the description of a new one is a significant zoological event. Its association with *Nephrops norvegicus* illustrates that even relatively well-known organisms can still yield surprising discoveries.

A few organisms have also been recorded in association with the British sea pens. The isopod crustacean *Astacilla longicornis* has a specialised, highly elongate body form and is sometimes found clinging to the rachis of *Funiculina quadrangularis*. Another associate of *Funiculina* is the brittlestar *Asteronyx loveni*, a species which uses its very long, prehensile arms to cling to the sea pen, so maintaining itself in an elevated position above the sea bed (Fujita & Ohta, 1988). *Asteronyx* is a deep-water form usually found below 100 m depth. In British waters it has been sporadically recorded from the west of Scotland, but Loch Hourn holds the only precisely-located inshore population (Dr J.D. McKenzie, personal communication).

3. Epifauna

In addition to the megafaunal burrowers and sea pens, the biotopes within this complex support a variety of large animals living on or just below the sediment surface. The burrowing anemone *Cerianthus lloydii* is common throughout British and Irish waters in a wide range of sediment types. The much larger *Pachycerianthus multiplicatus* has a very localised distribution on the western Scottish and Irish coasts (it is also known from Scandinavia). This species is characteristic of the deep mud biotopes CMU.SpMeg and CMU.SpMeg.Fun. Howson et al. (1994) listed it as present in only 16 of the 98 sea lochs covered in their report. The densest known populations are at the heads of Lochs Fyne (Howson & Davies, 1991) and Duich (Connor, 1989). These two anemones inhabit tubes embedded in the sediment and so are not strictly ‘epifauna’. Another large (non-burrowing) anemone sometimes recorded on *Nephrops* grounds is *Bolocera tuediae*. This anemone has frequently been seen surrounded by aggregations of pink shrimps, *Pandalus borealis*, (C.J. Chapman, personal communication), but the details of this association are not known.

Common epibenthic predators/scavengers occurring in these biotopes include shore crabs *Carcinus maenas*, edible crabs *Cancer pagurus*, swimming crabs *Liocarcinus depurator*, hermit crabs *Pagurus bernhardus* and the starfish *Asterias rubens* and *Crossaster papposus*. The surface-living brittlestars *Ophiura ophiura*, *O. albida* and *O. affinis* are common on the sandier mud biotopes (CMS.VirOph, CMS.VirOph.HAs) and present in lower numbers on the finer muds. The white, slug-like gastropod *Philine aperta* is often present at very high densities (> 100 m^{-2}) on the finer substrata. This species is a predator of polychaete worms, bivalves and foraminiferans at the sediment surface.

Most of the common inshore fish species can be encountered over soft mud biotopes but seldom in large numbers. The biotope complex is not a major habitat for any commercially-important species. Aside from the specialist burrowers, the most characteristic fish are probably the gobies *Gobius niger* and *Potamoschistus minutus*.

4. Predation

Little is known about the intensity or importance of predation on the characteristic species of the biotope complex. Birkeland (1974) described a complex interaction between the sea pen *Ptilosarcus guerneyi* and seven predator species (four starfish and three nudibranchs). In

British waters the nudibranch *Armina loveni* is a specialist predator on the sea pen *Virgularia mirabilis*. This sea slug is infrequently recorded, but is known to occur from Norway to western France. In Puget Sound, a related species, *Armina californica* is one of the predators of *Ptilosarcus guerneyi*. Birkeland (1974) found that the nudibranch fed preferentially on the largest sea pens. In the laboratory, individuals were found to eat an average of one *Ptilosarcus* every four days. *Armina* was an uncommon animal at the study site and its impact on the sea pen population appeared to be minimal. Another predator on *Ptilosarcus* was the sun star *Crossaster papposus*. This species is also common in British waters and so may be a potential predator on sea pens here. Amphipod crustaceans of the family Stegocephalidae also appear to feed on sea pens, but little is known of their ecology (Moore & Rainbow, 1984).

Many specimens of *Virgularia mirabilis* lack the uppermost part of the colony, a feature which has been attributed to nibbling by fish. Mackie (1987) found that extracts of *Pennatula phosphorea* inhibited feeding in sole *Solea solea*, suggesting that this sea pen may possibly have a chemical defense against fish predation.

Nephrops norvegicus is known to be eaten by a variety of bottom-feeding fish, including cod, haddock, skate and dogfish. In some areas up to 80% of cod stomachs are found to contain *Nephrops* (Howard, 1989). There are also numerous records of fish predation on thalassinidean mud-shrimps, for example Buchanan (1963), who found *Calocaris macandreae* in the stomachs of cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. Since these mud-shrimps rarely if ever appear on the sediment surface, the fish probably catch them by suction while they are engaged in activities (eg. sediment expulsion) in the upper reaches of their burrows. The echiuran *Maxmuelleria lankesteri* has also been recorded in the stomachs of Irish Sea cod. Rachor & Bartel (1981) found that *Echiurus echiurus* was an important food for fish in the German Bight.

5. *Sediment macrofauna*

The burrowing megafauna and larger epifauna of these biotopes are accompanied by a a diverse fauna of smaller animals living within the sediments. Animals retained by a sieve of 0.5 mm mesh size are classed as ‘macrofauna’ (those passing through a sieve of this grade fall within the ‘meiofauna’ and ‘microbiota’). The macrofauna of marine sediments has generated an enormous literature, particularly in the field of benthic pollution monitoring (review in Pearson & Rosenberg, 1978), and only a brief outline of its composition relevant to the general ecology of the biotope complex can be given here.

The organic-rich fine muds supporting the biotopes within this complex (CMU.SpMeg and CMU.SpMeg.Fun) will typically support 30 - 45 macrofaunal species in areas not suffering from gross organic pollution. The macrofauna is found largely in the top 10 cm of sediment, with a majority of individuals in the uppermost 3 cm. Polychaete worms usually dominate in number of species and individuals. Members of the families Spionidae (eg. *Prionospio* spp.) and Cirratulidae (eg. *Chaetozone setosa*, *Tharyx* spp.) are often the most common taxa. In samples from Loch Sween, spionids and cirratulids comprised up to 70% of the individual animals present (personal observations). These are all small slender worms, 2 - 3 cm long, which use long anterior palps or tentacles to collect organic particles in the sediment. Other small polychaetes important in this environment are *Scalibregma inflatum*, and species of the genera *Glycera*, *Nephtys* and *Pholoë*. Small bivalves such as *Mysella bidentata*, *Corbula gibba* and *Abra alba* may be abundant. Other groups frequently present in large numbers are nemertean and phoronid worms. The brittlestars *Amphiura filiformis* and *A. chiajei* are also often common, with *A. chiajei* predominating on the finer muds. Most of these animals are deposit-feeders, ingesting tiny organic particles and feeding on the bacterial layer coating the sediment grains. Suspension-feeders include *Amphiura filiformis* and *Corbula gibba*.

Other biotopes within the complex will also support a polychaete and bivalve-dominated macrofaunal community, but the mix of species will differ according to hydrodynamic conditions, sediment type and level of organic enrichment. In general, more suspension-feeding animals will be found as the sediment grade becomes coarser. The sandier muds with *Virgularia mirabilis* (biotope CMS.VirOph) will also usually have the *Amphiura* species in large numbers (with *A. filiformis* predominating), along with the large tube-dwelling polychaetes *Chaetopterus variopedatus* and *Lanice conchilega*. Other important polychaetes include *Goniada maculata*, *Nephtys incisa* and *Notomastus latericeus*. The three bivalve species mentioned in the fine-mud fauna above are also frequently common in this biotope.

Most of the typical macrofauna of British sediments have very wide or even cosmopolitan distributions. The unusual polychaete *Sternaspis scutata* is limited to the southern English examples of biotope IMU.PhiVir, but has a very broad distribution outside the British Isles.

6. Bioturbation and macrofaunal community structure

A phenomenon often reported in surveys of sediment macrofauna is the high level of spatial patchiness in species distribution and abundance. Cores taken less than a metre apart may show striking differences in faunal composition. Small-scale differences in sediment characteristics undoubtedly contribute to this variability, for example where localized patches of highly-enriched sediment are created by the decomposition of loose seaweed or other organic detritus. However, the sediment fauna itself may help to generate this spatial variability, a key factor being the disturbance to the sea bed (bioturbation) caused by the activities of the large burrowing megafauna. Where they occur in large numbers, megafaunal burrowers can have a profound influence on their environment. In the southern North Sea, *Callianassa subterranea* was estimated to turn over a total of 11 kg dry sediment m^{-2} $year^{-1}$ (Rowden & Jones, 1997), while in an Adriatic lagoon, the volume of water pumped through burrows by *Upogebia pusilla* during periods of neap tides almost equalled the inflow of water from the open sea (Dworschak, 1981).

Many studies have examined the effects of bioturbation on the smaller sediment fauna (Hall, 1994). Both enhancing and inhibitory effects have been found, depending on the identity of the larger burrowers and the nature of their activity. By constructing and ventilating burrows, megafauna may oxygenate the sediments and make them less compact by virtue of their bodily movements and digging activities. This will allow macrofauna to occupy otherwise uninhabitable deeper sediments and may locally enhance the food supply by stimulating bacterial growth. Thomsen & Altenbach (1993) found that the numbers and biomass of bacteria and foraminifera were up to three times higher around burrows of *Echiurus echiurus* than in the surrounding sediment. Enhancement of macrofaunal diversity and abundance has been recorded in sediments colonised by dense populations of enteropneust worms (Flint & Kalke, 1986) and echiurans (Rachor & Bartel, 1981; Stull et al., 1986), with a marked decline in community diversity following the disappearance of these larger burrowers.

Negative effects of burrowing megafauna on macrofaunal populations may arise directly by predation, or indirectly as a result of burial, increased turbidity or sediment compaction. Posey (1986) found that most sedentary macrofauna were much less abundant in a dense *Callianassa* bed than in adjacent areas with fewer *Callianassa*. Core samples taken from the vicinity of *Nephrops norvegicus* burrows and from nearby unburrowed sediment showed that the abundance of macrofauna was reduced in near-burrow areas (Smith, 1988) Tentaculate surface-feeding polychaetes were particularly affected. Laboratory observations suggested that these were excluded by the sediment ‘bulldozing’ activities of the crustaceans. However, a number of small, opportunistic nematode and oligochaete worm species were able to take advantage of this and colonize the disturbed patches.

The overall conclusion to be drawn from these studies is that a mix of megafaunal burrowers occurring in a sedimentary biotope will generate a complex and continually-shifting ‘mosaic’ of habitat patches experiencing different types and levels of disturbance. The differing responses to macrofaunal species to this patchiness will probably be a factor in the maintenance of local species diversity. The depth penetration and total abundance of fauna in the sediment may also be enhanced by the physical and chemical consequences of megafaunal activity. However, studies undertaken to date have provided no evidence that any single megafaunal burrower acts as a ‘keystone’ species whose activity is the dominant factor in determining the structure of the local biological community.

C. KEY POINTS FROM CHAPTER IV

- The community ecology of subtidal sediments is little-known in comparison with the more accessible and widely-studied intertidal biotopes.

- With the exception of *Nephrops norvegicus*, little is known about the life cycle and population dynamics of the characterising species. *Calocaris macandreae* is known to reproduce slowly, and maintain stable population densities for at least ten years. Sea pens are also probably long-lived and slow-growing, with patchy recuitment.

- *Nephrops norvegicus* populations seem to occur at higher densities on mixed sediments. Animals are active outside their burrows at a preferred light intensity which is found by night in shallow water, by day on deeper grounds, and around dawn and dusk at intermediate depths.

- Interconnections between megafaunal burrows are quite common where several species occur together, but these probably represent accidental contacts rather than symbiotic partnerships.

- Long-lasting burrows such as those of echiurans harbour a commensal fauna of bivalves and polychaetes. Some unusual sessile animals can be found growing on the bodies of burrowing crustaceans, including one recently-described species representing an entirely new animal phylum. The rarely-recorded deep-water brittlestar *Asteronyx loveni* occurs as a commensal of *Funiculina quadrangularis* at one known location in western Scotland.

- *Nephrops norvegicus*, *Maxmuelleria lankesteri* and thalassinidean species are all preyed upon by fish, but the importance of predation in the ecosystem is not known. The rare nudibranch *Armina loveni* is one of the few known specialist predators on British sea pens.

- The activities of the larger burrowers can either enhance or reduce the abundance of sediment macrofauna, depending on the species involved. The ‘mosaic’ of disturbance patches created by megafaunal activity may play a part in the maintenance of biodiversity in the sediment community.

- No single ‘keystone’ species has been identified in any of these biological communities.

V. SENSITIVITY TO NATURAL EVENTS

Assessment of the sensitivity of the ‘Sea pens and burrowing megafauna’ biotope complex to naturally-occurring agents of environmental change has to be largely subjective, given the short time period over which the system has been accessible to study. Detailed studies of these biotopes have been carried out at only a handful of sites, and most work is still at the stage of characterizing the communities and gaining information on the basic biology of their principal species. There has not been time to accumulate the long-term observations of community structure and response to natural events that are available for habitats such as the rocky intertidal. This chapter therefore consists largely of case studies illustrating factors which have been shown to cause changes in sea pen or megafaunal burrower populations.

A. CASE STUDIES OF POPULATION STABILITY AND CHANGE

There have been no long-term studies of British sea pen populations, so the degree of temporal stability they exhibit is unknown. In California, Davis & Van Blaricom (1978) monitored densities of the sea pansy *Renilla kollikeri* on a subtidal sand plain from March 1974 to September 1975 and compared these with figures recorded at the same site in the period 1957-63. The density of *Renilla* remained fairly constant at about 1.68 individuals m^{-2} throughout 1957-63. Mean density in 1974-75 was much lower (0.06 individuals m^{-2}). A major recruitment was observed in August 1974, the first seen at the study site since 1971. In the northern part of the study area, *Renilla* density decreased rapidly after the August larval settlement, eventually stabilizing at approximately pre-recruitment levels. Starfish predation was suggested as a cause of the post-recruitment population decrease. In the southern study area, the *Renilla* population stabilized at a higher density of 4 m^{-2}, possibly because starfish foraging was inhibited here by wave surge.

Information on changes in megafaunal burrower populations is also very fragmentary. Off the Northumberland coast, the density of *Calocaris macandreae* was found to be very stable, remaining at about 18 individuals m^{-2} over a period of ten years (Buchanan, 1974). In contrast, in the German Bight (southern North Sea) populations of *Echiurus echiurus* fluctuate widely over a much shorter time-scale (Rachor & Bartel, 1981). From 1973 to spring 1976, the echiuran was apparently absent from the study area in the eastern German Bight. A mass recruitment of juvenile worms was recorded in spring 1976, with extremely high densities (averaging 250 individuals m^{-2}) over an area of about 40 km^2. By mid-late summer 1977, this area had shrunk to about 12.5 km^2 and population density had dropped to 140 m^{-2}. In summer 1978 *Echiurus* was found only in about 2.5 km^2 at a density of 22 individuals m^{-2}. This population had disappeared entirely by autumn 1978. From these observations and earlier records, Rachor & Bartel (1981) noted that successful recruitment of *Echiurus* seemed to follow very cold or stormy winters, perhaps as consequence of increased oxygenation of the bottom sediments.

B. POTENTIAL AGENTS OF CHANGE

1. Physical disturbance

The biotopes within this complex are associated with physically-sheltered conditions of low wave exposure and weak tidal currents. They are therefore not generally subjected to major physical disturbance by storms even where they occur in relatively shallow water (eg. in many sea lochs). Examples of these biotopes occurring off more open coasts, such as in the North or Irish Seas, will generally be in water deep enough to be unaffected by storm events.

2. Weather conditions

In shallow sea loch environments, sedimentary biotopes will typically experience seasonal temperature changes over a range of about 10°C (from ~ 5 - 15°C). In unusually cold winters or warm summers temperatures outside this range might be experienced, but it is not known whether this will have any effect on the biological community. Megafauna which burrow deeply in the sediment will probably be buffered to some extent from temperature changes in the overlying water column. The example of *Echiurus echiurus* in the German Bight suggests that annual variation in temperature can alter community composition by its effects on recruitment, but there is too little information available on other species to say whether this is a widespread phenomenon.

Warm summer temperatures may lead to stratification of the water column and to conditions of hypoxia - a reduction in dissolved oxygen content - in the near-bottom water, This is especially likely to occur in semi-enclosed water bodies such as sea lochs. Hypoxia will be exacerbated by high levels of organic matter in the sediment, and its potential effects on biological communities will be discussed later in association with organic enrichment.

3. Organic enrichment

Large increases in the organic content of the bottom sediments and associated phenomena such as oxygen depletion can have a significant effect on benthic animals of all types, including megafaunal burrowers. In the present context, organic enrichment is most likely to occur as a consequence of human activities such as sewage sludge disposal or cage aquaculture, and its effects will therefore be reviewed in the following chapter.

4. Predation

Well-known examples of benthic communities substantially affected by sudden population increases in predator or grazer species include the crown-of-thorns starfish (*Acanthaster planci*) ‘outbreaks’ on Indo-Pacific coral reefs (Moran, 1986), and the periodic devastation of northern hemisphere kelp beds by sea urchins (Hagen, 1995). So far, however, there have been no recorded examples of such events in the biotopes discussed here.

5. Disease

Like all organisms, the species making up the biological communities discussed here are subject to a variety of pathogenic (disease-causing) and parasitic infections. Thalassinidean mud-shrimps are frequently parasitized by specialized isopod crustaceans known as bopyrids. The parasite lives in the gill chamber of the mud-shrimp and can inhibit the reproductive development of its host (Tucker, 1930). In the southern North Sea, Rowden & Jones (1994) found that up to 11% of *Callianassa subterranea* individuals were infected with a bopyrid parasite. Presumably the reproductive output of mud-shrimp populations will be reduced to some extent by these parasites but it is not known whether this has any wider consequences.

To date, the most significant disease process recorded in a species from this biotope complex is the recent identification of a syndinean dinoflagellate pathogen, *Hematodinium* sp., in *Nephrops norvegicus* from the west of Scotland (Field et al., 1992; Appleton & Vickerman, 1998). The Syndinea is a group of exclusively parasitic dinoflagellates, and members of the genus *Hematodinium* have emerged as serious pathogens of commercially-important crustaceans in several areas of the world in the last decade (Shields, 1994). In *Nephrops*, the parasite occurs in the blood and connective tissue spaces and appears to cause death by blocking the delivery of oxygen to the host's tissues (Taylor et al., 1996). *Hematodinium* is most prevalent in *Nephrops* during the spring and early summer when infected animals have an abnormal bright orange body colouration and milky white ventral abdomen caused by a dense concentration of parasite cells in the blood. Heavily-infected animals become moribund, spend more time out of their burrows than healthy animals and are probably less able to evade capture by predators or fishing gear. Heavy infestation with the parasite is fatal to the host.

In the Clyde Sea, peak occurrence of the disease occurred in 1991 and 1992, when up to 70% of trawled *Nephrops* were infected (UMBS Millport, 1996). The incidence then declined, with 10 - 20% occurrence at Clyde Sea sites in 1996 and 1997. Infestation rates in 1998 appear to have increased again (R.J.A. Atkinson, personal communication). The infestation is now also well-established in the Irish Sea and appears to be increasing in the North Sea. The ecological consequences of *Hematodinium* infestation and host mortality in *Nephrops* populations are unknown, but there are potential economic implications, since the disease adversely affects meat quality. Fortunately, infected meat is non-toxic, and fishing mortality largely masks the effects of disease mortality. So far, the *Nephrops* fishery has not suffered any serious decline. This parasitic infestation is probably not a new phenomenon, but was overlooked until the mid-1980s. Prevalence of the infection is probably cyclical, with a large peak in the early 1990s which prompted the recent increase in research. An intensive research programme is currently in progress to clarify the life cycle of the parasite, determine the mode of transmission and assess the consequences of the problem for the *Nephrops* fishery.

C. KEY POINTS FROM CHAPTER V

- Very little is known about the extent of naturally-occurring change in biotopes within this complex, or of the factors leading to it. Among the burrowing megafauna, examples are known of species with highly-stable populations and other species which experience wide fluctuations in abundance.

- Biotopes within this complex are generally sheltered from major physical disturbances. Unusual temperature extremes may affect recuitment rates but few supporting data are available.

- Organic enrichment and associated phenomena such as oxygen depletion are the most important known agents of change in soft-sediment communities, but are likely to occur mainly as a consequence of human activities.

- The only major biological agent known to affect a species in this biotope complex is the dinoflagellate parasite now prevalent in *Nephrops* populations from the west of Scotland, Irish Sea and North Sea. The ecological consequences of this infestation are unknown but evidence to date suggests that the *Nephrops* stocks have not been seriously affected.

VI. SENSITIVITY TO HUMAN ACTIVITIES

As was discussed in the previous chapter, the lack of long-term observational studies of biotopes within this complex hinders any assessment of their sensitivity to naturally-occurring events. The same is true in relation to human-induced changes in the environment. Observational evidence does indicate a sensitivity to particular human activities (eg. trawling, organic pollution), although more rigorous numerical data are still sorely needed. It is also possible to identify certain other activities that could potentially impact on these biotopes (based on examples known from other benthic habitats, or simply from general biological principles). These additional factors will be briefly mentioned even where they have not yet been shown to be important in any specific case.

The chapter will focus on processes occurring at a local or regional scale, and which are relevant to the monitoring and management of SACs. Human-induced environmental changes taking place globally, and over a longer time-scale (eg. global warming, sea level changes) may ultimately prove to be important, but their effects, magnitude and timing are currently unpredictable and beyond the scope of the present review.

A. ACTIVITIES KNOWN TO AFFECT THE BIOTOPE COMPLEX

1. Trawling and creeling

Nephrops norvegicus is the only species within this biotope complex to be the target of a large commercial fishery (a small-scale local fishery for *Munida rugosa* exists in the Clyde). The *Nephrops* fishery is of major economic importance and is pursued throughout most of the geographic extent of the biotopes in which the species occurs. This includes both shallow, semi-enclosed sea loch areas, and open-coast grounds in deeper water (eg. the Irish and North Seas). In British waters the *Nephrops* fishery has grown rapidly since its inception in the 1950s (Howard, 1989), and the species is now one of the most valuable shellfish resources in the north-eastern Atlantic. Because of its intensity and wide geographic coverage, the *Nephrops* fishery has the potential to affect the biotopes in question throughout their range. There are potential consequences both for the *Nephrops* populations themselves, and for the associated fauna of sea pens and megafaunal burrowers.

a. Impacts on *Nephrops* populations

The waters around Scotland yield approximately one-third of a total world *Nephrops* catch of about 64000 tonnes (1995 figures, Marine Laboratory, Aberdeen). In terms of *Nephrops* landings per unit area fished, the Firth of Forth is the most heavily fished area, whereas the Fladen Ground in the North Sea is relatively lightly exploited (SOAEFD, 1997). With the exception of the Fladen, most Scottish stocks appear to be fully or over-exploited. Considerable efforts are currently being made to develop reliable methods for stock assessment (Tuck et al., 1997b) as a necessary step towards determining the effects of the fishery on *Nephrops* populations.

Recent findings from the western Irish Sea suggests that the structure of some *Nephrops* populations may render them vulnerable to over-exploitation. A large (approximately 3400 km^2), discrete area of muddy sediments between the Isle of Man and the Irish coast supports a large *Nephrops* fishery (average yield 8252 tonnes year^{-1} between 1989 - 1993). In spring and summer a large near-surface gyre (a circulating water mass) forms over a static dome of colder bottom water left over from the previous winter (Hill et al., 1997). The existence of this circulation system coincides with the period when *Nephrops* larvae are present in the plankton. Larvae appear to be retained within the gyre and eventually settle back onto the underlying muddy sea bed rather than being carried by currents into areas of unsuitable substratum (Hill et al., 1996). The retention of larvae by the gyre may be essential for the maintenance of the local *Nephrops* population, which acts as a largely self-perpetuating unit. The situation may be complicated by the fact that some larval production occurs in early spring, prior to the establishment of the gyre, and the population may therefore not be entirely ‘closed’, but it is possible that over-exploitation of *Nephrops* in this area could lead to a self-perpetuating population decline due to a reduction in recruitment.

On a smaller spatial scale, observations using towed video have given some insight into the localised effects of trawling for *Nephrops* in sea lochs. In Loch Fyne, Howson & Davies (1991) observed the highest densities of *Nephrops* in areas of muddy substratum close to, or surrounded by, submarine rock outcrops or boulders. These features presumably give some protection from trawling, as boats will tend to avoid areas where there is a high risk of damage to the fishing gear. In the intensively-trawled areas of lower Loch Fyne Howson & Davies considered it likely that trawling had reduced the density of the *Nephrops* population. Atkinson (1989) came to similar conclusions in his survey of Loch Sween. Variations in the density of *Nephrops* burrows in different regions of the loch seemed likely to reflect differences in trawling pressure. Highest burrow densities were found where submerged rock pinnacles or arrays of anchored buoys limited access by trawlers. However, it is possible that other factors such as differences in sediment type around submarine rock outcrops might also contribute to this pattern, and identifying a direct cause-and-effect relationship is difficult in cases such as this (Hall et al., 1993).

These limited observations lead to the general conclusion that trawling can possibly reduce the density of *Nephrops* in the confined situations of sea lochs. It is also important to note that even where the local topography is unfavourable to trawling, sea loch populations are still usually subject to exploitation by creel fishing. However, the resilience of *Nephrops* populations to fishing pressure may be enhanced by the fact that juveniles and egg-carrying females remain within their burrows and are not usually caught in trawls (R.J.A. Atkinson, personal communication). Self-seeding populations such as that in the north-western Irish Sea are probably the exception rather than the rule, and most stocks have the potential to ‘bounce back’, even after heavy fishing pressure.

b. Impacts on other megafaunal burrowers

Atkinson (1989) concluded that trawling was unlikely to affect other megafaunal burrowers to any great extent. The deep-burrowing species (mud-shrimps and *Maxmuelleria lankesteri*) will usually be too far below the sediment surface to be displaced by towed fishing gear. The uppermost parts of burrows will be disrupted by trawling, but observations in Loch Sween have shown that surface openings are soon re-established following experimental disturbance (personal observations). However, in Loch Fyne, Howson & Davies (1991) found that the density of all burrow types was lower in frequently-trawled areas than in sites protected by submarine obstructions. The impact of bottom trawling on benthic communities has been the subject of intensive study in recent years (Auster et al., 1996; Kaiser & Spencer, 1996; Tuck et al., 1998), and research on the cumulative effects of trawling on deep-burrowing megafauna is currently under way in the Mediterranean (M.J. Kaiser, personal communication).

The indirect effects on the burrowing community arising from the selective removal of *Nephrops* are unknown.

c. Impacts on sea pen populations

Sessile animals such as sea pens which project above the sediment surface are clearly likely to be damaged or uprooted by the passage of a trawl. In Loch Sween, *Virgularia mirabilis* was more abundant in the vicinity of rock pinnacles than on open mud plains (Atkinson, 1989). Protection from trawling is one obvious explanation for this, but it must also be remembered that as suspension-feeders, sea pens may require a certain degree of water movement, and that more favourable conditions for growth may exist where local hydrography is modified by irregularities in the sea floor. In Loch Fyne, *Virgularia* was scarce on the deeper muds irrespective of whether or not these were trawled (Howson & Davies, 1991). At shallower depths where the species was more abundant, densities were similar at untrawled (3 - 4 individuals m^{-2}) and trawled (2 - 7 m^{-2}) sites. Howson & Davies concluded that there was no clear evidence that trawling had affected *Virgularia* densities in Loch Fyne. The resilience of *Virgularia* to trawling is supported by the findings of Tuck et al. (1998), who found no changes in density in a sea loch following experimental trawling carried out repeatedly over an 18-month period.

Hoare & Wilson (1977) observed that *Virgularia* was absent from areas of Holyhead Harbour subject to disturbance by dredging or boat moorings, although a direct cause-and - effect relationship was not demonstrated.

Virgularia mirabilis is able to withdraw rapidly into the sediment when disturbed, an ability which should provide some protection from dislodgement by trawls. *Pennatula phosphorea* is also able to withdraw, but the taller *Funiculina quadrangularis* cannot do so. This species may therefore be more vulnerable to human-induced disturbance of the sea floor, particularly by mobile fishing gear. It is possible that the apparent absence of *Funiculina* from open-coast *Nephrops* grounds may be a consequence of its susceptibility to trawl damage (D.W. Connor, personal communication).

Creeling for *Nephrops* is pursued in many coastal areas, including those in which trawling does not take place. This is consequently another possible source of damage to sea pens. However, an experimental study in Loch Broom found that sea pens were quite resilient to being smothered, dragged or uprooted by creels (Kinnear et al., 1996). All three species proved able to re-anchor themselves provided the basal peduncle remained in contact with the sediment surface, and mortality rates following experimental creel disturbance were very low.

The overall conclusion arising from these studies is that *Funiculina* is likely to be the sea pen most susceptible to damage by fishing gear, but that *Virgularia* and *Pennatula* will be much less affected.

2. Organic enrichment

The release of large quantities of nutrient-rich organic matter into the sea is one of the most widespread and important human impacts on the marine environment. Circumstances in which this occur include:

- Discharge of sewage from coastal outfalls
- Larger-scale dumping of treated sewage sludge at offshore sites
- Sedimentation of faeces and uneaten food around marine fish farms
- Release of organic effluent from industrial sites (eg. pulp mills, alginate factories)

These various forms of organic enrichment can all have profound effects on benthic communities, and these have been widely-studied in the context of pollution monitoring (Pearson & Rosenberg, 1978). Typically, a moderate input of organic matter can enhance the abundance and diversity of the benthic fauna by increasing the supply of food, but as the organic load rises the faunal diversity declines and the benthos becomes increasingly dominated by a small number of hardy, opportunistic species (usually polychaetes of the genus *Capitella*), which may be numerically extremely abundant. In grossly polluted situations, even these animals are excluded and the sediment surface becomes covered by a whitish blanket of bacteria (*Beggiatoa* spp.) which obtain energy by oxidising sulphide diffusing out of the anoxic sediments. The threshold levels of organic enrichment at which these successive stages occur will be determined by factors such as temperature, sediment type and local hydrography. Where organic matter is released into the sea from a point source (eg. a salmon cage or sewage outfall), a gradient of faunal and sedimentary change will be produced, with progressively more impacted conditions encountered with increasing proximity to the source.

The burrowing megafauna has been regarded as belonging to the ‘normal’ (ie. unimpacted) sediment community, and to be excluded from areas of high organic enrichment (Pearson & Rosenberg, 1976). The critical factor in causing this exclusion may be the oxygen depletion (hypoxia) that is often associated with organic pollution. Hypoxia results from the elevated biological oxygen demand of degradative microbial processes, stimulated by the input of organic matter. Large, active animals with high respiratory demands will be the most affected by oxygen depletion. Bagge & Munch-Petersen (1979) reported that catches of *Nephrops novegicus* in the Kattegat (Denmark) were greatest in September when the concentration of dissolved oxygen in the bottom water was at its lowest. Low levels of oxygen within their burrows probably forced the *Nephrops* onto the sediment surface where they were more vulnerable to capture by fishing gear.

Several studies have found that thalassinidean mud-shrimp burrows are often very depleted in oxygen and enriched in sulphide, and that the shrimps themselves have physiological mechanisms that allow them to tolerate these conditions (Anderson et al., 1991; Astall et al., 1997a, b; Johns et al., 1997). These animals are therefore highly resistant to environmental oxygen depletion, and some species can withstand total anoxia for several days (R.J.A. Atkinson, personal communication). However, even mud-shrimps have their limits of tolerance. Stachowitsch (1984) recorded individuals of *Upogebia tipica*, *Jaxea nocturna* and *Axius stirhynchus* abandoning their burrows during a severe episode of oxygen depletion in the Adriatic. Christiansen & Stene (1998) observed specimens of *Callianassa subterranea* killed by upwelling of anoxic, sulphide-rich water in a Norwegian fiord. Organic enrichment will have other adverse effects besides hypoxia. These can include burial by large volumes of material (for example, in sludge dumping grounds), excess turbidity, changes in sediment characteristics that may inhibit the construction of burrows, and the presence of associated toxins (present in sewage sludge). All these factors may contribute to the exclusion of megafaunal burrowers from the most polluted situations.

Very little has been recorded concerning the sensitivity of sea pens to organic pollution, but it is reasonable to suppose that they will be susceptible to the same adverse effects as the other components of the benthic fauna. Hoare & Wilson (1977) noted that *Virgularia mirabilis* was absent from part of Holyhead Harbour heavily affected by sewage pollution. Both *Virgularia mirabilis* and *Pennatula phosphorea* were found to be abundant near the head of Loch Harport, Skye, close to a distillery outfall discharging water enriched in malt and yeast residues and other soluble organic compounds (Nickell & Anderson, 1997). Sediment organic carbon content in the study area was < 5%, and macrofaunal analysis indicated that the distillery effluent had very little effect on the benthic fauna.

a. Case study: the Garroch Head sludge dumping ground

Although the general observation that burrowing megafauna are absent from highly polluted areas appears to hold true, these animals do nevertheless flourish in many localities where the sediments are naturally rich in organic matter (for example, in many Scottish sea lochs). There is little information on the critical environmental thresholds causing changes in these communities. The only study to examine the distribution and abundance of megafaunal burrowers along a gradient of organic enrichment is that of Smith (1988), who carried out a towed video survey around the Garroch Head sludge dumping ground south of the Isle of Bute in the Firth of Clyde. Water depth was generally 70 - 80 m, but reached 100 m in places. The burrowing megafauna observed or identified from their burrow openings were *Nephrops novegicus, Calocaris macandreae, Callianassa subterranea, Lumpenus lampraetiformis* and *Cepola rubescens*. As predicted, megafaunal abundance declined as the centre of the dumping ground was approached. At the centre, the sediment contained about 10% organic carbon. Burrowing megafauna were abundant in areas of < 4% organic carbon, and absent where this exceeded 6%. The snake-blenny *Lumpenus lampraetiformis* seemed to have the highest tolerance, and extended furthest into the dumping ground. *Calocaris macandreae* did not extend as far along the enrichment gradient as *Lumpenus* or *Nephrops*. Epifauna such as whelks and hermit crabs also did not extend into areas of highest enrichment. The burrowing anemone *Cerianthus lloydii* was found at the sample site nearest to the dump centre, but was most abundant at an intermediate level of enrichment.

b. Effects of salmon farming in Scottish sea lochs

Cage aquaculture of Atlantic salmon has become a major industry along the west coast of Scotland, and few sea lochs are now untouched by its effects (Black, 1996). The rain of fish faeces and uneaten food from moored cages to the sea bed can cause local enrichment, progressing in severe cases to complete faunal exclusion and the development of bacterial mats on the sediment surface (Dixon, 1986; Brown et al., 1987; Gowen & Bradbury, 1987). The radius over which a salmon farm affects the bottom sediments will depend on local factors such as the size of the farm, depth of water and current speed. In some circumstances effects on sediment chemistry and faunal composition are limited to the sea bed directly underlying the fish cages, and out to a distance of only ~15 m from them (Brown et al., 1987). In contrast, Weston (1990) found detectable effects on sediment chemistry out to 45 m from a fish farm, while benthic community effects were found to at least 150 m distance.

Megafaunal burrowers are certainly absent from heavily-impacted sea beds below salmon cages, but as for other forms of organic pollution there has been no systematic study of this. The threshold levels of enrichment causing changes in megafaunal communities around sea loch salmon farms have not been determined, and information is largely anecdotal at present.

Atkinson (1989) recorded changes in the south basin of Caol Scotnish, a narrow upper arm of Loch Sween, apparently associated with the installation of salmon cages there. In 1987, most of the fine mud bottom of the basin was clear of *Beggiatoa*, with bacterial mats restricted to the immediate vicinity of the salmon cages. The density of megafaunal burrows (*Maxmuelleria lankesteri, Callianassa subterranea* and *Jaxea nocturna*) was relatively high in the unimpacted areas, ranging from 1 - 5 m^{-2}. In 1988 a carpet of *Beggiatoa* covered the sea bed throughout the south basin and the sediment was close to becoming totally anoxic. Burrows were much fewer than in 1987 (0.46 m^{-2}) and confined to small patches of *Beggiatoa*-free sediment. In the year separating these observations salmon cages had been positioned at both ends of the south basin (they were previously near one shore in the centre of the basin) and production had been increased. Although the salmon cages were removed from Caol Scotnish in 1989, sediment conditions continued to deteriorate, with *Beggiatoa* cover increasing further (Dr L.A. Nickell, personal communication). Some recovery was apparent by 1990, with megafaunal burrow openings reappearing. The large size of individuals of *Callianassa subterranea* and *Maxmuelleria lankesteri* collected at this time suggested that these were not recent recruits, and that the megafaunal burrowers had persisted in this area of the loch during the period of peak enrichment.

Such observations suggest that the interaction between sedimentary organic content and megafaunal burrowers may be more complex than previously believed, and that some species may persist in highly-enriched conditions even when burrow openings are rare or absent.

B. ACTIVITIES POTENTIALLY AFFECTING THE BIOTOPE COMPLEX

1. Other pollutants

There are no recorded cases of biotopes within this complex being seriously impacted by pollution processes other than organic enrichment, but on general biological principles it can be assumed that the various forms of contaminant shown to damage other benthic communities could also have adverse effects on the systems discussed here. Potentially harmful contaminants could include oil or oil-based drilling muds, pesticides, polychlorinated biphenyls (PCBs) and heavy metals.

Specific examples of known sensitivity to pollutants are rare, probably because burrowing megafauna are generally too difficult to sample to be included in standard pollution monitoring studies. In the North Sea, Daan et al. (1992) found that *Callianassa subterranea* decreased in density towards drilling sites contaminated by oil-based muds. Distribution patterns suggested that this was one of the more sensitive species in the sediment fauna, and experienced environmental stress even at distances of 1 - 2 km from the contaminant source. Following the wreck of the oil tanker *Braer* off the coast of Shetland in 1993, a fishery exclusion zone was established in the contaminated area. At present, *Nephrops norvegicus* is the only species for which this closure still operates (C.J. Chapman, personal communication). The low water currents associated with muddy sediments makes this type of habitat highly vulnerable to pollutants, which may persist in the environment for several years.

In the Scottish salmon farming industry, a variety of chemical compounds have been used to combat infestation of the fish by parasitic crustaceans (‘salmon lice’), and there has been concern about the possible effects of these pesticides on the benthic fauna. Ivermectin, an anti-louse treatment now coming into use within the industry, has recently been shown to be highly toxic to sediment-dwelling polychaetes (Black et al., 1997; Thain et al., 1997) and epibenthic shrimps (Burridge et al., 1993). It is reasonable to suppose that ivermectin (and perhaps other compounds used in the industry) might also be toxic to burrowing megafauna in the vicinity of salmon farms. In Washington State, USA, the pesticide carbamyl has been used to control populations of thalassinidean mud-shrimps whose activities are detrimental to the survival of cultivated oysters (Brooks, 1993).

Communities containing sea pens and abundant burrowing megafauna exist in the north-eastern Irish Sea in areas heavily contaminated by past discharges of long-lived radionuclides from the British Nuclear Fuels Plc reprocessing plant at Sellafield, Cumbria (Hughes & Atkinson, 1997). No obvious effects of Sellafield discharges could be observed here, although the burrowing fauna probably have a major influence on the distribution of radionuclides within the sediments (Kershaw et al., 1983).

In Nova Scotia, Pemberton et al. (1976) found that the extremely deep-burrowing mud-shrimp *Axius serratus* was most abundant in highly polluted sediments adjacent to urban, industrialised shores, areas barren of living foraminiferans, molluscs and ostracods. These observations suggest that the animal is one of the more pollution-tolerant members of the local benthic fauna, contrasting with the findings on North Sea *Callianassa* quoted above. The apparent diversity of responses and physiological abilities within the general category of ‘burrowing megafauna’ highlights the need for more research into the effects of environmental pollution on these animals.

2. Introduced species

There is currently increasing concern about the effects on marine ecosystems arising from the introduction of non-native species, this process often occurring accidentally as a result of human activities (eg. transport in ships’ ballast water) (Carlton, 1996). To date, a number of non-native species have become established in British waters, some very locally, others distributed more widely (Eno et al., 1997). The biotopes discussed here have not yet been subject to any biological invasions, but there is always the potential for this to occur.

C. ACTIVITIES UNLIKELY TO AFFECT THE BIOTOPE COMPLEX

With the exception of *Nephrops norvegicus* (and, to a small extent, *Munida rugosa*), no organisms are collected or harvested from these biotopes. Sedimentary habitats are generally unattractive to recreational divers, and there is no likelihood of environmental damage by this means (divers may occasionally collect small numbers of *Nephrops* for personal consumption).

None of the known examples of the biotope complex are in areas likely to be subject to coastal alteration, construction of tidal barrages or other large-scale environmental modifications. The fine sediments on which the biotopes typically exist are not targets for sea bed extraction.

D. KEY POINTS FROM CHAPTER VI

- Observational evidence suggests that trawling for *Nephrops norvegicus* and organic pollution are currently the two human activities most likely to affect this biotope complex.

- Most *Nephrops* stocks around the UK are believed to be fully-exploited. Local hydrographic conditions may lead to localised recruitment in some stocks and render them more vulnerable to over-exploitation.

- There is evidence that in sea lochs, trawling can locally deplete *Nephrops* populations. The effects on other burrowing megafauna are less clear, but one would expect deep-burrowing species to be relatively unaffected by this form of disturbance. The sea pen *Funiculina quadrangularis* is probably vulnerable to trawl damage, but the other species are likely to be more resilient. Creeling probably has no significant adverse effects.

- Heavy organic pollution excludes large, active megafauna such as *Nephrops norvegicus*, and probably also sea pens. Hypoxia is probably the most damaging consequence of organic enrichment. Deep-burrowing megafauna may also be excluded from heavily-impacted areas by hypoxia, physical burial or changes in sediment properties, but the critical thresholds causing change have not been measured.

- There are only scattered observations of responses to other forms of pollution, but there is evidence of megafaunal sensitivity to drilling muds. The anti-parasite chemicals used in the salmon farming industry are also toxic to some sediment-dwelling organisms.

- The introduction of non-indigenous species is a potential, but highly unpredictable problem in all coastal marine ecosystems, including those discussed here. There are no current examples known from this biotope complex.

- Other human activities in the marine environment seem unlikely to affect the biotopes discussed here.

VII. MONITORING AND SURVEILLANCE OPTIONS

A variety of techniques exists for surveying subtidal sedimentary biotopes. Different techniques provide different types and quality of information. The choice of method(s) to be used will therefore depend on the type of data required, and on the purpose of the survey, which may be either initial mapping and faunal characterization over a large area, or repeated monitoring at a smaller spatial scale. The availability and cost of the equipment required will also be a factor.

This chapter will review the methods available, summarize the advantages and disadvantages of each, and discuss examples where particular techniques have been applied to the ‘Sea pens and burrowing megafauna’ biotope complex.

It is worth noting at this stage that all these monitoring techniques require appropriate training and practical expertise to be employed effectively. In common with most other field investigations in the marine environment, success is usually also dependent on favourable weather conditions.

A. MONITORING TECHNIQUES

1. Remote sampling

This heading covers all equipment lowered by cable from the deck of a ship to the sea bed, then hauled back aboard with a sample of the substratum. Variants of this general pattern have been developed for different sediment types and include the Petersen, van Veen and Smith-McIntyre grabs, the Forster anchor-dredge and the Reineck box-corer. Detailed descriptions and illustrations of these and other models can be found in Holme (1971). Sediment samples required for detailed macrofaunal analysis are generally sieved through 1.0 mm or 0.5 mm mesh, and the recovered fauna fixed (4% formalin) and preserved (70% ethanol) for later examination.

All these sampling devices require to be operated from a hard-hulled boat with suitably-sized winch and A-frame. Box-corers are large enough for their use generally to be restricted to ocean-going research vessels. The standard area sampled by the most widely-used grabs is 0.1 m^2. In most macrofaunal studies, replicate samples will be taken, totalling 0.5 or 1.0 m^2 per station. Anchor-dredges take an unstandardized ‘bite’ out of the substratum and are therefore only semi-quantitative sampling devices. Specimen collection in the field can usually be achieved quickly in good weather conditions, but the sorting and identification of the fauna is very time-consuming and labour-intensive. There has therefore been much debate on the best sampling strategy to employ to maximize the cost-effectiveness of the analysis (Kingston & Riddle, 1989).

Grabs of various kinds have been used as standard sampling devices in countless benthic studies dating back over a century. Their great advantage is that the sampling of a standardized substratum area allows precise quantification of animal densities. Their disadvantage in the present context is that they do not penetrate the sediment deeply enough to reliably sample the deep-burrowing megafauna. Larger, mobile animals (eg. *Nephrops*) and epifauna occurring at relatively low densities (eg. sea pens in many areas) will also rarely be captured. The recovery of small patches of sediment also gives very little information on sea bed topography or burrow types. The deep-burrowing megafauna can be collected in anchor-dredges, but accurate density measurements are not possible, and the other interpretive problems of grab-sampling also apply.

Advantages and disadvantages of remote sampling

Advantages

- Allows precise measurement of densities of the smaller sediment fauna
- No depth or time limitations on sampling
- Field operation relatively simple
- Standard equipment readily available
- Water turbidity unimportant

Disadvantages

- Will not reliably sample:
  - Deep-burrowing megafauna
  - Large, mobile animals (eg. *Nephrops*)
  - Large epifauna at low densities (eg. sea pens)

- Gives little information on bottom topography or burrow types
- Standard sampling area very small (0.1 m^2 per grab)
- Analysis of samples time-consuming and labour-intensive
- Equipment needs hard boat to operate. May be unable to access very shallow areas or enclosed inlets

2. Diving

SCUBA diving has been used increasingly since the 1970s for field studies of the ecology of burrowing megafauna, and most of our knowledge of species such as *Maxmuelleria lankesteri* could not have been gained by any other means. Diving has also been the mainstay of the MNCR biotope surveys around the UK. The overwhelming advantage of the technique is that it allows close-up observations, precise deployment of static camera equipment and application of methods such as resin-casting (Atkinson & Chapman, 1984) that have proved invaluable for burrow identification. Research dives can be carried out from small dories or inflatable boats, or if necessary from the shore, allowing access to shallow or enclosed inlets that larger boats cannot reach.

However, diving does have a number of important drawbacks. Using compressed air as a breathing gas entails strict depth and time limitations. For practical purposes, it is difficult to carry out detailed observations or experiments at depths below 30 m, and most field studies of burrowing megafauna have been conducted in much shallower water. The use of alternative breathing gases promises to extend the depth and time limits for diving studies, but these have not yet come into general use in UK scientific diving. Any form of diving entails exposure to physical hazards (eg. decompression sickness), and as a result the conduct of professional diving operations in the UK is strictly controlled by legislation. Standard training and operational requirements for scientists diving at work are enforced by the Health and Safety Executive.

Divers can examine the sea floor at a finer resolution than any photographic technique, but only relatively small areas can be covered on a single dive. The technique is therefore more suited to repeated monitoring of small fixed sites than to habitat mapping on a scale of kilometres. Observations may be hindered or prevented entirely if the water is highly turbid, which is often the case over the fine-sediment biotopes discussed here. Working effectively over soft muddy sea beds requires a high level of diving expertise, in particular excellent buoyancy control and confidence in low-visibility conditions. These skills are lacking even in some quite experienced divers, but are not difficult to master with sufficient practice.

Advantages and disadvantages of diving

Advantages

- Allows first-hand observation at close range
- Allows accurate density measurements of sea floor features (burrow openings, sea pens)
- Allows repeated monitoring of fixed study sites
- Benthic samples can be collected (eg. hand-cores, burrow resin casts)
- Equipment readily available, relatively inexpensive compared with ROVs or underwater video
- Can be carried out from small boats or from the shore, allowing access to very shallow or semi-enclosed waters

Disadvantages

- Strict depth and time constraints
- Has potential physical hazards (eg. decompression sickness)
- Operations subject to strict legislative controls
- Only possible to cover small areas on individual dives
- Effectiveness can be limited by water turbidity

3. Towed underwater video

Towed video provides a means to visually survey large expanses of sea floor without the depth or time constraints associated with diving. The basic apparatus involved is relatively simple, consisting of a low-light sensitive video camera mounted on a lightweight, runnered metal sledge, towed slowly over the sea bottom by a ship. A number of camera models suitable for this work are now available from commercial manufacturers. The camera is mounted on the sled facing obliquely forwards, usually 70 - 100 cm above the substratum. One or two quartz-iodide lamps are positioned at the front of the sledge, pointing vertically or obliquely downwards to illuminate the sea bed within the camera's field of view. Red filters can be fitted to the lights to minimize disturbance to light-sensitive benthic animals. The camera is connected to a video recorder on board ship by an umbilical cable loosely attached to the towing warp every few metres along its length.

For optimum picture quality, towing speed has to be carefully controlled and kept at 1 knot or below as far as possible. Positional information during the tow can be recorded using the ship's navigational system (Decca or GPS). The visual field of the camera can be established prior to the survey by deploying the system with a calibration scale (graduated rule or marked string) fixed to the lower part of the sledge within view of the camera. Analysis of the resulting videotapes usually consists of counting the features of interest (eg. burrow openings, benthic animals) within a strip of known width traversed by the moving camera sledge. The frequency of counts or linear extent of the transect to be analyzed depends on the objectives of the survey and on the time available for the work (videotape analysis can be very time-consuming).

Although the equipment required for towed video surveys is relatively simple, it is expensive and generally confined to large marine laboratories or academic institutions.

Towed video is one of the most valuable tools in the study of megafaunal burrowing communities, and has been used intensively for this purpose in the west of Scotland (Smith, 1988; Atkinson, 1989; Howson & Davies, 1991; Tuck et al., 1997b), the north-eastern Irish Sea (Hughes & Atkinson, 1997), and in the Mediterranean (Marrs et al., 1996). To some extent, the method is not independent of diving studies, since the latter have provided much of the detailed information on burrow types essential for the accurate interpretation of sea floor video recordings. The resolution of camera observations is also lower than that of diving studies, so that smaller burrow openings or fine topographic details may be missed. This deficiency can be partly rectified by mounting a time-lapse still photographic camera on the video sledge,set to take pictures at intervals along the video transect. Still photographs usually give better resolution than videotape, and allow easier quantification of bottom features.

Care must be taken in selection of deployment areas in order to minimize the risk of snagging the camera sledge on wrecks, rock pinnacles or other obstructions. If it is necessary to work near underwater obstructions, a video or still camera mounted on a frame suspended below the ship can be used as an alternative to a towed sledge (C.J. Chapman, personal communication). Grabs or other benthic sampling gear could also be mounted on the frame, allowing samples to be taken. The main drawback to the suspended frame method is that the support vessel has to drift, so that there is little control over transect direction.

Advantages and disadvantages of towed video

Advantages

- Able to survey large expanses of sea floor quickly
- Allows precise density measurements of features of interest (eg. burrow openings, sea pens)
- No depth or time constraints (in coastal waters)
- Gives much information on sea bed topography and burrow types present, also on behaviour of benthic animals.

Disadvantages

- Equipment needs hard boat to operate. May be unable to access very shallow waters or enclosed inlets
- Equipment readily available but expensive
- Analysis of videotapes can be very time-consuming
- Not possible to collect benthic samples
- Provides no information on smaller sediment fauna
- Effectiveness can be limited by water turbidity
- Care required in choice of towing path (need to avoid wrecks, rock outcrops and other submarine obstructions)

4. Remotely-operated vehicles (ROVs)

ROVs are video camera systems mounted in a compact submersible vehicle whose movements are controlled by a surface operator via an umbilical cable (Auster, 1993). The capacities of ROVs are in some respects intermediate between those of SCUBA diving and towed video. Operations are free from the depth and time constraints imposed on human divers, but have a radius of operation defined by the length of the umbilical cable. Surveying outside this radius is achieved by moving the support vessel. An ROV has the advantage over towed video of being able to hover over a selected point or ‘retrace its steps’, allowing the operator to closely examine a feature of interest. However, quantification of features on the sea bed is more difficult than from a towed video recording, as an ROV does not always remain at a fixed distance from the substratum, and the field of view may therefore change. Because the movements of the ROV are controlled by the surface operator, surveys using this method are by nature more selective than video transects, and so may not give a representative view of the sea floor characters.

Some models of ROV have mechanical ‘arms’ controlled by the surface operator and so have the capacity to take benthic samples.

ROVs are used extensively in the offshore oil and gas industry but have not so far been widely employed in scientific studies in the UK. To date there are no published examples of their application in studies of the biotope complex discussed here.

Advantages and disadvantages of ROVs

Advantages

- No time constraints. Depth range limited by length of umbilical but most models can access depths likely to be encountered in UK coastal waters
- Able to cover wide areas (relative to capacity of human divers)
- Mobility allows close-up examination of sea bed
- Give much information on sea bed topography and burrow types present
- Deployment areas less restricted than towed video. Can be used over mixed substrata or in areas with submarine obstructions
- Some models able to collect benthic samples

Disadvantages

- Equipment needs a hard boat to operate. May be unable to access very shallow waters or enclosed inlets
- Equipment very expensive
- Precise quantification of sea bed features difficult due to changes in field of view
- Effectiveness can be limited by water turbidity (the ROV motors themselves may disturb the bottom sediments)
- Provide only limited information on smaller sediment fauna
- Sampling of sea floor features is non-random

5. Acoustic surveys

Acoustic surveys using the recently-developed RoxAnn^{TM} system are becoming increasingly important in the large-scale mapping of benthic biotopes (Greenstreet et al., 1997). RoxAnn^{TM} is an electronic system connected to the transducer of a conventional echo-sounder in parallel with the existing display. The system functions by processing the first and second echoes returned from the sea bed to derive values for the roughness (ie. topographic irregularity) and hardness (ie. substratum type, rock/sand/mud etc.) of the sea floor. By plotting the roughness and hardness functions against each other and integrating this information with values for water depth, a detailed map of the distribution of substratum types in a survey area can be produced.

The great advantage of RoxAnn^{TM} is that information on substratum types over wide expanses of sea floor (ie. on a scale of tens of kilometres) can be gathered very rapidly, in far less time than it would take to collect and analyse grab samples over such an area (Greenstreet et al., 1997). In addition, the system is sensitive not only to the physical characteristics of the substratum, but also to certain biotic characteristics such as the presence of organisms projecting above the sea bed, or to the presence of large burrows in the sediment. The technique therefore clearly has enormous potential for rapid mapping of marine biotopes.

However, RoxAnn^{TM} data cannot be used in isolation. The substratum types distinguished by the system in its present form must be ‘ground-truthed’, ie. checked by analysis of grab samples, diver survey or photographic observations. In some cases the system distinguishes more sediment ‘types’ than can be recognized by traditional particle size analysis (Greenstreet et al., 1997). Although broad biotope categories can be identified, their precise species composition must still be determined by other means.

Because of its recent origins, RoxAnn^{TM} is only now coming into widespread use as a tool for benthic habitat mapping, and the capabilities and limitations of the system are still in the process of being defined. It has been used in surveys of several candidate SACs, including Strangford Lough (Magorrian et al., 1995), Loch nam Madadh (Entec, 1996), the Sound of Arisaig (Davies et al., 1996) and the Berwickshire/North Northumberland Coast (Foster-Smith et al., 1996). In all of these areas, sedimentary biotopes with sea pens and burrowing megafauna were identified and mapped. This aspect of marine technology is evolving rapidly, and other comparable acoustic systems will doubtless become available in the near future.

Advantages and disadvantages of RoxAnn^{TM}

Advantages

- No depth (within coastal waters) or time limitations
- Allows substrata to be mapped rapidly over large areas
- Water turbidity unimportant

Disadvantages

- Equipment needs a hard boat to operate. May be unable to access very shallow waters or enclosed inlets

- Equipment very expensive
- Results need to be 'ground-truthed' by other methods (eg. grab sampling, towed video)
- Does not provide details of biological community composition or species abundance
- Not able to collect benthic samples

The table below summarizes the capabilities of the various monitoring techniques.

	Remote sampling	**Diving**	**Towed video**	**ROV**	**RoxAnn™**
Equipment widely available	Yes	Yes	No	No	No
Hard boat required	Yes	No	Yes	Yes	Yes
Physical hazards	No	Yes	No	No	No
Analytical time/effort required	Time- and labour-intensive	Depends on tasks undertaken	Time- and labour-intensive	Time- and labour-intensive	Relatively low compared to remote sampling
Depth/time limitations[1]	None	Strict	None	None	None
Geographic constraints[2]	Yes	No	Yes	Yes	Yes
Seabed topographic constraints[3]	No	No	Yes	No	No
Limited by water turbidity	No	Yes	Yes	Yes	No
Sample collection	Yes	Yes	No	Yes (some models)	No
Close-up observation	No	Yes	No	Yes	No
Areal coverage	Very low (per sample)	Low	Very high	High	Very high
Information on topography and larger fauna	No	Yes	Yes	Yes	Yes (faunal data limited)
Information on smaller fauna	Yes	Yes (if cores taken)	No[4]	Yes (some models)	No
Burrow/faunal density measurements	Yes	Yes	Yes	Yes (less accurate than towed video)	No

1. Refers to depths likely to be encountered in UK coastal waters (ie. < 200 m)
2. Access to very shallow water or narrowly enclosed inlets
3. Deployment constrained by mixed substrata or where submarine obstructions present
4. Can be overcome using suspended grab/camera system (see text)

B. PROVISIONAL MONITORING SCHEME RELEVANT TO SACs

Having outlined the capabilities and limitations of the various monitoring techniques, it is possible to suggest a provisional scheme by which the distribution, composition and ‘health’ of an example of the biotope complex within an SAC could be assessed. It is assumed that although the main responsibility for this work will rest with a local SAC site officer, manpower and technical support will be available from the relevant national conservation agency (EN, SNH, CCW, DOE/NI) and from the JNCC. Collaboration with academic experts based at universities or public sector research institutions should also be strongly encouraged and would be essential if certain options (eg. burrow resin-casting) were to be pursued.

1. Determining the presence and extent of the biotope complex

The presence of an example of the biotope complex within an SAC can be established by diving (eg. MNCR survey), observation using towed video or ROV, by consulting literature records of species distributions, or simply inferred from the existence of a local *Nephrops* fishery. The spatial extent of the relevant sedimentary habitats would be most effectively mapped using RoxAnn^{TM}, backed up by localized grab sampling or direct observation (diving, towed video, ROV). This initial habitat survey has already been achieved for many of the candidate SACs.

2. Initial characterization of the biological community

For an assessment of the scientific and conservation importance of an example of the biotope complex within an SAC, its species composition must be determined so that it can be compared with examples known from elsewhere. For the larger animals this requires a visual survey, either by divers (if water depth allows), towed video or ROV. Species such as *Nephrops norvegicus*, *Goneplax rhomboides*, *Cepola rubescens*, *Pachycerianthus multiplicatus* and the three sea pens are highly conspicuous and easily identified, either first-hand or on videotape. Identification of the more cryptic, deeper-burrowing megafauna (echiuran worms, thalassinidean mud-shrimps) relies on observation of relatively subtle diagnostic features of burrow openings and ejecta mounds, since the animals themselves are unlikely to be seen at the sediment surface. Guides to the identification of megafaunal surface traces can be found in Atkinson (1986), Atkinson & Nash (1985) and Hughes et al. (1996b, for *Maxmuelleria lankesteri*). A detailed key is provided by Marrs et al. (1996). In general, characterization of this element of the fauna can be fairly difficult even for experienced observers. Definitive identifications can be obtained by the resin-casting of burrows (Atkinson & Chapman, 1984), but this is a specialized and time-consuming technique requiring considerable expertise, and only feasible in relatively shallow waters (< 30 m). In the UK, this expertise exists in only a few academic institutions.

The composition of the sediment macrofauna can only be determined by examination of samples taken in grabs or cores. This is a highly labour-intensive process requiring taxonomic expertise. Numerous academic institutions and private environmental consultancies around the UK have the capacity to carry out these analyses, but financial costs may be considerable.

It is recommended that the initial faunal survey of a sedimentary biotope within an SAC should involve identification of burrowing megafauna by experienced observers using towed video or ROV recordings. These should be backed-up by first-hand diving observations if water depth allows, but enough is now known about the surface features associated with individual species for reliable identifications to be possible from videotape if good image quality is achieved. Resin-casting is probably unnecessary at the initial stage but would be worth pursuing if the visual survey reveals distinctive burrow types of unknown origin (eg. Tuck & Atkinson, 1995) in water depths accessible to divers. A small number of grab or core samples should also be taken in each of the major sediment types identified for characterization of the smaller fauna. A detailed consideration of the merits of different sampling strategies relative to the information obtained can be found in Kingston & Riddle (1989).

3. Monitoring of change in the biotope

If a biotope example within an SAC is deemed to be important for scientific or conservation-related reasons, it will be necessary to establish a programme of repeated observations or measurements to determine whether changes are occurring in any important parameters, and to identify the causes of any observed change. The practical objectives will clearly be to keep the time, labour and financial cost involved as low as possible while maximising the usefulness of the information obtained.

For routine monitoring, the abundance of the larger, more conspicuous fauna can be taken as an indicator of the general ‘health’ of the ecosystem. As discussed in Chapter VI, sea pens and *Nephrops norvegicus* are the species likely to be directly affected by trawling or organic enrichment (the most likely agents of change under current circumstances). The abundance of the larger animals can be assessed relatively easily (see detailed discussion below), and is a more immediately-apparent indicator of change than the results of costly and time-consuming macrofaunal analyses. The MNCR biotope classification system is explicitly based on the larger organisms recorded on diving surveys, and so reflects this emphasis.

a. Visual survey methods

Visual monitoring can be carried out either by divers or by remote means (towed video, ROV). Which method is used will depend on local circumstances (water depth may preclude diving) and on logistic factors (the availability of research vessels and video systems). Diving-based surveys can re-visit precisely located study areas and provide information on changes at a very small spatial scale. Study sites can be buoyed, then simple rope transect lines or grids (composed of negatively-buoyant line) can be pegged out on the sea floor to give a standardized counting area. Atkinson (1989) used a rope transect 200 m x 2 m in size to map megafaunal burrows in Loch Sween. Deployment of a transect of this size can be achieved by slowly paying it out from a small boat, then pinning the corners to the substratum. Shorter transect lines (eg. 20m long) can be taken down by a diver wrapped around a central post, pegged at one end, then paid out as the diver swims slowly over the bottom.

For repeated monitoring, rope grids or transect lines can be left in position indefinitely, but if visits are to be infrequent (eg. only one or a few occasions per year) it is probably best to remove them after each visit. Structures left on the sea bed will rapidly become fouled by attached organisms. Rope grids will also tend to trap loose seaweed, which will decompose and alter the sediment characteristics by localized organic enrichment of the study area. Fixed structures are also vulnerable to damage by fishing gear or boat anchors, and close liaison with the local community will be required to avoid this if grids, transects or camera systems are to be left in place for extended periods.

The length and duration of towed video surveys will probably be determined by the available ship-time, but it is quite possible to survey virtually the full linear extent of lochs as large as Fyne and Sween in a few days (Atkinson, 1989; Howson & Davies, 1991). Analysis of the resulting videotapes will usually take far longer than the time spent in the field, and this factor should be borne in mind when planning a towed video (or ROV) survey. It is very easy to generate more videotape than there is time to analyze, and some selectivity is usually necessary. For example, Atkinson (1989) examined in detail video records of stretches of sea bed 200 m long by 1 m wide. The sections for analysis can be taken at regular intervals along the ship's path, but in practice, the occurrence of stretches of poor visibility may disrupt the regular spacing of sampling areas. The area of sea floor surveyed needs to be large enough to take account of the patchy distributions of many megafaunal burrowers. A high-resolution still camera used in conjunction with the towed video will provide information on subtle sediment features and small burrow openings.

b. Features to quantify

i. Sea pens

Extended sea pens are easily counted, either by first-hand observation or on videotape, except perhaps when populations are very dense, in which case a semi-quantitative abundance scale could be used (ie. occasional/frequent/abundant etc.). The periodic retraction of colonies of *Virgularia* and *Pennatula* into the substratum is a factor that could lead to errors in density estimates, as more pens will usually be present than are visible above the surface at any given time. Kinnear et al. (1996) noted the difficulty of accurately estimating *Virgularia* densities from towed video recordings. Birkeland (1974) found that the apparent density of *Ptilosarcus guerneyi* at his study sites varied from 0 - 5 colonies m^{-2} to 10 - 30 m^{-2}, depending on the proportion of colonies extended. The average proportion of extended colonies was 26%. There was no obvious relationship between extension and tidal cycle, current strength or direction, turbidity, weather, season or time of day. Colonies were not synchronized in their behaviour, a feature also found by Hoare & Wilson (1977) for *Virgularia mirabilis* in Holyhead Harbour.

In the light of this behaviour pattern, counts of expanded sea pens should be regarded as giving minimum estimates of population density. If the retraction behaviour of colonies is not synchronized, this source of error should 'average out' when comparing sets of observations (ie. if, for example, 50% of colonies are extended at any given time, an observed density difference on successive observations is indicative of a population change, even if the absolute number of pens present is not known). The timing of expansion cycles, and the absolute number of colonies present, could be determined by observation of small areas of sea floor using a static video or time-lapse still camera deployed on the sea bottom for a period of a few days.

ii. Megafaunal burrow openings and mounds

Burrow openings and sediment mounds can also be counted easily on dived transects or on good-quality video recordings. In the context of SAC monitoring it is recommended that counts should be made of broad categories of feature (eg. 'Large/small mound', 'Large/small burrow opening' etc.), rather than attempting to estimate precisely the population densities of the various species present (unless specialist help is available). There are numerous complicating factors involved in the latter exercise, and the time required to achieve it is far greater than for a basic count of surface features. The problems in converting from surface features to population densities include:

- Megafaunal mounds and burrow openings often show features diagnostic of particular species, but most bioturbated sediments contain many simple holes (large or small) that even an experienced observer will find difficult to identify. This ‘uncertainty factor’ is particularly acute in analyses of towed video recordings whose resolution may not be sufficient to show subtle identification features.

- The number of surface openings per individual burrow system is variable in many species (eg. *Calocaris macandreae*, *Jaxea nocturna*, *Callianassa subterranea*), so that converting from one parameter to the other is at best an approximation. In the north-eastern Irish Sea, megafaunal population density figures derived from surface mound and hole counts were found to underestimate the actual numbers extracted from box-core samples (Hughes & Atkinson, 1997). In the case of *Callianassa subterranea* a four-fold discrepancy was found, due partly to the presence of large numbers of small juveniles whose burrow openings were invisible at the scale of resolution of the towed video.

- At close range, a diver can quite easily distinguish the extent of an individual *Nephrops* burrow system by noting the relative orientations of the various openings. This is harder to achieve from a video recording, which may give only a fleeting view at a low level of resolution. The occurrence of vacant burrows, and others occupied by several animals (adult-juvenile complexes) creates problems in estimating animal densities from burrow densities. Again, if specialist help is not available, it is probably best to make a simple count of burrow openings rather than try to estimate the number of burrow systems present.

For these reasons, it is probably best to use the total number of mounds and burrow openings seen in a survey area as an indicator of the density and activity level of the megafaunal burrowing community. More precise, species-level density estimates can be made if sites are surveyed by experienced observers (especially if diving work is possible), but it is assumed that this will not always be possible. Specimens of the larger, more conspicuous megafauna (*Nephrops norvegicus, Goneplax rhomboides, Cepola rubescens*) may be seen above the sediment surface and should also be counted, but the number seen will usually be only be a small (and indeterminate) proportion of the local population.

Suggested basic categories of megafaunal surface features for monitoring purposes are listed in the table below, with guidance on the likely or potential creators of these. Size categories are very approximate, as all categories will show a continuous variation in size, with considerable overlap between the features made by different species. Marrs et al. (1996) give a more detailed guide to megafaunal surface features, incorporating the different size categories of these.

Basic category	Size & appearance	Potential creator
Sediment mound	Large, conical or domed, 20 - 40 cm diameter. May have a central burrow opening	Maxmuelleria lankesteri. Possibly other echiuran worms
	Small, < 10 cm diameter. May have a central burrow opening	Callianassa subterranea, Jaxea nocturna
Hole in sediment surface, penetrating at an oblique angle	Large, up to 10cm across	Nephrops norvegicus. Animal may be visible in or near burrow opening
	Smaller, much < 10cm across	Lesueurigobius friesii, Goneplax rhomboides, or small Nephrops norvegicus. Animal may be visible in or near burrow opening
Hole in sediment surface, penetrating vertically	Large, circular, up to 20 cm diameter, at plane of sediment surface	Cepola rubescens. Animal may be visible in or near burrow opening
	Small, circular, much < 10 cm diameter	Any thalassinidean crustaceans, echiuran worms, probably others
	Small, circular, in groups of 3 (or multiples of 3)	Calocaris macandreae
	Very small, slit-like, in clusters	Maera loveni
Star - shaped trace on the sediment surface	Up to 70 cm in diameter. Linear tracks may radiate from a central burrow opening.	Maxmuelleria lankesteri. Possibly other echiuran worms

Atkinson (1989) and Marrs et al. (1996) found that counts of burrow openings and mounds made by divers agreed fairly well with those made over the same ground from towed video recordings. Diver observation allows a finer scale of resolution than is obtainable by video, so that more small surface features are likely to be recorded. Care should therefore be taken if figures obtained by the two methods are to be compared.

iii. Larger epifauna

The larger epifaunal animals such as crabs, hermit crabs and starfish can be easily counted if desired. The burrowing anemones *Cerianthus lloydii* and (especially) *Pachycerianthus multiplicatus* should also be conspicuous when extended. Both species can withdraw into their tubes below the sediment surface, and population density estimates will therefore be subject to the same qualifications as for the sea pens discussed earlier.

iv. Condition of the sediment

The occurrence and extent of any surface patches of black, reduced sediment colonised by bacterial mats (*Beggiatoa* spp.) should be noted, as this will indicate a localized increase in sediment organic content. Such localized enrichment is a normal seasonal occurrence in many places, for example, in shallow sea lochs receiving a large input of loose seaweed, terrestrial leaf litter and settling phytoplankton, and so is not necessarily an indicator of adverse environmental changes. However, particular attention should be paid to the extent of these patches if the site is potentially influenced by local human input of organic matter (eg. a salmon farm or sewage outfall).

If sediment samples can be collected, it is possible to measure the organic content simply and easily by combustion. Small amounts of sediment (a few grammes) are freeze-dried, finely-ground, then heated to 500°C for about 15 hours in a muffle furnace. After cooling, the samples are re-weighed, and the weight loss gives a measure of the organic content. The apparatus required to carry out this analysis (freeze-dryer, muffle furnace, accurate balance) is unlikely to be available on-site at a marine SAC, but will be standard equipment at any academic institution likely to be taking part in an SAC monitoring programme. Sediment samples can be stored frozen if immediate analysis is not possible.

v. Trawling

The passage of a *Nephrops* trawl will generally leave conspicuous tracks on the sea bed, and the occurrence of these during a visual survey should be noted. A bottom trawl will leave two parallel linear tracks.

c. Monitoring potential agents of environmental change

In addition to determining the composition of the biological community and monitoring it for any evidence of natural or human-induced change, any SAC management scheme will also have to identify and assess the potential causes of environmental change at that locality. In the context of the ‘Sea pens and burrowing megafauna’ biotope complex, these are most likely to be the *Nephrops* fishery and any localized sources of organic pollution.

i. Fishing effort

The frequency of trawler visits to a locality should ideally be recorded, as should the number of boats engaged in creel fishing for *Nephrops*. The estimation of trawling pressure may be difficult because site observation is unlikely to be continuous, and trawlers have been known to operate at night in order to avoid detection. Within an SAC, fishing activity could be monitored by the requirement to record accurate catch and effort data in logbooks provided for the purpose. Needless to say, gaining any of this information will require an SAC officer to maintain good relations with the local community and regional fisherman’s organization, both of which will be represented on the local SAC management group.

ii. Organic pollution

Only a few candidate marine SACs are in locations so remote as to be unaffected by the human input of organic matter to the sea. In most sites harbouring the ‘Sea pens and burrowing megafauna’ biotope complex there will be some degree of sewage input, while sites in the west of Scotland will be potentially affected by salmon or shellfish farming. Point sources of organic matter in or close to a marine SAC should be identified, and also the quantities of material involved. Data on volumes of effluent emitted from sewage outfalls or tonnage deposited at sludge disposal grounds will be obtainable from the relevant regional water authorities or environmental agencies. Aquaculture sites should be monitored for fish tonnage (which will determine the output of waste from the farm), and for the usage of anti-parasite chemical treaments. Computer models are now available to predict the dispersal distances and sedimentation rates of particulate organic matter from sewage outfalls and fish farms, and these should be an important aid to management of marine sites in the future (see Chapter VIII).

C. KEY POINTS FROM CHAPTER VII

- The various techniques available for mapping and characterizing the biotope complex provide different types of information. Remote sampling will not reliably detect large or deep-burrowing animals. Diving provides high-resolution data but can only be employed in relatively shallow water. Video observations allow monitoring of bottom topography and faunal distributions over large areas. RoxAnn$^{\text{TM}}$ is a highly effective means of mapping the extent of sedimentary biotopes but must be ‘ground-truthed’ using other methods.

- For basic mapping of the biotope complex within an SAC, a RoxAnn$^{\text{TM}}$ survey backed up by grab-sampling and towed video is recommended.

- Detailed characterization of burrowing megafauna should involve diving or towed video surveys by experienced observers.

- For routine biological monitoring the larger fauna (sea pens, megafaunal surface traces, epifauna) should be used as indicators of the condition of the biotope. These are all relatively easy to count first-hand or on videotape. Megafaunal abundance should be assessed from surface features grouped into simple categories, as precise estimation of species population density is a complex task with many potential sources of error.

- Potential agents of environmental change in an SAC should also be identified and monitored. For this biotope complex the most important examples will be the intensity of the local *Nephrops* fishery, and any sources of organic input to the marine environment (eg. sewage disposal, aquaculture).

VIII. GAPS AND REQUIREMENTS FOR FURTHER RESEARCH

It will have become clear from the preceding chapters that our understanding of the structure and dynamics of the biotopes in question is still very patchy. Considerable advances have been made over the past decade in studies of some of the major characterizing species, but there is still little information on ecological relationships at the population or community level. In the context of SAC management, initial surveys have confirmed the existence of the biotope complex in several of the candidate sites, but in none of them is there detailed information on community composition and species abundance.

The following list outlines some of the main deficiencies in our current knowledge, focusing on questions directly relevant to the management of the biotope complex within SACs.

A. COMMUNITY COMPOSITION WITHIN CANDIDATE SACs

1. Issue to be addressed

For all candidate SACs known or believed likely to include examples of the biotope complex, it is necessary to quantify the abundance of the three sea pens and any associated species of national conservation importance (eg. *Pachycerianthus multiplicatus, Asteronyx loveni*). Identification of the burrowing megafauna present in each site is also required, with at least a semi-quantitative assessment of their relative abundance.

2. How to address this

Quantitative surveys of the sea floor by towed video, still camera or ROV, supplemented by diving observations where water depth allows. These surveys should be carried out by observers with experience of megafaunal burrowing communities and the survey techniques involved.

B. POPULATION DYNAMICS OF SEA PENS

1. Issue to be addressed

Nothing is known of the growth, mortality or recruitment rates of the three British sea pen species. It is therefore difficult to assess the resilience of populations to natural or human-induced changes in the coastal environment.

2. How to address this

Detailed diver monitoring of population turnover in fixed quadrats established at suitable coastal sites. For *Virgularia mirabilis* this could be done in a range of substrata, to determine whether population dynamics vary in different biotopes. Studies of *Funiculina quadrangularis* in deeper mud sites would probably allow comparable data to be collected on the rare anemone *Pachycerianthus multiplicatus*, with which it often co-occurs. This observational study would be relatively easy to carry out in the field, but would have to be maintained for a period commensurate with the probable life-span of these animals (ie. several years).

C. EFFECTS OF TRAWLING ON SEA PENS AND BURROWING MEGAFAUNA

1. Issue to be addressed

As discussed in Chapter VI, there is observational evidence that trawling can deplete local populations of *Nephrops norvegicus*, but the effects on sea pens and deep-burrowing megafauna are less certain, with some disagreement between the findings of towed video surveys (Atkinson, 1989; Howson & Davies, 1991). This important management-related question needs to be addressed systematically, ideally with data from both observational and experimental studies. Some work relevant to this issue is currently in progress (M.J. Kaiser, personal communication), but little has yet appeared in the mainstream scientific literature (Tuck et al., 1998).

2. How to address this

Quantitative towed video surveys of sea pen and burrower densities in areas experiencing known levels of trawl disturbance (eg. untrawled, rarely trawled, frequently trawled). This observational element of the study should be combined with experimental trawling over grounds previously characterized by towed video. Ideally, diver surveys of the experimentally-trawled areas would be carried out for fine-scale measurements of burrow regeneration rates, and to determine the proportion of sea pens that are uprooted or damaged by trawl passage. Experiments could also be conducted to measure subsequent recovery and survival of sea pens following trawl passage. Time-lapse still photography or video could be used to monitor post-trawl recovery in areas where diving is not possible.

The results of this study would help to determine whether exclusion of mobile fishing gear from defined areas should be considered as a measure to protect examples of these biotopes, particularly those containing the more vulnerable sea pen *Funiculina quadrangularis*.

D. THRESHOLD EFFECTS OF ORGANIC ENRICHMENT

1. Issue to be addressed

The responses of sediment macrofaunal communities to organic enrichment are now well-established, and the successional changes in species composition are widely used as environmental indicators in pollution monitoring studies. The larger, megafaunal burrowers will also be affected by local organic enrichment, but there are few data on the threshold levels of enrichment leading to community change, or on the effects of associated contaminants such as the anti-parasite chemicals used in cage aquaculture. Determining the spatial extent of influence by local sources of organic pollution (eg, salmon farms) will be particularly important to examples of the biotope complex in sea lochs or other semi-enclosed water bodies. The best-known examples of the ‘Sea pens and burrowing megafauna’ biotope complex are found in sea lochs and these are potentially vulnerable to disturbance by future expansion of the aquaculture industry in the west of Scotland.

2. How to address this

Diver-surveyed transects should be monitored in the vicinity of point sources of organic matter (salmon farms would be the obvious choice), and the distribution of megafaunal burrowers and sea pens recorded along the enrichment gradient. Computer models are now available (or actively under development) to predict levels of particulate deposition and environmental change around organic discharges (Cromey et al., 1996; Gillibrand & Turrell, 1997). Faunal distribution patterns would be used in conjunction with relevant model simulations to predict the likely effects of organic discharges on sea pen/megafaunal biotopes in semi-enclosed waters. This would make an important contribution to soft-sediment biotope management in SACs.

E. GENETIC INTERCHANGE BETWEEN LOCAL POPULATIONS

1. Issue to be addressed

The case of *Nephrops norvegicus* in the western Irish Sea (see Chapter VI) demonstrates that local hydrographic factors can affect the population structure and recruitment potential of benthic organisms. Species with planktonic larval stages, once throught to be capable of unrestricted genetic interchange over huge distances, may in some cases exist as a series of semi-isolated local populations with a much smaller recruitment 'radius'. This is likely to be even more true for species which lack an extended planktonic phase in their life cycle (probable examples from this biotope complex include sea pens and *Maxmuelleria lankesteri*). Limited larval dispersal may render species vulnerable to local extinction in the face of environmental pressures, if declining populations cannot be replenished by an inflow of recruits from elsewhere. The extent to which this situation exists in species from the 'Sea pens and burrowing megafauna' biotope complex, and the degree of genetic diversity within species from coastal ecosystems generally, is only now beginning to be investigated.

2. How to address this

A range of biochemical and molecular genetic techniques is available to measure the degree of genetic interchange between populations. In the context of SAC management, appropriate techniques could be applied to species deemed to be of conservation importance, and which appear to have a fragmented or localized distribution. The anthozoans *Funiculina quadrangularis* and *Pachycerianthus multiplicatus* would be obvious candidates, and interesting comparisons could be made with the population structure of the more widespread sea pens *Virgularia mirabilis* and *Pennatula phosphorea*. The body form of these anthozoans is such that the required tissue samples could probably be obtained without much damage to the animals and it would not be necessary to collect entire specimens. A genetic study of this kind would be complementary to the investigation of population dynamics proposed under (A) above.

IX. SYNTHESIS AND APPLICATION TO MARINE SAC MANAGEMENT

The preceding chapters have reviewed the available information on the distribution and ecology of the ‘Sea pens and burrowing megafauna’ biotope complex, and outlined the main potential agents of natural and human-induced change. It is possible now to consider the relevance of these factors to those candidate SACs in which the biotope complex occurs, and to assess the overall importance of the biotope complex in conservation terms. This chapter will also assess the suitability of the various monitoring options discussed in Chapter VII to particular sites, and the suitability of the SACs for addressing the research needs listed in Chapter VIII.

A. BIODIVERSITY, CONSERVATION IMPORTANCE AND SENSITIVITY OF THE BIOTOPE COMPLEX

1. Importance

The criteria for assessing the ‘importance’ of a species or community from a conservation-related perspective have been the subject of much debate. They are perhaps especially difficult to establish in the marine environment, where basic knowledge of distributions, life cycles and ecological functioning is still at a low level compared with the terrestrial situation. A number of criteria (not necessarily exhaustive) for assessing conservation importance are listed below, with details of their relevance to the ‘Sea pens and burrowing megafauna’ biotope complex. Criteria include those listed by Hiscock (submitted).

Habitats, communities or species may be considered ‘important’ from a conservation - related perspective if they are:

a. Rare or very restricted in distribution

Of the MNCR-defined biotopes included within this complex, the most restricted are CMU.SpMeg.Fun and IMU.PhiVir, both of which are confined to a small number of Scottish sea lochs (IMU.PhiVir has one isolated example in Portland Harbour). The sea loch representatives are distributed along a large stretch of the western Scottish coastline, but their collective spatial extent must be fairly small.

Species falling within this category are the sea pen *Funiculina quadrangularis*, the anemones *Pachycerianthus multiplicatus* and *Scolanthus callimorphus*, and the brittlestar *Asteronyx loveni.* All of these species do occur outside British waters, so that their conservation importance must be defined in a British context. Some megafaunal burrowers (eg. *Axius stirhynchus*) are known from only a small number of records, but these animals are too easily overlooked to be classed with any confidence as truly rare.

b. In decline or have been

None of the biotopes or species considered here are known to be currently declining. Existing records are inadequate to determine whether any declines have occurred in the recent past.

c. A high proportion of the regional or world population or extent

Biotopes with sea pens and megafauna have certainly been best-characterized and studied in British waters, but as discussed in Chapter II, similar biological communities are known from sedimentary habitats in many parts of the world. The anemone *Pachycerianthus multiplicatus* is known only from Scotland, Ireland and Scandinavia, so that British waters might conceivably hold a significant proportion of its total population.

d. Particularly good or extensive examples of their type

British and Irish waters do support good examples of the biotopes in question, with a high diversity of burrowing megafauna and several sea pen species. Their perceived importance may change as information is gained from other regions, but at present the British representatives are probably the best-known examples of their type.

e. Keystone species providing a habitat for other species

The various small invertebrates found as commensals in megafaunal burrows are also found as members of the general sediment fauna rather than being specialized burrow associates. The one example known in this category is the brittlestar *Asteronyx loveni*, which appears to be an obligate commensal of large anthozoans such as *Funiculina quadrangularis*.

f. Biotopes with a particularly high species richness

Marine sediments do support a large number of invertebrate species, especially if the entire size range of animals is considered. Biotopes characterized by sea pens and burrowing megafauna are not known to be unusually species-rich, but have not been compared systematically with sediments lacking this component of the fauna. It is possible that the patchwork of disturbance created by megafaunal burrowers may promote a higher local species diversity (of macro- and meiofauna) than would otherwise exist.

g. Biotopes important for the efficient functioning of regional ecosystems

Marine sediments are certainly important in the geochemical cycling of carbon, nutrients and metals in coastal environments. Bioturbation is known to affect geochemical processes but no studies have yet been able to assess its importance at the ecosystem level (ie. comparing the efficiency of cycling through bioturbated and non-bioturbated sediments).

h. Of high aesthetic, symbolic or recreational importance

The biotope complex does not possess any features within this category.

This assessment leads to the overall conclusion that the conservation importance of the ‘Sea pens and burrowing megafauna’ biotope complex lies in:

- The restricted distribution and spatial extent of the biotopes and species listed under (a) above.

- The fact that the British representatives are particularly good examples of their type.

2. Sensitivity

As discussed in Chapters V and VI, the biotopes within this complex (including CMU.SpMeg.Fun and IMU.PhiVir, defined above as being of conservation importance) are sensitive to disturbance by trawling and organic pollution, and probably by chemical contamination of various kinds. The ability of these biotopes to recover after disturbance (ie. return to their original state) is not well-understood. Sediment macrofaunal communities can recover following the cessation of organic enrichment, although the time required for this to occur is strongly dependent on local conditions (Pereira, 1997). The life cycles of some animal species may act as a barrier to recolonization following local disappearance. This will be true especially of species with low reproductive rates, and short-lived larvae with low dispersal abilities (Hiscock, submitted). Species with a sessile or sedentary lifestyle as adults will clearly also be unable to recolonize an area other than by larval dispersal.

The life cycles of most of the characteristic species of this biotope complex are poorly-known, but the studies reviewed in Chapter IV suggest that taxa with poor colonization ability will include the three sea pens, *Pachycerianthus multiplicatus*, *Calocaris macandreae* and possibly *Maxmuelleria lankesteri*. Local extinction might not be easily (or ever) reversed in these species, a feature of particular importance to those with fragmented distributions (eg. *Funiculina, Pachycerianthus*).

3. Feasibility of management

The biotopes and species defined above as being of conservation importance are limited in their distribution within the UK to semi-enclosed water bodies of relatively small spatial extent (sea lochs, Portland Harbour). In these circumstances, effective habitat management to promote their survival is a feasible proposition. This would involve monitoring of, and possibly regulation of, those human activities likely to damage the species and communities of interest, namely the use of mobile fishing gear and the discharge of organic material into the sea.

Examples of the ‘Sea pens and burrowing megafauna’ biotope complex existing in open sea areas (Clyde, Irish Sea, Minches, North Sea) may also be subject to management, but any measures taken (eg. closure of areas to trawling) will come within the context of fishery regulation, these areas being the major commercial *Nephrops* grounds.

B. SUMMARY OF THE BIOTOPE COMPLEX IN ‘DEMONSTRATION’ SACs

In the following sections, ‘status and monitoring value’ summarize the extent of our current knowledge of the biotope complex in each SAC, and make a provisional assessment of the relative importance of the site from a conservation perspective. ‘Potential management concerns’ and ‘Recommended action’ are self-explanatory.

1. Loch nam Madadh

a. Status and monitoring value

Loch nam Madadh probably contains good examples of the biotopes CMU.SpMeg, CMU.SpMeg.Fun and CMU.VirOph. The nationally rare *Funiculina quadrangularis* and *Pachycerianthus multiplicatus* are present (Entec, 1996), species found in very few other candidate or possible SACs. The spatial extent of the sediment biotopes within the loch system has been mapped, but we still lack data on sea pen abundance, and details of the species composition of the burrowing megafauna.

b. Potential management concerns

The density of human habitation in the loch area is low. Lochmaddy township discharges some sewage into the loch. There are a number of sites leased for salmon or shellfish cultivation, all in the outer islands and channels of the loch system (Howson, 1991). A small amount of fuel oil contamination and general marine litter is likely to arise from the ferry terminal and other boating activities in Lochmaddy Harbour. There is also small-scale creeling for *Nephrops*. The generally low intensity of human activities in the area suggests that there are unlikely to be any significant impacts on the biotope complex at present, although the effects of any future expansion of salmon farming in the loch system should be monitored. Loch nam Madadh is a fiardic sea loch, with maximum depths at its entrance (Howson, 1991). The finer muds with *Pennatula, Funiculina* and burrowing megafauna are found in this outer, deep region which continues into the open sea. In this relatively open and well-flushed area they are likely to be less vulnerable to the impacts of aquaculture than similar biotopes located in the more enclosed upper reaches of fiordic sea lochs.

c. Recommended action

A systematic survey using towed video or ROV should be carried out to give more precise information on biotope distributions and species abundances. Only at the outer edge of the loch system are water depths of over 30 m reached, so that supplementary diver observations or transect counts would be possible throughout almost all of the areas of interest.

2. Sound of Arisaig

a. Status and monitoring value

The state of knowledge of the biotope complex in this area essentially mirrors that described above for Loch nam Madadh. Sediment biotopes are extensive, with records of both sea pens

(*Virgularia mirabilis*) and burrowing megafauna, but details of community composition and species abundances are lacking.

b. Potential management concerns

Small discharges of sewage effluent take place from housing in the Arisaig area, but the local population density is so low that the effects of this will be minimal (Howson, 1990). Sites have been leased for salmon and shellfish farming in Loch Ailort, Loch Ceann Traigh and Loch Moidart, and there are further experimental aquaculture-related activities in and around the Sea Fish Industry Authority research station at Ardtoe. The effects of aquaculture are likely to be limited to areas of restricted water circulation in upper Loch Ailort and the north channel of Loch Moidart. The megafaunally-burrowed muds recorded by Davis & Hall-Spencer (1996) are in areas relatively open to the sea and unlikely to be affected by the current levels of aquaculture in the sea lochs.

There is some local creel fishing for *Nephrops* in the Sound of Arisaig area. It is not known if trawling is pursued this close inshore, but any occurrence of this should be monitored for its potential effects on the mud biotope along the Open Coast.

c. Recommended action

A quantitative survey by towed video would be highly desirable to provide more information on the communities present in the area. The megafaunally-burrowed muds in Loch Ceann Traigh and in the Open Coast area (Davies & Hall-Spencer, 1996) are at depths (30 - 60 m) beyond effective diving range.

3. Strangford Lough

a. Status and monitoring value

The biological diversity and recognised conservation importance of Strangford Lough have led to its major biotopes being mapped in some detail (Erwin, 1977; Magorrian et al., 1995). As for Loch nam Madadh and the Sound of Arisaig, our knowledge of the local sea pen/megafauna biotope is limited to its spatial extent and the presence of a few conspicuous species (*Virgularia mirabilis*, *Nephrops norvegicus*, *Goneplax rhomboides*). An accurate assessment of the representativeness (and hence conservation importance) of this community relative to others of its type awaits a more detailed quantitative survey.

b. Potential management concerns

Strangford Lough supports a much larger human population than either of the Scottish SACs discussed above. The largest town is Newtownards on the northern shore. Other villages contribute to a total lough-side population of about 60,000. There are seven main sewage outfalls discharging effluent after various degrees of treatment (Service, 1993). The finer sediments have an organic carbon content mostly in the range 2 - 5% (one station with a value of 6.8% was found). The sediments therefore have a high organic content, but are within the range recorded for naturally-enriched sea loch sediments. Service (1993) found high chromium concentrations in the sediment at some stations, associated with tannery effluent discharged through the sewage outfall at Killyleagh. Past discharges of chromium exceeded 10 tonnes per year, but this quantity has since been reduced 10-fold. No strong spatial trends were found in the distribution of other heavy metals in the lough. Magorrian et al. (1995) found high densities of *Nephrops norvegicus* on the mud grounds in the central part of the lough, suggesting that megafaunal communities have not been adversely affected by effluent discharges, but it would be advisable to have more information on the dispersal of particulate organic matter in relation to biotope distributions. Strangford Lough also contains extensive and very dense beds of epifaunal suspension-feeders (brittlestars *Ophiothrix fragilis*, and horse mussels *Modiolus modiolus*), and it is possible that the filtering activities of these animals may play a part in ameliorating the effects of effluent discharges into the lough.

There is a small *Nephrops* fishery within Strangford Lough, mainly carried out by potting (R. Briggs, personal communication). This is unlikely to cause any significant damage to the biotopes of interest.

c. Recommended action

It would be desirable to have more detailed information on the species composition and abundance of the soft-sediment communities in Strangford Lough. The mud grounds in the lough are mostly at depths below 30 m (Magorrian et al., 1995), so that a video survey would be required. The mud substrata with high *Nephrops* densities are rather patchy, and broken by areas of harder, rougher ground, but Magorrian et al. (1995) were able to successfully employ a towed camera system in the lough.

4. Cardigan Bay

Unlike the three localities discussed above, Cardigan Bay has been proposed as a candidate marine SAC not on the basis of its benthic communities but because of its importance to an Annex II marine mammal species, the bottlenose dolphin, *Tursiops truncatus*. The available information shows that sediments burrowed by thalassinidean crustaceans do occur in the bay, but appear to occupy a fairly small proportion of its area. While it would clearly be useful to have more detailed information on community composition, it is unlikely that Cardigan Bay supports any of the biotopes or species of conservation importance, as defined in this report. No measures specifically targeted on sediment biotopes are therefore recommended. Measures undertaken to maintain the quality of the area as a dolphin habitat (eg. reducing human pollutant inputs of all kinds) will also contribute to the preservation of the bay’s benthic biotopes.

5. Plymouth Sound & Estuaries

a. Status and monitoring value

Information on the current distribution of burrowing megafauna in Plymouth Sound is limited, but past records suggest that a high diversity of species may be present. The sound is not an important locality for sea pens, although *Virgularia mirabilis* appears to be sparsely present.

b. Potential managment concerns

Substantial amounts of sewage enter Plymouth Sound, either directly, or via discharges into the estuaries of the Plym and Tamar. Much of this is untreated (Devon Wildlife Trust, 1993). There are no major industrial effluents entering the sound, but a considerable amount of oil, antifoulants and litter must originate from shipping and recreational boats in the area. There is little commercial fishing within the sound. Periodic dredging is carried out to keep navigational channels open.

Overall, the human influence on Plymouth Sound is so extensive and of such long standing that its existing biological communities are probably robust and able to maintain themselves without the need for active conservation measures. Any sensitive species particularly vulnerable to man-made environmental changes would probably have disappeared long ago. The local examples of the biotope complex are therefore not considered to be under any threat, or to require any active management.

c. Recommended action

The sediment biotopes within Plymouth Sound probably do not include species of high conservation importance, but an updating of the rather fragmentary information on their character would be useful. Most of the sedimentary substrata within the sound are in relatively shallow water, so that diving could be used to supplement any observations made using towed video or ROV.

6. Chesil & the Fleet

a. Status and monitoring value

Sea pens and burrowing megafauna appear to be absent from the Fleet proper, but are recorded within Portland Harbour. The harbour lies outside the proposed boundaries of the SAC, but the extension of these should be considered, as the community within Portland Harbour is of a type uncommon in southern Britain, and contains several species of regional or national conservation importance. Dyrynda's (1984) observation of numerous *Virgularia mirabilis* is interesting, as this species is generally uncommon in southern Britain. Other unusual records included *Cepola rubescens*. and the anemone *Scolanthus callimorphus*, which is known only from one other locality in the British Isles (western Ireland).

b. Potential management concerns

The range of human influences on Portland Harbour must be comparable to that in the northern section of Plymouth Sound, and leads to the same general conclusions about the robustness of the species and communities there. However, given the apparent distinctiveness of the Portland examples, it would be desirable to have a more detailed assessment of current and projected human impacts on the sedimentary biotopes here.

c. Recommended action

An updating of Dyrynda's (1984) survey of Portland Harbour would be valuable. Information on current status could be gained most easily by diving, as the water depth in the outer harbour is only about 10 m.

7. Berwickshire & North Northumberland Coast

a. Status and monitoring value

Information on the biotope complex in this candidate SAC is limited to a description of the spatial extent of the silty sand substratum, one record of *Virgularia mirabilis* and some observations of unspecified megafaunal burrows.

b. Potential management concerns

The benthic biotopes in the area must experience some sewage input from the coastal communities, but this is unlikely to be of much significance along this open, current-swept coastline. Some trawling for *Nephrops norvegicus* occurs in this area (J. Kinnear, personal communication). However, with so little information on the biological community it is not possible to assess its conservation importance or assess the significance of human impacts upon it.

c. Recommended action

A detailed biological survey using towed video is highly desirable. The areas inferred to support sea pens and megafauna are well below the depth range accessible to divers.

C. OTHER CANDIDATE OR POSSIBLE SACs

1. Lochs Alsh, Duich & Long

Of the localities designated as candidate or possible SACs, this loch system contains the richest and best-characterized examples of the 'Sea pens and burrowing megafauna' biotope complex (Connor, 1989). *Virgularia mirabilis* occurs throughout all three lochs, but the richest community appears to exist in deep muds at the head of Loch Duich, including forests of *Funiculina quadrangularis* and a large population of *Pachycerianthus multiplicatus*. Burrowing megafauna include *Nephrops norvegicus*, *Callianassa subterranea*, *Calocaris macandreae* and *Lesueurigobius friesii*. At the time of Connor's (1989) report there appeared to be little threat to the biotope complex, although he noted that leases for salmon farms had been granted in Lochs Alsh and Duich. An expansion of fish farming in Loch Duich might have some adverse effects on the benthic communities due to the highly-enclosed situation of the loch. Monitoring the effects of any new aquaculture developments should therefore be the highest managment priority if the site is designated as an SAC.

D. SUITABILITY OF SACs FOR ADDRESSING RESEARCH NEEDS

Chapter VIII outlined several areas of research that would contribute to the development of management policies relevant to this biotope complex. The present chapter has made clear that details of community composition and species abundance are lacking for almost all the proposed SACs, Loch Duich being the best-known at present. The table at the end of this chapter summarizes the state of knowledge of the various sites, and lists their perceived relative importance in conservation terms.

The proposed study of sea pen population dynamics could be carried out in Loch nam Madadh, Loch Alsh/Duich or Portland Harbour, all of which contain populations of *Virgularia mirabilis* in water accessible to divers. The Scottish sites also have the other two sea pen species. A Comparison of Portland Harbour with a Scottish locality would be interesting, as the former is a geographically marginal population probably experiencing a greater range of human impacts.

The effects of experimental trawling on sea pens and megafaunal burrowers could be studied in the Sound of Arisaig, or off the Berwickshire coast if the biotope is shown to have the extent inferred by Foster-Smith et al. (1996), although follow-up diving observations of the trawl paths would not be possible. Whether potentially destructive studies of this kind would be allowed within an SAC is doubtful. The distribution of sea pens, megafaunal burrowers and other benthic biota in relation to local inputs of organic matter (aquaculture, sewage outfalls) could be studied in any of the relevant SACs, and should certainly form part of any routine monitoring programme in semi-enclosed sites with restricted water circulation (eg. Strangford Loch, Loch Duich).

Studies of genetic differentiation between populations could clearly involve SACs in which the species of interest were found. In the case of species with highly localized distributions (eg. *Funiculina quadrangularis*, *Pachycerianthus multiplicatus*), genetic evidence would probably confirm suspicions that isolated populations are self-seeding, and hence susceptible to local extinction if their environments are disrupted. The genetic population structure of other, more widespread species (eg. *Virgularia mirabilis*, *Callianassa subterranea*) should also be investigated, as this might well reveal hitherto unrecognized barriers to larval dispersal created by coastal geography or hydrographic patterns. Data from studies of this kind would therefore help to determine the likelihood of community recovery following a disturbance event.

E. SUMMARY TABLE

The table below summarises the perceived status of the biotope complex within each SAC, its importance relative to others of its type, and recommended management options. Summaries are presented for seven 'demonstration' candidate SACs, and one possible SAC (Loch Alsh/Duich/Long system).

Loch nam Madadh	**Status and monitoring value:** Probably good examples in a near-pristine environment. Contains species of national conservation importance. **Potential management concerns:** Probably none at present

	Recommended action: Quantitative survey of communities by towed video and diving
Loch Duich etc.	**Status and monitoring value:** Good examples in a near-pristine environment. Contains species of national conservation importance. **Potential management concerns:** Probably none at present, but expansion of aquaculture should be monitored. **Recommended action**: Population census of *Pachycerianthus, Funiculina* and further identification of burrowing megafauna would be valuable.
Sound of Arisaig	**Status and monitoring value:** Biotopes extensive, possibly good examples in a near-pristine environment, but community composition poorly known. **Potential management concerns:** *Nephrops* trawling? Possibly none. **Recommended action:** Quantitative survey of communities by towed video.
Strangford Lough	**Status and monitoring value:** Probably good examples, but community composition not known in detail. **Potential management concerns:** Probably none at present. **Recommended action:** Quantitative survey of communities by towed video/ROV.
Cardigan Bay	**Status and monitoring value:** Little-known. Two mud-shrimp species recorded, both nationally common and widespread. **Potential management concerns:** Probably none. **Recommended action:** None. Benthic sedimentary biotopes incidental to conservation importance of the area.
Plymouth Sound & Estuaries	**Status and monitoring value:** Biotope details not known. Variety of burrowing megafauna present, but no records of nationally-rare species Site much influenced by human activity. **Potential management concerns:** Probably none. Any existing communities must be highly tolerant of human impacts. **Recommended action:** Diving or video survey of megafaunal distributions could be made, but not a high priority.
Chesil & the Fleet (Portland Harbour)	**Status and monitoring value:** Possibly a good example of a regionally-uncommon biotope. Contains a nationally-rare anemone and red band-fish (rare in SACs). **Potential management concerns:** Unknown. Site much influenced by human activity, so existing communities must be fairly robust.

	Recommended action: Diving survey to provide information on current status and possible human impacts.
Berwickshire & N. Northumberland Coast	**Status and monitoring value:** Biotope possibly extensive, but community composition largely unknown. **Potential management concerns:** Unknown. Possibly none. **Recommended action:** Quantitative survey of communities by towed video.

It can be seen from the table that the sites definitely known to contain good examples of the biotope complex, or in which nationally-rare species are known to occur, are Loch nam Madadh, Loch Duich, Strangford Lough and Portland Harbour.

The Sound of Arisaig and Berwickshire/North Northumberland contain extensive and potentially good examples of the biotope complex and should be investigated further.

The conservation importance of the biotope complex is probably lowest in Plymouth Sound and Cardigan Bay.

LITERATURE CITED AND KEY BACKGROUND READING

Key references for background reading on the ecology of the biotope complex, its main characterizing species, and potential human influences upon it are shown in boldface.

Allen, J.A., 1967. The fauna of the Clyde Sea area. Crustacea: Euphausiacea and Decapoda. *Scottish Marine Biological Association, Millport.*

Anderson, S.J., Atkinson, R.J.A. & Taylor, A.C., 1991. Behavioural and respiratory adaptations of the mud-burrowing shrimp *Calocaris macandreae* Bell (Thalassinidea: Crustacea) to the burrow environment. *Ophelia*, 34: 143-156.

Appleton, P.L. & Vickerman, K., 1998. *In vitro* cultivation and developmental cycle in culture of a parasitic dinoflagellate (*Hematodinium* sp.) associated with mortality of the Norway lobster (*Nephrops norvegicus*) in British waters. *Parasitology*, 116: 115-130.

Astall, C.M., Anderson, S.J. & Taylor, A.C., 1997a. Comparative studies of the branchial morphology, gill area and gill ultrastructure of some thalassinidean mud-shrimps (Crustacea: Decapoda: Thalassinidea). *Journal of Zoology*, 241: 665-688.

Astall, C.M., Taylor, A.C. & Atkinson, R.J.A., 1997b. Behavioural and physiological implications of a burrow-dwelling lifestyle for two species of Upogebiid mud-shrimp (Crustacea: Thalassinidea). *Estuarine, Coastal and Shelf Science*, 44: 155-168.

Atkinson, R.J.A., 1974a. Behavioural ecology of the mud-burrowing crab *Goneplax rhomboides*. *Marine Biology*, 25: 239-252.

Atkinson, R.J.A., 1974b. Spatial distribution of *Nephrops* burrows. *Estuarine and Coastal Marine Science*, 2: 171-176.

Atkinson, R.J.A., 1986. Mud-burrowing megafauna of the Clyde Sea area. *Proceedings of the Royal Society of Edinburgh*, 90 (B): 351-361.

Atkinson, R.J.A., 1989. Baseline survey of the burrowing megafauna of Loch Sween PMNR and an investigation of the effects of trawling on the benthic megafauna. *Report to the Nature Conservancy Council from the University Marine Biological Station, Millport.*

Atkinson, R.J.A. & Chapman, C.J., 1984. Resin casting: a technique for investigating burrows in sublittoral sediments. *Progress in Underwater Science*, 9: 15-25.

Atkinson, R.J.A., Froglia, C., Arneri, E. & Antolini, B., 1997. Observations on the burrows and burrowing behaviour of *Squilla mantis* (L.) (Crustacea: Stomatopoda). *P.S.Z.N. I. Marine Ecology*, 18: 337-359.

Atkinson, R.J.A., Froglia, C., Arneri, E. & Antolini, B., in press. Observations of the burrows and burrowing behaviour of *Brachynotus gemellari* and of the burrows of several other species occurring on *Squilla* grounds off Ancona, Central Adriatic. *Scientia Marina.*

Atkinson, R.J.A., Moore, P.G. & Morgan, P.J., 1982. The burrows and burrowing behaviour of *Maera loveni* (Crustacea: Amphipoda). *Journal of Zoology,* 198: 399-416.

Atkinson, R.J.A. & Nash, R.D.M., 1985. Burrows and their inhabitants. *Progress in Underwater Science,* 10: 109-115.

Atkinson, R.J.A. & Nash, R.D.M., 1990. Some preliminary observations on the burrows of *Callianassa subterranea* (Montagu) (Decapoda: Thalassinidea) from the west coast of Scotland. *Journal of Natural History,* 24: 403-413.

Atkinson, R.J.A., Pelster, B., Bridges, C.R., Taylor, A.C. & Morris, S., 1987. Behavioural and physiological adaptations to a burrowing lifestyle in the snake blenny, *Lumpenus lampraetiformis* and the red band-fish, *Cepola rubescens. Journal of Fish Biology,* 31: 639-659.

Atkinson, R.J.A. & Pullin, R.S.V., 1996. Observations on the burrows and burrowing behaviour of the red band-fish, *Cepola rubescens* L. *P.S.Z.N.I. Marine Ecology,* 17: 23-40.

Atkinson, R.J.A., Pullin, R.S.V. & Dipper, F.A., 1977. Studies on the red band fish, *Cepola rubescens. Journal of Zoology,* 182: 369-384.

Atkinson, R.J.A. & Taylor, A.C., 1991. Burrows and burrowing behaviour of fish. In: *The environmental impact of burrowing animals and animal burrows. Symposia of the Zoological Society of London, No. 63.* eds. Meadows, P.S. & Meadows, A., Clarendon Press, Oxford, pp. 133-155.

Auster, P.J., 1993. ROVs for science. *Marine Technology Society Journal*, 26: 3-4.

Auster, P.J., Malatesta, R.J., Langton, R.W., Watling, L., Valentine, P.C., Donaldson, C.L., Langton, E.W., Sheppard, A.N. & Babb, I.G., 1996. The impacts of mobile fishing gear on sea floor habitats in the Gulf of Maine (north-west Atlantic): implications for conservation of fish populations. *Reviews in Fisheries Science,* 4: 185-202.

Bagge, O & Munch-Petersen, S., 1979. Some possible factors governing the catchability of Norway lobster in the Kattegat. *Rapports et Proces-Verbaux des Réunions, Conseil Internationale pour l'exploration de la mer,* 175: 143-146.

Bailey, N., Howard, F.G., & Chapman, C.J., 1986. Clyde *Nephrops*: biology and fisheries. *Proceedings of the Royal Society of Edinburgh,* 90(B): 501-518.

Barnes, H., 1963. Underwater television. *Oceanography and Marine Biology Annual Review,* 1: 115-128.

Birkeland, C., 1974. Interactions between a sea pen and seven of its predators. *Ecological Monographs,* 44: 211-232.

Black, K.D., (ed.) 1996. Aquaculture and sea lochs. *Scottish Association for Marine Science, Oban*.

Black, K.D., Fleming, S., Nickell, T.D. & Pereira, P.M.F., 1997. The effects of ivermectin, used to control sea lice on caged farmed salmonids, on benthic infauna. *ICES Journal of Marine Science*, 54: 276-279.

Brooks, K.M., 1993. Impacts on benthic invertebrate communities caused by aerial application of carbamyl to control burrowing shrimp in Willapa Bay, WA. *Journal of Shellfish Research*, 12: 146.

Brown, J.R., Gowen, J.R. & McCluskey, S.D., 1987. The effects of salmon farming on the benthos of a Scottish sea loch. *Journal of Experimental Marine Biology and Ecology*, 109: 39-51.

Buchanan, J.B., 1963. The biology of *Calocaris macandreae* (Crustacea: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom*, 43: 729-747.

Buchanan, J.B., 1974. A study of long term population stability in a benthic crustacean. *Proceedings of the Challenger Society*, 4: 252-253.

Buchanan, J.B., 1984. Sediment analysis. In: *IBP Handbook No. 16. Methods for the study of marine benthos.* Blackwell Scientific Publications, Oxford. pp. 41-65.

Burridge, L.E. & Haya, K., 1993. The lethality of ivermectin, a potential agent for treatment of salmonids against sea lice, to the shrimp *Crangon septemspinosa*. *Aquaculture*, 117: 9-14.

Calderon-Perez, J.A., 1981. Some aspects of the biology of *Calocaris macandreae* Bell (Crustacea: Decapoda: Thalassinidea) in Isle of Man waters. *Ph.D Thesis, University of Liverpool.*

Carlton, J.T., 1996. Marine bioinvasions: the alteration of marine ecosystems by nonindigenous species. *Oceanography*, 9: 36-42.

Chapman, C.J., 1979. Some observations on populations of Norway lobster, *Nephrops norvegicus* (L.) using diving, television and photography. *Rapports et Proces-verbaux des Réunions, Conseil Internationale pour l'exploration de la mer,* 175: 127-133.

Chapman, C.J., 1980. Ecology of juvenile and adult *Nephrops*. In: *The biology and management of lobsters (2),* eds. Cobb, J.S. & Phillips, B.F., London, Academic Press, pp. 143-178.

Chapman, C.J. & Bailey, N., 1987. Biological research on fish and shellfish stocks. Recent progress in Norway lobster research. In: *Developments in fisheries research in Scotland.* eds. Bailey, R.S. & Farrish, B.B., Fishing News Books Ltd., Farnham. pp. 99-111.

Chapman, C.J. & Howard, F.G., 1988. Environmental influences on Norway lobster (*Nephrops norvegicus*) populations and their implications for fishery management. *Symposia of the Zoological Society of London,* 59: 343-353.

Chapman, C.J., Johnstone, A.D.F. & Rice, A.L., 1975. The behaviour and ecology of the Norway lobster, *Nephrops norvegicus* (L.). In: *Proceedings of the 9th European Marine Biology Symposium*, ed. Barnes, H., Aberdeen University Press, pp. 59- 74.

Chapman, C.J. & Rice, A.L., 1971. Some direct observations on the ecology and behaviour of the Norway lobster *Nephrops norvegicus. Marine Biology,* 10: 321-329.

Chia, F.S. & Crawford, B.J., 1973. Some observations on gametogenesis, larval development and substratum selection of the sea pen *Ptilosarcus guerneyi. Marine Biology,* 23: 73-82.

Christiansen, M.E. & Stene, R.O., 1998. Occurrence of the thalassinid *Callianassa subterranea* (Montagu) (Crustacea, Decapoda) on the coast of southern Norway. *Sarsia*, 83: 75-77.

Connor, D.W., 1989. Survey of Loch Duich, Loch Long and Loch Alsh. *Marine Nature Conservation Review Report MNCR/SR/010/89 (Nature Conservancy Council CSD Report No. 977).*

Connor, D.W., 1990. *Amalosoma eddystonense* Stephen 1956, an echiuran new to Scotland, with notes on its proboscis and habitat. *Porcupine Newsletter,* 4: 226-228.

Connor, D.W., Dalkin, M.J., Hill, T.O., Holt, R.H.F. & Sanderson, W.G., 1997. Marine Nature Conservation Review: Marine biotope classification for Britain and Ireland. Volume 2. Sublittoral biotopes. Version 97.06. *Joint Nature Conservation Committee Report No. 230.*

Conway Morris, S., 1995. A new phylum from the lobster's lips. *Nature,* 378: 661-662.

Covey, R., 1991. Benthic marine ecosystems in Great Britain: a review of current knowledge. Eastern England and English Channel (MNCR Coastal Sectors 6 and 7). *Nature Conservancy Council CSD Report No. 1172 (MNCR Report No. MNCR/OR/08).*

Covey, R., 1992. Sublittoral survey of the north coast of the outer Solway (Mull of Galloway to Auchencairn). *Nature Conservancy Council CSD Report No. 1193 (MNCR Report MNCR/SR/15).*

Cromey, C.J., Black, K.D., Edwards, A. & Jack, I.A., 1996. Forecasting the deposition and biological effects of excess carbon from sewage discharges. *Final Report to the Forth River Purification Board.*

Cutts, N. & Hemingway, K., 1996. The Solway Firth: broad scale habitat mapping. *Scottish Natural Heritage Research, Survey and Monitoring Report No. 46.*

Daan, R., van het Groenewoud, H., de Jong, S.A. & Mulder, M., 1992. Physico-chemical and biological features of a drilling site in the North Sea, 1 year after discharges of oil-contaminated drill cuttings. *Marine Ecology Progress Series,* 91: 37-45.

Davies, J., 1997. Chapter 8. Western Channel (Durlston Head to Cape Cornwall, including the Isles of Scilly) (MNCR Sector 8). In: *Marine Nature Conservation Review. Benthic marine ecosystems: a review of current knowledge for Great Britain and the north-east Atlantic.* ed. Hiscock, K. *Peterborough, Joint Nature Conservation Committee (Coasts and Seas of the United Kingdom. MNCR Series).*

Davies, J. & Hall-Spencer, J., 1996. Mapping of the benthic biotopes in the proposed Sound of Arisaig Special Area of Conservation. *Scottish Natural Heritage Research, Survey and Monitoring Report No. 83.*

Davis, N. & Van Blaricom, G.R., 1978. Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow water. *Limnology and Oceanography,* 23: 417-427.

Devon Wildlife Trust, 1993. Marine survey report. Plymouth Sound and approaches. A report on the wildlife resource of Plymouth Sound and the adjacent open coast.

Ditadi, A.S.F., 1982. On the burrows of echiuran worms (Echiura): a survey. *Boletim Zoologica, Universidade do Sao Paulo*, 7: 21-36.

Dixon, I., 1986. Fish farm surveys in Shetland, August 1986. Summary of survey results, Volume 1. *Report to the Nature Conservancy Council, Shetland Islands Council and Shetland Salmon Farmers Association from the Field Studies Council Oil Pollution Research Unit, Orielton, Pembroke, Dyfed.*

Dworschak, P.C., 1981. The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea). *Journal of Experimental Biology and Ecology,* 52: 25-35.

Dworschak, P.C., 1983. The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea) I. The burrows. *P.S.Z.N.I. Marine Ecology,* 4: 19-43.

Dyer, M.F., Fry, W.G., Fry, P.D. & Cranmer, G.J., 1982. A series of North Sea benthos surveys with trawl and headline camera. *Journal of the Marine Biological Association of the United Kingdom,* 62: 297-313.

Dyrynda, P., 1984. Investigation of the subtidal ecology of the Fleet Lagoon (Dorset). *Nature Conservancy Council CSD Report No. 530.*

Eggleston, D., 1971. Synchronization between moulting in *Calocaris macandreae* (Decapoda) and reproduction in its epibiont *Triticella korenii* (Polyzoa Ectoprocta). *Journal of the Marine Biological Association of the United Kingdom,* 51: 404-410.

Emblow, C.S., 1992. Survey of the sublittoral hard substrata from Morecambe Bay to Whitehaven. *Peterborough, Joint Nature Conservation Committee Report No. 28 (MNCR Report No. MNCR/SR/19).*

Eno, N.C., Clark, R.A. & Sanderson, W.G. (eds.), 1997. Non-native species in British waters: a review and directory. *Joint Nature Conservation Committee, Peterborough.*

Entec, 1996. Broad scale habitat mapping of intertidal and subtidal coastal areas: Loch Maddy, North Uist. *Scottish Natural Heritage Research, Survey and Monitoring Report No. 76.*

Erwin, D.G., 1977. A diving survey of Strangford Lough: the benthic communities and their relation to substrate - a preliminary account. In: *Biology of Benthic Organisms. Proceedings 11th European Marine Biology Symposium, Galway, 1976.* eds. Keegan, B.F., Ó Céidigh, P., & Boaden, P.J.S., Oxford, Pergamon Press, pp. 215-224.

Field, R.H., Chapman, C.J., Taylor, A.C., Neil, D.M. & Vickerman, K., 1992. Infection of the Norway lobster *Nephrops norvegicus* by a *Hematodinium* - like species of dinoflagellate on the west coast of Scotland. *Diseases of Aquatic Organisms*, 13: 1-15.

Fisher, W.K. & MacGinitie, G.E., 1928. The natural history of an echiuroid worm. *Annals and Magazine of Natural History, Ser. 10 (1)* : 204-213.

Flint, R.W. & Kalke, R.D., 1986. Biological enhancement of estuarine benthic community structure. *Marine Ecology Progress Series,* 31: 23-33.

Foss, G., 1962. Some observations on the ecology of *Myxine glutinosa* L. Preliminary communication. *Sarsia,* 7: 17-22.

Foss, G., 1968. Behaviour of *Myxine glutinosa* L. in natural habitat. Investigation of the mud biotope by a suction technique. *Sarsia,* 31: 1-13.

Foster-Smith, R.L., Sotheran, I., Foster-Smith, J.L. & Bunker, F., 1996. Mapping survey of the sublittoral and littoral biotopes of the Berwickshire coast. *Scottish Natural Heritage Research, Survey and Monitoring Report, No. 60.*

Fujita, T. & Ohta, S., 1988. Photographic observations of the lifestyle of a deep-sea ophiuroid, *Asteronyx loveni* (Echinodermata). *Deep-Sea Research (A)*, 35: 2029-2043.

Funch, P. & Kristensen, R.M., 1995. Cycliophora is a new phylum with affinities to Entoprocta and Ectoprocta. *Nature,* 378: 711-714.

Gibson, R.N. & Ezzi, I.A., 1978. The biology of a Scottish population of Fries' goby, *Lesueurigobius friesii. Journal of Fish Biology,* 12: 371-389.

Gillibrand, P.A. & Turrell, W.R., 1997. The use of simple models in the regulation of the impact of fish farms on water quality in Scottish sea lochs. *Aquaculture*, 159: 33-46.

Gordon, J.D.M. & Duncan, J.A.R., 1979. Some notes on the biology of the snake blenny *Lumpenus lampraetiformis* on the west coast of Scotland. *Journal of the Marine Biological Association of the United Kingdom,* 59: 413-419.

Gowen, J.R. & Bradbury, N.B., 1987. The ecological impact of salmonid farming in coastal waters: a review. *Oceanography and Marine Biology Annual Review,* 25: 563-575.

Greenstreet, S.P.R., Tuck, I.D., Grewar, G.N., Armstrong, E., Reid, D.G. & Wright, P.J., 1997. An assessment of the acoustic survey technique, RoxAnn, as a means of mapping seabed habitat. *ICES Journal of Marine Science,* 54: 939-959.

Hagen, N.T., 1995. Sea urchin outbreaks and epizootic disease as regulating mechanisms in coastal ecosystems. In: *Biology and Ecology of Shallow Coastal Waters. Proceedings 28th European Marine Biology Symposium, Iraklio, Crete, 1993.*eds. Eleftheriou, A., Ansell, A.D. & Smith, C.J., Fredensborg, Olsen & Olsen, pp. 303-308.

Hall, S.J., 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology Annual Review,* 32: 179-239.

Hall, S.J., Robertson, M.R., Basford, D.J. & Heaney, S.D., 1993. The possible effects of fishing disturbance in the northern North Sea: an analysis of spatial patterns in community structure around a wreck. *Netherlands Journal of Sea Research,* 31: 201-208.

Hardisty, M.W., 1979. *Biology of the cyclostomes.* London: Chapman & Hall.

Hayward, P.J. & Ryland, J.S., 1990. The Marine Fauna of the British Isles and North-West Europe. Volume 1: Introduction and Protozoans to Arthropods. Oxford, Clarendon Press.

Hensley, R.T., 1996. A preliminary survey of benthos from the *Nephrops norvegicus* mud grounds in the north-western Irish Sea. *Estuarine, Coastal and Shelf Science,* 42: 457-465.

Hill, A.E., Brown, J. & Fernand, L., 1996. The western Irish Sea gyre: a retention system for Norway lobster (*Nephrops norvegicus*)? *Oceanologia Acta,* 19: 357-368.

Hill, A.E., Brown, J. & Fernand, L., 1997. The summer gyre in the western Irish Sea: shelf sea paradigms and management implications. *Estuarine, Coastal and Shelf Science,* 44, Suppl. A: 83-95.

Hill, T.O., Emblow, C.S. & Northen, K.O., 1996. Marine Nature Conservation Review Sector 6. Inlets in eastern England: Area summaries. *Peterborough, JNCC (Coasts and seas of the UK, MNCR Series).*

Hiscock, K., 1984. Sublittoral survey of Bardsey and the Lleyn Peninsula, August 13th to 27th 1983. Volume 1, Survey Report. *Report to the Nature Conservancy Council from the Field Studies Council Oil Pollution Research Unit, Orielton, Pembroke, Dyfed.*

Hiscock, K., submitted. Identifying marine ‘sensitive areas’ - the importance of understanding life-cycles. Paper submitted for publication in the proceedings of the symposium on *Aquatic life cycle strategies: survival in a variable environment,* April 1997.

Hiscock, K. & Moore, J., 1986. Surveys of harbours, rias and estuaries in southern Britain: Plymouth area including the Yealm. Volume 1, Report. *Report to the Nature Conservancy Council from the Field Studies Council Oil Pollution Research Unit, Orielton, Pembroke, Dyfed.*

Hoare, R. & Wilson, E.H., 1976. The macrofauna of soft substrates off the coast of Lundy. *Reports of the Lundy Field Society,* 27: 53-58.

Hoare, R. & Wilson, E.H., 1977. Observations of the behaviour and distribution of *Virgularia mirabilis* O.F. Müller (Coelenterata: Pennatulacea) in Holyhead Harbour, Anglesey. In: *Biology of Benthic Organisms. Proceedings 11th European Marine Biology Symposium, Galway, 1976.* eds. Keegan, B.F., Ó Céidigh, P. & Boaden, P.J.S., Oxford, Pergamon Press, pp. 329-337.

Holme, N.A., 1971. Macrofauna sampling. In: *IBP Handbook No. 16, Methods for the study of marine benthos, 2nd edition.* eds. Holme, N.A. & McIntyre, A.D.. Blackwell Scientific Publications, Oxford & Edinburgh. pp. 80-130.

Howard, F.G., 1989. The Norway lobster. *Department of Agriculture and Fisheries for Scotland, Scottish Fisheries Information Pamphlet No. 7. Second edition.*

Howson, C.M., 1988. Marine Nature Conservation Review. Survey of Shetland, Foula and Fair Isle, 1987. Volume 1, Report. *Report to the Nature Conservancy Council from the Field Studies Council Oil Pollution Research Unit, Orielton, Pembroke, Dyfed.*

Howson, C.M., 1990. Marine Nature Conservation Review Surveys of Scottish sealochs. Sealochs of Arisaig and Moidart. *Report to the Joint Nature Conservation Committee from the University Marine Biological Station, Millport.*

Howson, C.M., 1991. Marine Nature Conservation Review Surveys of Scottish sealochs. The sealochs of North and South Uist and Benbecula. Volume 1, Report. *Report to the Joint Nature Conservation Committee from the University Marine Biological Station, Millport.*

Howson, C.M., Connor, D.W. & Holt, R.H.F., 1994. The Scottish sealochs - an account of surveys undertaken for the Marine Nature Conservation Review. *Joint Nature Conservation Committee Report No. 164 (Marine Nature Conservation Review Report MNCR/SR/27)*.

Howson, C.M. & Davies, L.M., 1991. Marine Nature Conservation Review, Surveys of Scottish sealochs. A towed video survey of Loch Fyne. Volume 1 - Report.

Report to the Nature Conservancy Council from the University Marine Biological Station, Millport.

Hughes, D.J., Ansell, A.D., Atkinson, R.J.A. & Nickell, L.A., 1993. Underwater television observations of surface activity of the echiuran worm *Maxmuelleria lankesteri* (Echiura: Bonelliidae). *Journal of Natural History,* 27: 219-248.

Hughes, D.J., Ansell, A.D. & Atkinson, R.J.A., 1994. Resource utilization by a sedentary surface deposit feeder, the echiuran worm *Maxmuelleria lankesteri. Marine Ecology Progress Series,* 112: 267-275.

Hughes, D.J., Ansell, A.D. & Atkinson, R.J.A., 1996a. Sediment bioturbation by the echiuran worm *Maxmuelleria lankesteri* (Herdman) and its consequences for radionuclide dispersal in Irish Sea sediments. *Journal of Experimental Marine Biology and Ecology,* 195: 203-220.

Hughes, D.J., Ansell, A.D. & Atkinson, R.J.A., 1996b. Distribution, ecology and life cycle of *Maxmuelleria lankesteri* (Echiura: Bonelliidae): a review with notes on field identification. *Journal of the Marine Biological Association of the United Kingdom*, 76: 897-908.

Hughes, D.J. & Atkinson, R.J.A., 1997. A towed video survey of megafaunal bioturbation in the north-eastern Irish Sea. *Journal of the Marine Biological Association of the United Kingdom*, 77: 635-653.

Hughes, D.J., Marrs, S.J., Smith, C.J. & Atkinson, R.J.A., in press. Observations of the echiuran worm *Bonellia viridis* in the deep basin of the northern Evoikos Gulf, Greece.*Journal of the Marine Biological Association of the United Kingdom.*

Johns, A.R., Taylor, A.C., Atkinson, R.J.A. & Grieshaber, M.K., 1997. Sulphide metabolism in thalassinidean crustacea. *Journal of the Marine Biological Association of the United Kingdom,* 77: 127-144.

Kaiser, M.J. & Spencer, B.E., 1996. The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology,* 65: 348-358.

Kastendiek, J., 1976. Behavior of the sea pansy *Renilla kollikeri* Pfeffer (Coelenterata: Pennatulacea) and its influence on the distribution and biological interactions of the species. *Biological Bulletin (Woods Hole),* 151: 518-537.

Kershaw, P.J., Swift, D.J., Pentreath, R.J. & Lovett, M.B., 1983. Plutonium redistribution by biological activity in Irish Sea sediments. *Nature*, 306: 774-775.

Kingston, P.F. & Riddle, M.J., 1989. Cost effectiveness of benthic faunal monitoring. *Marine Pollution Bulletin,* 20: 490-496.

Kinnear, J.A.M., Barkel, P.J., Mojseiwicz, W.R., Chapman, C.J., Holbrow, A.J., Barnes, C. & Greathead, C.F.F., 1996. Effects of *Nephrops* creels on the environment. *Fisheries Research Services Report No. 2/96.*

Künitzer, A., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dörjes, J., Duineveld, G.C.A., Eleftheriou, A., Heip, C., Herman, P., Kingston, P., Niermann, U., Rachor, E., Rumohr, H. & de Wilde, P.A.J., 1992. The benthic infauna of the North Sea: species distribution and assemblages. *ICES Journal of Marine Science*, 49: 127-143.

Langton, R.W., Langton, E.W., Theroux, R.B. & Uzmann, J.R., 1990. Distribution, behaviour and abundance of sea pens, *Pennatula aculeata*, in the Gulf of Maine. *Marine Biology*, 107: 463-469.

Lee, H. & Swartz, R.C., 1980. Biological processes affecting the distribution of pollutants in marine sediments. Part II. Biodeposition and bioturbation. In: *Contaminants and sediments, Volume 2.*, ed. Baker, R.A., Science Publishers, Ann Arbor, Michigan. pp. 555-605.

Mackie, A.M., 1987. Preliminary studies on the chemical defenses of the British octocorals *Alcyonium digitatum* and *Pennatula phosphorea. Comparative Biochemistry and Physiology (A)*, 86: 629-632.

Mackie, A.S.Y., Oliver, P.G. & Rees, E.I.S., 1995. Benthic biodiversity in the southern Irish Sea. *Studies in marine biodiversity and systematics from the National Museum of Wales. BIOMÔR Reports.*

Magorrian, B.H., Service, M. & Clarke, W., 1995. An acoustic bottom classification survey of Strangford Lough, Northern Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 75: 987-992.

Manuel, R.L., 1981 (revised 1988). British Anthozoa. *Synopses of the British Fauna, N.S., No. 18.* London, Academic Press.

Marine Biological Association, 1957. Plymouth Marine Fauna, 3rd Edition.

Marrs, S.J., Atkinson, R.J.A., Smith, C.J. & Hills, J.M., 1996. Calibration of the towed underwater TV technique for use in stock assessment of *Nephrops norvegicus. Final Report to the European Commission, Ref. No. 94/069.*

McIntyre, A.D., 1971. Marine zoobenthos in the light of recent research. In: *The Ocean World. Proceedings of the Joint Oceanographic Assembly (Tokyo, 1970),* ed. Uda, M., Tokyo, Japan Society for the Promotion of Science. pp. 139-141.

Mills, J.L., 1997.Chapter 11. Liverpool Bay and the Solway (Rhôs-on-Sea to the Mull of Galloway) (MNCR Sector 11). In: *Marine Nature Conservation Review. Benthic marine ecosystems: a review of current knowledge for Great Britain and the north-east Atlantic.* ed. Hiscock, K., *Peterborough, Joint Nature Conservation Committee (Coasts and Seas of the United Kingdom. MNCR Series).*

Moore, P.G. & Rainbow, P.S., 1984. Ferratin crystals in the gut caecae of *Stegocephaloides christianensis* Boeck and other Stegocephalidae (Crustacea: Amphipoda): a functional interpretation. *Philosophical Transactions of the Royal Society of London, (B)*, 306: 219-245.

Moran, P.J., 1986. The *Acanthaster* phenomenon. *Oceanography and Marine Biology Annual Review,* 24: 379-480.

Nash, R.D.M., 1980. Laboratory observations on the burrowing of the snake blenny *Lumpenus lampraetiformis* (Walbaum) in soft sediments. *Journal of Fish Biology,* 16: 639-648.

Nash, R.D.M., Chapman, C.J., Atkinson, R.J.A. & Morgan, P.J., 1984. Observations on the burrows and burrowing behaviour of *Calocaris macandreae* (Crustacea: Decapoda: Thalassinoidea). *Journal of Zoology,* 202: 425-439.

Nichol, J.A.C., 1958. Observations on the luminescence of *Pennatula phosphorea* with a note on the luminescence of *Virgularia mirabilis*. *Journal of the Marine Biological Association of the United Kingdom,* 37: 551-563.

Nickell, L.A. & Atkinson, R.J.A., 1995. Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean burrow morphology. *Marine Ecology Progress Series,* 128: 181-197.

Nickell, L.A., Atkinson, R.J.A., Hughes, D.J., Ansell, A.D. & Smith, C.J. 1995a. Burrow morphology of the echiuran worm *Maxmuelleria lankesteri* (Echiura: Bonelliidae), and a brief review of burrow structure and related ecology of the Echiura. *Journal of Natural History*, 29: 871-885.

Nickell, L.A., Hughes, D.J. & Atkinson, R.J.A., 1995b. Megafaunal bioturbation in organically-enriched Scottish sea lochs. In: *Biology and Ecology of Shallow Coastal Waters. Proceedings of the 28th European Marine Biology Symposium, Iraklio, Crete, 1993.* eds. Eleftheriou, A., Ansell, A.D. & Smith, C.J., Fredensborg: Olsen & Olsen. pp. 315-322.

Nickell, T.D. & Anderson, S.J., 1997. Environmental assessment of Loch Harport. Report prepared for United Distillers. *Altra Safety and Environment Ltd., Report UDI 911.*

Ohta, S., 1984. Star-shaped feeding traces produced by echiuran worms on the deep-sea floor of the Bay of Bengal. *Deep-Sea Research (A),* 31: 1415-1432.

Pearson, T.H. & Rosenberg, R., 1976. A comparative study of the effects on the marine environment of wastes from cellulose indistries in Scotland and Sweden. *Ambio,* 5: 77-79.

Pearson, T.H. & Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology Annual Review,* 16: 229-331.

Pemberton, G.S., Risk, M.J. & Buckley, D.E., 1976. Supershrimp: deep bioturbation in the Strait of Canso, Nova Scotia. *Science,* 192: 790-791.

Pereira, P.M.F., 1997. Macrobenthic succession and changes in sediment biogeochemistry following marine fish farming. *Ph.D thesis, University of Stirling.*

Pervesler, P. & Dworschak, P.C., 1985 Burrows of *Jaxea nocturna* Nardo in the Gulf of Trieste. *Senckenbergiana Maritima*, 17: 33-53.

Posey, M.H., 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis. Marine Ecology Progress Series,* 31: 15-22.

Rachor, E. & Bartel, S., 1981. Occurrence and ecological significance of the spoon-worm *Echiurus echiurus* in the German Bight. *Veröffentlichungen Instituts Meeresforschung Bremerhaven,* 19: 71-88.

Reineck, H.-E., Gutmann, W.F. & Hertweck, G., 1967. Das Schlickgebiet südlich Helgoland als Beispiel rezenter Schelfablerungen. *Senckenbergiana Lethaea,* 48: 219-275.

Rice, A.L. & Chapman, C.J., 1971. Observations on the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans, *Nephrops norvegicus* and *Goneplax rhomboides. Marine Biology,* 10: 330-342.

Rice, A.L. & Johnstone, A.D.F., 1972. The burrowing behaviour of the gobiid fish *Lesueurigobius friesii. Zeitschrift für Tierpsychologie*, 30: 431-438.

Rogers, A.D. & Nash, R.D.M., 1996. A new species of *Ochetostoma* (Echiura, Echiuridae) found in the Azores with notes on its ecology. *Journal of the Marine Biological Association of the United Kingdom,* 76: 467-478.

Rostron, D.R., 1992. Sublittoral benthic sediment communities of Morecambe Bay. *Joint Nature Conservation Committee Report No. 47, from Subsea Survey, Pembroke. (MNCR Report No. MNCR/SR/22).*

Rowden, A.A. & Jones, M.B., 1994. A contribution to the biology of the burrowing mud shrimp, *Callianassa subterranea* (Decapoda: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom,* 74: 623-635.

Rowden, A.A. & Jones, M.B., 1995. The burrow structure of the mud shrimp *Callianassa subterranea* (Decapoda: Thalassinidea) from the North Sea. *Journal of Natural History,* 29: 1155-1165.

Rowden, A.A. & Jones, M.B., 1997. Recent mud shrimp burrows and bioturbation. *Porcupine Newsletter,* 6: 153-158.

Scottish Office Agriculture, Environment and Fisheries Department, 1997. Marine Laboratory, Aberdeen, Annual Review 1994-1995.

Service, M., 1993. The structure and chemistry of the superficial sediments of Strangford Lough, Northern Ireland. *Marine Pollution Bulletin,* 26: 343-345.

Shields, J.D., 1994. The parasitic dinoflagellates of marine crustaceans. *Annual Review of Fish Diseases,* 4: 241-271.

Shinn, E.A., 1968. Burrowing in recent lime sediments of Florida and the Bahamas. *Journal of Paleontology,* 42: 879-894.

Smith, C.J., 1988. Effects of megafaunal/macrofaunal burrowing interactions on benthic community structure. *Ph.D thesis, University of Glasgow.*

Stachowitsch, M., 1984. Mass mortality in the Gulf of Trieste: the course of community destruction. *P.S.Z.N.I. Marine Ecology,* 5: 243-264.

Stephen, A.C., 1934. The Echiuridae, Sipunclidae and Priapulidae of Scottish and adjacent waters. *Proceedings of the Royal Physical Society, Vol. XXIII, Part 4.,* 159-185.

Stull, J.K., Haydock, C.I. & Montagne, D.E., 1986. Effects of *Listriolobus pelodes* (Echiura) on coastal shelf benthic communities and sediments modified by a major California wastewater discharge. *Estuarine, Coastal and Shelf Science,* 22: 1-17.

Suchanek, T.H. & Colin, P.L., 1986. Rates and effects of bioturbation by invertebrates and fishes at Enewetak and Bikini Atolls. *Bulletin of Marine Science,* 38: 25-34.

Suchanek, T.H., Colin, P.L., McMurtry, G.M. & Suchanek, C.S., 1986. Bioturbation and redistribution of sediment radionuclides in Enewetak Atoll Lagoon by callianassid shrimp: biological aspects. *Bulletin of Marine Science,* 38: 144-154.

Swift, D.J., 1993. The macrobenthic infauna off Sellafield (north-eastern Irish Sea) with special reference to bioturbation. *Journal of the Marine Biological Association of the United Kingdom*, 73: 143-162.

Taylor, A.C., Field, R.H. & Parslow-Williams, P.J., 1996. The effects of *Hematodinium* sp. infection on aspects of the respiratory physiology of the Norway lobster, *Nephrops norvegicus. Journal of Experimental Marine Biology and Ecology,* 207: 217-228.

Thain, J.E., Davies, I.M., Rae, G.H. & Allen, Y.T., 1997. Acute toxicity of ivermectin to the lugworm *Arenicola marina. Aquaculture*, 159: 47-52.

Thomsen, L. & Altenbach, A.V., 1993. Vertical and areal distribution of foraminiferal abundance and biomass in microhabitats around inhabited tubes of marine echiurids. *Marine Micropaleontology*, 20: 303-309.

Tuck, I.D. & Atkinson, R.J.A., 1995. Unidentifed burrow surface trace from the Clyde Sea area. *Netherlands Journal of Sea Research,* 34: 331-335.

Tuck, I.D., Atkinson, R.J.A. & Chapman, C.J., 1994. The structure and seasonal variability in the spatial distribution of *Nephrops norvegicus* burrows. *Ophelia,* 40: 13-25.

Tuck, I.D., Chapman, C.J. & Atkinson, R.J.A., 1997a. Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland - I. Growth and density. *ICES Journal of Marine Science,* 54: 125-135.

Tuck, I.D., Chapman, C.J., Atkinson, R.J.A., Bailey, N. & Smith, R.S.M., 1997b. A comparison of methods for stock assessment of the Norway lobster, *Nephrops norvegicus,* in the Firth of Clyde. *Fisheries Research,* 32: 89-100.

Tuck, I.D., Hall, S.J., Robertson, M.R., Armstrong, E. & Basford, D.J., 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Marine Ecology Progress Series*, 162: 227-242.

Tucker, B.W., 1930. On the effects of an epicaridan parasite, *Gyge branchialis,* on *Upogebia littoralis. Quarterly Journal of Microscopical Science,* 74: 1-118.

Tully, O. & Hillis, J.P., 1995. Causes and spatial scales of variability in population structure of *Nephrops norvegicus* (L.) in the Irish Sea. *Fisheries Research,* 21: 329-347.

Tunberg, B., 1986. Studies on the population ecology of *Upogebia deltaura* (Leach) (Crustacea, Thalassinidea). *Estuarine, Coastal and Shelf Science,* 22: 753-765.

University Marine Biological Station, Millport, 1996. Twenty-sixth annual report, 1 August 1995 - 31 July 1996.

Weston, D.P., 1990. Quantitative examination of macrobenthic community changes along an organic enrichment gradient. *Marine Ecology Progress Series,* 61: 233-244.

Witbaard, R. & Duineveld, G.C.A., 1989. Some aspects of the biology and ecology of the burrowing shrimp *Callianassa subterranea* (Montagu) (Thalassinidea) from the southern North Sea. *Sarsia*, 74: 209-219.

Ziebis, W., Forster, S., Huettel, M. & Jørgensen, B.B., 1996. Complex burrows of the mud shrimp *Callianassa truncata* and their geochemical impact in the sea bed. *Nature,* 382: 619-622.