SUBTIDAL BRITTLESTAR BEDS

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

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August 1998

Prepared for Scottish Association for Marine Science (SAMS) for the

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Acknowledgements

I would like to thank the various reviewers of this report for their constructive suggestions and for access to unpublished information. Special thanks are due to Brendan Ball and Janette Allen. I am also grateful to all others who provided information on particular sites, and to Jane Dodd and Elvira Poloczanska for their help in the field.

Citation: Hughes, D.J. 1998. Subtidal brittlestar beds (volume IV). An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science (UK Marine SACs Project). 78 Pages.

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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 biotopes characterized by dense aggregations of epifaunal brittlestars. Brittlestar beds can occur on two of the broad habitats defined in Annex I of the Habitats Directive, namely 'Reefs' and 'Sandbanks covered by sea water at all times'. Examples can also be found in geographic areas regarded as 'Large shallow inlets and bays'.

Nature and importance of the biotope complex

Brittlestars are echinoderms with a well-defined central disc and long, sometimes spiny arms. They are the most species-rich class of living echinoderms and occur in virtually all benthic environments worldwide, from the intertidal zone to the deep sea. The 'Subtidal brittlestar beds' biotope complex is defined by the occurrence of brittlestars at high densities (hundreds or thousands m^{-2}), living epifaunally on bedrock, boulder, gravel or sedimentary substrata. About 20 species of brittlestars occur in coastal waters of the British Isles, but only a few of these form beds. The main bed-forming species are *Ophiothrix fragilis* and *Ophiocomina nigra,* with rare examples formed by *Ophiopholis aculeata.* Brittlestars of the genus *Ophiura* sometimes occur on sedimentary substrata in large numbers, but not usually in such dense aggregations as the other species. Beds may be formed by one species only, or contain a mixture of several. None of the bed-forming brittlestar species occur solely in dense aggregations. All are common and widespread at lower densities in other benthic biotopes around the British Isles.

Brittlestar beds currently have no economic importance. However, they are of considerable scientific interest as living examples of an 'anachronistic' community. Dense aggregations of epifaunal suspension-feeders, including brittlestars, were common during the Paleozoic and early Mesozoic eras on marine soft substrata, but became much less common following the later Mesozoic evolutionary radiation of teleost fish, decapod crustaceans and other predatory groups. The occurrence of this community type may have been restricted over geological time-scales by predation, and the living brittlestar beds have therefore received much attention from ecologists studying the influence of predation as a structuring factor in the marine environment.

Living brittlestar beds are widespread and common around Britain and Ireland, but are fairly rare on a global scale. The British representatives are the best-known and most intensively-studied examples of their kind. Brittlestar beds represent major concentrations of benthic biomass and may play an important role in the functioning of their local ecosystems. They may also have potential as biological indicators of natural or human-induced change in the coastal environment.

Distribution in the UK and elsewhere

In the MNCR biotope classification, the biotopes MCR.Oph and MCR.OPh.Oacu are characterized by mass occurrence of brittlestars, the latter case including the rare *Ophiopholis*-dominated beds. Beds classed within MCR.Oph are found widely around Britain and Ireland, appearing to be absent only from most of the English North Sea coast. Beds are present in eight of the 12 'demonstration' candidate SACs and probably absent from the remaining four. They also occur in several other candidate or possible SACs. In the 'demonstration' group of SACs, brittlestar beds appear to be most extensive in Strangford Lough, and along the Berwickshire/North Northumberland Coast. *Ophiothrix* beds also exist around the Llyn Peninsula, but the distribution and extent of these has been less-thoroughly mapped. A bed dominated by *Ophiocomina* is known from near Papa Stour in Shetland. The Loch Alsh/Duich/Long system (a possible SAC) contains the only *Ophiopholis*-dominated beds known from a candidate or possible SAC.

Outside Britain and Ireland, extensive *Ophiothrix* beds exist on the French side of the English Channel, and temporary aggregations of this species have also been recorded in the Dutch Oosterschelde Estuary. Shallow-water aggregations of other brittlestar species are also known from the Mediterranean and Adriatic Seas, from an isolated salt water lake in the Bahamas, and from the Antarctic, California and Japan. Brittlestars are an important element of the deep-sea benthos. Populations may extend across very wide areas of sea floor (for example, around northern Japan), but densities do not approach those of the coastal aggregations.

Environmental requirements

Brittlestar beds are usually found in conditions of full marine salinity, the only recorded exceptions being those of the Dutch Oosterschelde Estuary. Depth occurrence is roughly from 10 - 70 m. The upper or lower depth boundaries of beds may be very abrupt. Beds can exist in a variety of hydrodynamic regimes, with weak to moderately strong wave exposure and tidal streams. Tidal streams are often weak over beds in semi-enclosed water bodies such as sea lochs, but are typically stronger over those on open coasts. Current speeds of up to 1.5 $m\ s^{-1}$ have been recorded over brittlestar beds in the Dover Strait during spring tides.

Brittlestar beds are also known from a wide range of substratum types, from bedrock to coarse sand or mixed sediments. The most common substrata are probably cobbles, gravel and mixed coarse sediments. Beds are generally on level or gently-sloping bottoms rather than on vertical cliffs or overhangs. The occurrence of brittlestar beds is not limited by temperature except in very shallow water, where temperature extremes may be encountered. Heavy sedimentation will inhibit bed occurrence by clogging the brittlestar feeding organs. It has been argued that beds occur only where predation pressure by fish or crabs is low, a modern ecological analogue of their suggested limitation by predators over evolutionary time. There is evidence from field experiments that brittlestars in rocky reef habitats are more subject to predation than those in beds. A 'halo' of clear substratum can sometimes be seen where a brittlestar bed approaches a rocky reef, perhaps indicating the foraging radius of rock-dwelling crabs and fish.

Biology and ecological functioning

Aggregations of *Ophiothrix fragilis* result from the active association of animals with their conspecifics (ie. true social behaviour is displayed), rather than simply from the individual responses of the brittlestars to features of their physical environment. *Ophiocomina nigra* is less tolerant than *Ophiothrix fragilis* of close contact with conspecifics. Individuals of this species often show a dispersed, non-random spatial distribution, this pattern only breaking down at very high local population densities. Individuals of *Ophiocomina nigra* will maintain a dispersed distribution from each other even when mixed with much larger numbers of *Ophiothrix*.

For *Ophiothrix fragilis*, the advantages of living in dense aggregations include increased stability in strong currents (isolated animals or small groups are easily swept away), enhanced feeding success and ease of fertilization. *Ophiothrix* is primarily a suspension-feeder, trapping phytoplankton and detritus on the tube feet of arms extended into the current. Feeding takes place mainly at current speeds of about 0.2 m s^{-1} or below. When current speed exceeds 0.3 m s^{-1}, the animals cease feeding, flatten themselves against the substratum and link arms, so increasing their collective stability in the current. When feeding, the forest of extended arms may act like a baffle, slowing down the flow of water over the bed, causing an increased deposition of particles and so enhancing the feeding success of the animals. *Ophiocomina nigra* is a highly versatile feeder, able to suspension-feed, graze benthic detritus or scavenge on carrion.

Brittlestar beds may have abrupt boundaries but usually have a patchy internal structure, with localized concentrations of higher animal density. *Ophiothrix* densities of up to 2000 animals m^{-2} have been recorded. *Ophiothrix* beds may consist of large adults and tiny, newly-settled juveniles, which cling to the adult arms and feed on material trapped by their tube feet. Animals of intermediate size have been found living away from the beds, in nearby rock habitats or among clumps of sessile epifauna. *Ophiothrix* has a lengthy breeding season, with some spawning taking place throughout the summer and autumn. Settlement is at its peak in September/October, but some recruitment may take place at other times of year. New recruits settle on the arms of adult individuals. Life-span is probably 2 - 8 years. *Ophiocomina nigra* grows slowly and lives for up to 14 years. Spawning appears to take place over a limited period during the summer. Small males can be found clinging to the central discs of larger female specimens. These pairs may act as ‘triggers’ for spawning in the rest of the local population. Juvenile *Ophiocomina* do not settle among established adults. Aggregations therefore may comprise animals of one age-class, representing a single recruitment episode.

Dense brittlestar aggregations on bedrock may smother and exclude other epifaunal animals. However, on sedimentary substrata a rich fauna of smaller animals may be found beneath the brittlestar layer. The sediment fauna does not appear to be restricted in numbers or growth by the carpet of brittlestars, and may actually benefit from the increased deposition of organic matter in the beds. Several species of large, mobile crustaceans and echinoderms can be found on brittlestar beds. Brittlestar predators include the starfish *Asterias rubens* and *Luidia ciliaris* and the crabs *Cancer pagurus* and *Necora puber*. There are no known examples of species that are obligate or specialist associates of brittlestar beds.

It is thought that dense *Ophiothrix* beds may play an important role in local nutrient cycles by filtration and concentration of suspended particulate matter, and by the excretion of nitrogenous waste.

Sensitivity to natural events

Records from several areas suggest that brittlestar beds can persist for years or decades, but details of long-term fluctuations are available only for the western English Channel. In the Plymouth area, dense *Ophiothrix* beds were recorded at the turn of the century, but were apparently absent during the 1920s and 30s. Beds were recorded again from the early 1950s onwards, and persisted until the late 1960s. From about 1970 onwards, the extent and density of *Ophiothrix* populations declined rapidly and only scattered individuals were present by the end of the decade. The 1970s decline of *Ophiothrix* was associated with an increased abundance of the predatory starfish *Luidia ciliaris* in the Plymouth area. There are suggestions that the cyclical changes earlier in the century were also related to the abundance of *Luidia*. Increased numbers of *Luidia* were not recorded on the French side of the Channel and *Ophiothrix* beds there did not decline in parallel with those near Plymouth. The ultimate cause of these fluctuations may be the Russell Cycle, a multidecadal oceanographic process involving the periodically increased penetration of Atlantic water into the western Channel. An influx of Atlantic water may bring increased numbers of starfish larvae, or create the conditions necessary for their settlement and survival.

A rapid (2 - 3 days) mass mortality of *Ophiothrix quinquemaculata* has been recorded in the Gulf of Trieste, Adriatic Sea. This occurred as a result of severe oxygen depletion brought about by a combination of hot weather, poor water exchange and heavy organic enrichment. In the shallow waters of the Dutch Oosterschelde Estuary, *Ophiothrix fragilis* aggregations were found to be temperature-sensitive, building up after mild winters and suffering mass mortality when winter temperatures were unusually cold. These examples are likely to be relevant to British beds only in shallow, semi-enclosed water bodies such as sea lochs. In open-coast areas, severe hypoxia is less likely to occur and most beds will be sheltered by water depth from extremes of temperature.

Several examples are known of echinoderm populations being severely reduced over wide geographic areas by epidemic disease. Brittlestar beds would appear to offer ideal conditions for the spread of pathogens, but so far no cases of this have been reported.

Sensitivity to human activities

There are very few recorded instances of brittlestar beds being directly affected by human activity. Beds are generally avoided by fishermen, and no species are harvested from them. It has been suggested that human overfishing may even lead to the proliferation of brittlestar beds as a consequence of reduced predation pressure, but so far there is no firm evidence that this has occurred. Moderate levels of organic input (eg. sewage, aquaculture waste) to the sea may be beneficial to suspension-feeding brittlestars but excessive enrichment is likely to be harmful. The threshold levels of organic pollution involved have not been determined, and are likely to depend on local hydrography. Other forms of marine pollution can be expected to harm brittlestar beds (eg. diesel oil toxicity to brittlestars has been demonstrated), but there are no recorded examples of this occurring. Coastal alteration (eg. building of breakwaters, spoil dumping) could have positive or negative effects on local brittlestar populations, depending on the nature of the changes.

Introduced organisms (especially parasites or pathogens) are a potential threat in all coastal ecosystems. So far, brittlestar beds have not been affected, but the mass mortality of the urchin *Diadema antillarum* in the Caribbean (possibly caused by an introduced pathogen) shows that even widespread and abundant species can be vulnerable.

Monitoring options

Several techniques are available for determining the extent and composition of brittlestar beds. Towed video surveys are likely to be constrained by sea bed topography, and diving surveys by depth and currents. ROVs are less subject to these constraints. Acoustic surveys using RoxAnn^{TM} can distinguish dense brittlestar beds, and have been shown to be capable of mapping the extent of these features. Determination of species composition and animal densities requires either grab sampling (where ground type permits) or visual observation. For basic mapping of brittlestar beds within an SAC, a RoxAnn^{TM} survey backed up by grab sampling and/or a visual survey is recommended. A combination of methods appropriate to the water depth and substratum type could be used for repeat monitoring of the extent and density of the aggregations. In addition to brittlestar densities, the numbers of other epifauna, especially predators such as *Luidia ciliaris,* should be recorded. Human activities having the potential to affect the beds (eg. sewage disposal, salmon farming) should be identified, and their intensity monitored in relation to observed changes in bed extent or composition.

Gaps in knowledge

The biology of brittlestars, and the ecology of their aggregations, is fairly well-known in comparison with many other subtidal biotopes. The major gaps in knowledge relate to the temporal persistence of the beds, and the effects of natural and human-induced environmental change upon them. Brittlestar beds show a number of features that could make them potentially useful biological indicators of change in the coastal environment. They are easily-defined biotopes, dominated by a small number of species, whose biology and ecological requirements are relatively well-known. Beds are conspicuous and relatively easy to monitor. They occur around the British Isles, with the same dominant species, making regional comparisons possible. Brittlestar beds are known to be persistent on a scale of years to decades, but can also decline and disappear rapidly if conditions (eg. temperature, oxygen supply) change. They are sensitive to environmental change at a range of scales, from short-term, localized events (eg. hypoxia) to major oceanographic cycles occurring over decades. The distribution and extent of beds around the UK could be affected both by long-term natural processes (eg. changes in hydrography), and by a variety of more immediate human impacts on the coastal environment. Regular monitoring of beds at selected localities around the British Isles (some perhaps within SACs) could provide useful information about the state of coastal ecosystems and the changes occurring within them. It would be valuable to supplement this with more detailed information on the role of beds in local ecological processes such as carbon and nutrient cycling.

Assessment of biodiversity and conservation importance, and recommended actions

The conservation importance of brittlestar beds lies in the rarity of the *Ophiopholis*-dominated biotope (MCR.Oph.Oacu), and more generally, in the fact that the British Isles contains a large proportion of the known examples of this community type. The British and Irish examples are the best-known and most intensively-studied of their kind. Beds may also be locally important in ecosystem functions such as carbon and nutrient cycling. Fluctuations in the extent of brittlestar beds show that these biotopes are sensitive to environmental change (eg. predation pressure, hypoxia). It may be possible to take measures to preserve the integrity of beds, at least with respect to local management of human activities. However, the biotope complex as a whole is not known to be declining and probably faces no current threats.

With respect to the series of ‘demonstration’ candidate SACs, the best-developed beds are known from Strangford Lough and the Berwickshire/North Northumberland Coast. Strangford Lough contains very dense *Ophiothrix* (with some *Ophiocomina*) aggregations, while the Berwickshire coast supports beds on a variety of substrata, with examples dominated by *Ophiothrix, Ophiocomina* and *Ophiura albida.* An *Ophiocomina* bed is known from the Papa Stour SAC. All three sites could be usefully included in a bed monitoring scheme. *Ophiothrix* beds are also present near the Llyn Peninsula, but further information on their extent and distribution is required. The dense populations of *Ophiura* spp. recorded from the Wash are not represented in any other candidate SAC, but little is known of the dynamics of these beds.

Brittlestar aggregations in Loch nam Madadh and the Sound of Arisaig appear to be confined to localized boulder and bedrock outcrops and occupy only a small proportion of the benthic environment at these sites. These two candidate SACs are therefore of lesser importance to this biotope complex. The *Ophiopholis*-dominated beds in the Loch Alsh possible SAC are important because of the rarity of this biotope variant and should be monitored for any possible effects of aquaculture in this loch system.

I. INTRODUCTION

Dense aggregations of brittlestars, sometimes covering hundreds of square metres and comprising hundreds or thousands of individuals m^{-2}, can be found on a variety of substrata in UK coastal waters. Although found widely around the British and Irish coasts, beds of this kind are uncommon on a global scale and are of considerable interest to scientists studying the evolutionary history of marine benthic communities. The spatial extent of these aggregations, and the animal biomass they represent, mean that brittlestar beds may play an important role in the ecology of British coastal seas. They may also have some potential as indicators of natural or human-induced changes in the marine environment. The important scientific and ecological aspects of these beds justifies a review of their dynamics and sensitivity characteristics from a conservation-related perspective.

The objective of this report is to summarize and review the available information on the **'Subtidal brittlestar beds'** 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

Brittlestars form a class (Ophiuroidea) within the Phylum Echinodermata. Echinoderms are a major group of exclusively marine invertebrates characterized by five-fold radial symmetry and a body wall containing calcareous skeletal plates. All echinoderms also have a unique water vascular system which communicates with the surrounding sea water and operates, by means of hydrostatic pressure, rows of radially-arranged suckers or 'tube feet'. Brittlestars have long arms and a relatively-small, well-defined central disc. The tube feet do not have terminal suckers as in other echinoderms, and they are used more for food capture than for locomotion.

The Ophiuroidea is the largest living echinoderm class, comprising about 1800 species, with representatives in all benthic environments from the intertidal zone to the deep ocean, and found in all temperate, tropical and polar seas. There are about 20 species in British coastal and shelf seas (shallow-water species are illustrated in Picton, 1993). In British waters, brittlestars are common members of the benthic fauna of both hard and soft substrata. Some species live epifaunally on or among rocks, others on the surface of sandy or muddy bottoms, and others partially buried below the sediment surface. Brittlestars of some kind can be found in almost any marine benthic biotope in the British Isles, and are often common members of the fauna. In some areas, however, they occur in dense aggregations on the sea bed, with hundreds or even thousands of individuals m^{-2}, and sometimes to the virtual exclusion of any other animals. These brittlestar beds occur on a variety of substrata, from solid bedrock to boulders, gravel, sand or mixed sediments, usually in conditions with fairly strong tidal streams. Beds may be patchy and local in distribution or may cover several km^2 of sea bed.

Only a few species of the British brittlestar fauna occur in dense aggregations. Individual beds may be formed by a single species or contain a mixture of several. None of the bed-forming brittlestar species occurs exclusively in dense aggregations. All can be found in smaller numbers in other benthic biotopes. There is therefore no clear-cut population density above which a 'bed' can be defined. Nevertheless, there are certain benthic communities around the

UK and Ireland so numerically dominated by brittlestars that they have been recognized as distinct biotopes within the MNCR classification (see Chapter II), and it is these biotopes with which this report will be concerned. The bed-forming species are *Ophiothrix fragilis, Ophiocomina nigra* and, more rarely, *Ophiopholis aculeata*. Epifaunal, sediment-dwelling brittlestars of the genus *Ophiura* may also occur in large numbers but do not usually dominate their biotopes to the same extent as the other species. These *Ophiura* aggregations will be mentioned where relevant. The infaunal brittlestars *Amphiura filiformis* and *A. chiajei* live partially buried in muddy sediments and may reach densities of > 1000 m^2. However, these infaunal populations are not normally considered as brittlestar 'beds' and will not be considered further here.

Subtidal brittlestar beds can be found in several of the habitats defined in Annex I of the EU Habitats Directive. Examples occurring on hard substrata come within the category of **'Reefs'**, while some of those on gravel or mixed sedimentary substrata can be classed within **'Sandbanks covered by sea water at all times'** (provided these are shallower than 20 m depth). Geographically, examples can be found in **'Large shallow inlets and bays'**.

2. Major constituent species

a. *Ophiothrix fragilis*

This is a large brittlestar with long, spiny arms. The central disc is up to 20 mm in diameter. Colour is very variable, commonly brown or grey, but sometimes patterned with red, yellow or orange. The arms are usually banded with dark and light colours. *Ophiothrix fragilis* is very common all round the British and Irish coasts from the lower intertidal zone downwards. It occurs in a wide variety of benthic biotopes on hard substrata, among algae or sessile animals, and also on sandy or shelly bottoms. The species is widely distributed in the eastern Atlantic from Norway to South Africa. *Ophiothrix fragilis* is the species most commonly found in dense aggregations in British waters.

Ophiothrix fragilis is generally considered a single species and is not subdivided by researchers in the UK and Ireland. However, French workers recognize a number of varieties based on morphological differences, termed *echinata, pentaphyllum, lusitanica* and *abildgaardi* (Koehler, 1921). It is possible that differences between varieties may explain some of the inconsistencies in findings concerning the life cycle and population dynamics of the species (see Chapter IV).

b. *Ophiocomina nigra*

The smooth disc of *Ophiocomina nigra* is up to 25 mm in diameter. The arms are long, with a less 'bristly' appearance than those of *Ophiothrix fragilis*. The arm spines are prominent, but neatly arranged like the teeth of a comb. Individuals are uniformly coloured with no bold patterns. Colour ranges from jet black, through various shades of brown, to orange. Colour appears to be related to water depth, with darker shades predominating in shallower water (Fontaine, 1962). *Ophiocomina nigra* is usually found in fairly sheltered sites with some water movement, on bedrock, boulders or gravel, sometimes in mixed populations with *Ophiothrix fragilis*. It is common around the British Isles apart from the southern North Sea. Total geographic range is from Norway to the Azores and the Mediterranean.

c. *Ophiopholis aculeata*

The disc of *Ophiopholis aculeata* is covered with prominent large plates and is usually about 15 mm in diameter. The arms bear fairly short, robust spines. Colour is brown or reddish with darker bands on the arms. This species is typically an inconspicuous inhabitant of crevices or borings in rock, but forms dense beds in a few localities in Scotland (see Chapter II). *Ophiopholis aculeata* is a circumpolar cold water brittlestar reaching its southern limit of distribution in the English Channel.

d. *Ophiura* spp.

In British coastal waters, this genus comprises the species *O. ophiura* (*O. texturata* is a synonym for this species), *O. albida, O. robusta* and *O. affinis,* all of which are active brittlestars living on sand, muddy sand and gravel, or on silt-covered rock surfaces. *Ophiura* species have narrow, tapering, relatively short arms with inconspicuous spines. The arms are generally held stiffly out from the central disc. *Ophiura ophiura* is the largest species, with a disk up to 30 mm in diameter, and is a uniform sandy grey-brown colour. *Ophiura albida* and *O. robusta* are much smaller (disk to 15 mm diameter) with a pair of conspicuous white spots on the upper disk at the base of each arm. *Ophiura affinis* is smaller still (disk diameter 8 mm), grey-brown with darker banding on the arms. *Ophiura ophiura, O. albida* and *O. affinis* occur off all British coasts and range from Norway to the Mediterranean. *Ophiura robusta* is a boreal species which reaches only the northern half of the British Isles.

Ophiura species occur at high densities in some situations and are occasionally found as minor components of beds dominated by *Ophiothrix* or *Ophiocomina.* Aggregations of *Ophiura* spp. have received less attention than those of *Ophiothrix* or *Ophiocomina,* and much less is known of their ecology and dynamics (Tyler, 1976).

3. Importance of the biotope complex

a. Economic importance

Brittlestar beds are currently of no economic importance. No species are harvested from them and they are not thought to be significant feeding or nursery grounds for any commercially-important fish or shellfish.

b. Scientific importance

The living brittlestar beds have attracted considerable scientific attention as prime examples of an ‘anachronistic’ community, ie. a community type that was common in the distant past but is relatively rare today (Aronson, 1989). In the Paleozoic era (roughly 570 - 245 million years ago), the fossil record shows that sandy or muddy substrata in shallow coastal waters typically supported dense populations of sessile or sedentary animals living above the sediment surface, and feeding on plankton or other suspended matter in the water column. These epifaunal suspension-feeders included many species of brachiopods, stalked crinoids (‘sea lilies’) and other groups that are now either extinct or uncommon in modern marine communities. Brittlestars first appear in the Ordovician Period (roughly 500 - 420 m.y. ago), and the fossil record shows that in some circumstances they formed dense aggregations similar to those that exist today (Aronson & Sues, 1988). A major change in marine benthic communities occurred during the succeeding Mesozoic Era, during which dense populations of epifaunal suspension-feeders largely disappeared from sedimentary habitats in shallow water, which became dominated instead by groups such as bivalves which typically live buried within the substratum. This ‘Mesozoic marine revolution’ (Vermeij, 1977, 1987) appears to be associated with the evolutionary radiation of groups of marine predators able to tackle hard-shelled prey. These predatory groups include the decapod crustaceans (crabs, lobsters), teleost fishes and neogastropod snails (eg. whelks).

Fossilized brittlestar beds begin to decline in frequency during the Jurassic period (roughly 208 - 140 m.y. ago) and are rare in later deposits (Aronson, 1992) The living examples have a restricted geographic distribution today (see Chapter II). The association between the decline of a major community type and changes in predation intensity has attracted much attention from ecologists studying the dynamics of marine ecosystems over evolutionary time-scales. The British brittlestar beds have been studied by workers from as far afield as Japan and the United States, partly to test the hypothesis that modern beds exist where predation pressure is low (Aronson, 1989). Brittlestar beds thus provide a rare opportunity to experimentally test hypotheses concerned with community changes over evolutionary time, as opposed to relying solely on inferences drawn from the fossil record (Aronson, 1992).

c. Biodiversity and conservation importance

Species existing in dense aggregations consisting of millions of individuals are by definition not rare, and even without these aggregations the three main bed-forming species are widespread and common throughout British and European waters. However, as outlined above, the community type represented by brittlestar beds is fairly uncommon in the modern world. Beds do exist elsewhere (see Chapter II), but are particularly numerous in the British Isles. The British representatives are the best-known examples of their kind and have the longest history of scientific study. They should therefore be considered generically as being of conservation importance.

There is evidence (considered in more detail in Chapter IV) to suggest that massive aggregations of suspension-feeding brittlestars can have an important effect on water quality in coastal environments and may even help counteract some of the potentially harmful effects of eutrophication (proliferation of planktonic algae) caused by human input of nutrients into the sea. The beds may therefore play a significant role in the ecological functioning of coastal seas. Conversely, the distribution and extent of these conspicuous biological features may be potentially valuable indicators of climatic, oceanographic or human-induced changes in the coastal environment.

The conservation importance of brittlestar beds will be assessed comprehensively in Chapter IX after a full review of their distribution, ecology and sensitivity to change.

B. KEY POINTS FROM CHAPTER I

- The ‘Subtidal brittlestar beds’ biotope complex is defined by the occurrence of dense aggregations of brittlestars, at densities of hundreds or thousands m^{-2}, living epifaunally on bedrock, boulder, gravel or sedimentary substrata.

- The main bed-forming brittlestar species are *Ophiothrix fragilis* and *Ophiocomina nigra*, with rare examples formed by *Ophiopholis aculeata*. Brittlestars of the genus *Ophiura* also sometimes occur on sedimentary substrata in large numbers.

- None of the bed-forming brittlestar species occur solely in dense aggregations. All are widespread and often common in other benthic biotopes around the British Isles.

- Brittlestar beds are not sites of fisheries and currently have no economic importance.

- The beds are of high scientific importance as living examples of an ‘anachronistic’ community, resembling the dense aggregations of epifaunal suspension-feeders that dominated marine soft substrata during the Paleozoic Era. These communities became much less common following the Mesozoic radiation of ‘modern’ groups of marine predators.

- Living brittlestar beds are widespread around the British Isles but uncommon on a global scale. The British representatives are the best-known and best-studied examples of their kind. Beds have important effects on local water quality and are potential indicators of natural or human-induced changes in the coastal environment.

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 (MNCR), and summarize 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 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 recognisable **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**. The current version of the MNCR biotope classification (Connor et al., 1997) lists two biotopes characterized by high abundances of epifaunal brittlestars. These are summarized below:

1. MNCR Code **MCR.Oph**	*Ophiothrix fragilis* and/or *Ophiocomina nigra* beds on slightly tide-swept circalittoral rock or mixed substrata.

Moderately exposed or sheltered slightly tide-swept rock or mixed substrata with dense brittlestar beds, usually dominated by *Ophiothrix*, but often with *Ophiocomina* amongst them. *Ophiocomina* may be the dominant species at some sites. Crusts of coralline algae occur on the underlying rocks, along with the tubeworm *Pomatoceros triqueter*. *Alcyonium digitatum* and a few species of sea anemones and hydroids may occur sparsely on protruding rocks. The large predatory starfish *Luidia ciliaris* and *Crossaster papposus* are also typically present. This biotope represents the ‘standard’ brittlestar bed type, and occurs widely around the British Isles (see Section B below).

2. MNCR Code **MCR.Oph.Oacu**	*Ophiopholis aculeata* beds on slightly tide-swept circalittoral rock or mixed substrata.

This is a variant of the MCR.Oph biotope, distinguished by the occurrence of large numbers of *Ophiopholis aculeata* (*Ophiothrix* and *Ophiocomina* are also common in this biotope). Physical conditions and associated fauna are similar to those of MCR.Oph. *Ophiopholis* - dominated beds are rare, known from localities in Shetland, Ireland and in the Loch Alsh/Duich/Long system in the west of Scotland (Connor, 1989).

A few other biotopes defined in the MNCR system may support brittlestars in large numbers, but not consistently, or not in such abundance as to constitute ‘beds’.

B. DISTRIBUTION WITHIN THE BRITISH ISLES

1. General distribution

Figure 1 summarizes the general distribution of brittlestar beds around the British Isles.

The typical *Ophiothrix/Ophiocomina* beds (MCR.Oph) are found widely around the northern, western and southern British Isles (Aronson, 1989). Examples are known from Shetland (Howson, 1988), from many localities on the western Scottish coasts (Howson et al., 1994) and in the Clyde Sea (Gorzula, 1976). Extensive beds occur around the Isle of Man (Chadwick, 1886; Brun, 1969), off the Llyn Peninsula (Hiscock, 1984), Pembrokeshire (Aronson, 1989), and in the Bristol Channel (George & Warwick, 1985). Inshore brittlestar beds have been studied in south-west England (Warner, 1971), while those further offshore in the western English Channel have yielded data on long-term fluctuations in spatial extent (Holme, 1984). Further east in the Channel, *Ophiothrix* beds are a dominant community type in the Dover Strait (Davoult, 1990; Migné & Davoult, 1997).

On the east coast of the UK, *Ophiothrix/Ophiocomina* beds are known from Berwickshire (Pagett, 1984; Foster-Smith et al., 1996), but appear to be absent from the stretch of coast between this area and the Dover Strait. In Ireland, beds have been recorded from several localities on the southern, eastern and western coasts (Keegan et al., 1985; Ball et al., 1995).

2. Occurrence within 'demonstration' candidate SACs

The occurrence or non-occurrence of subtidal brittlestar beds in the 12 'demonstration' SACs included within the UK Marine SACs Project is summarized in the table below.

Brittlestar beds definitely present	Brittlestar beds probably absent
Papa Stour	Solway Firth
Loch nam Madadh	Cardigan Bay
Sound of Arisaig	Plymouth Sound & Estuaries
Strangford Lough	Chesil & the Fleet
Morecambe Bay	
Llyn Peninsula & the Sarnau	
The Wash & North Norfolk Coast	
Berwickshire & North Northumberland Coast	

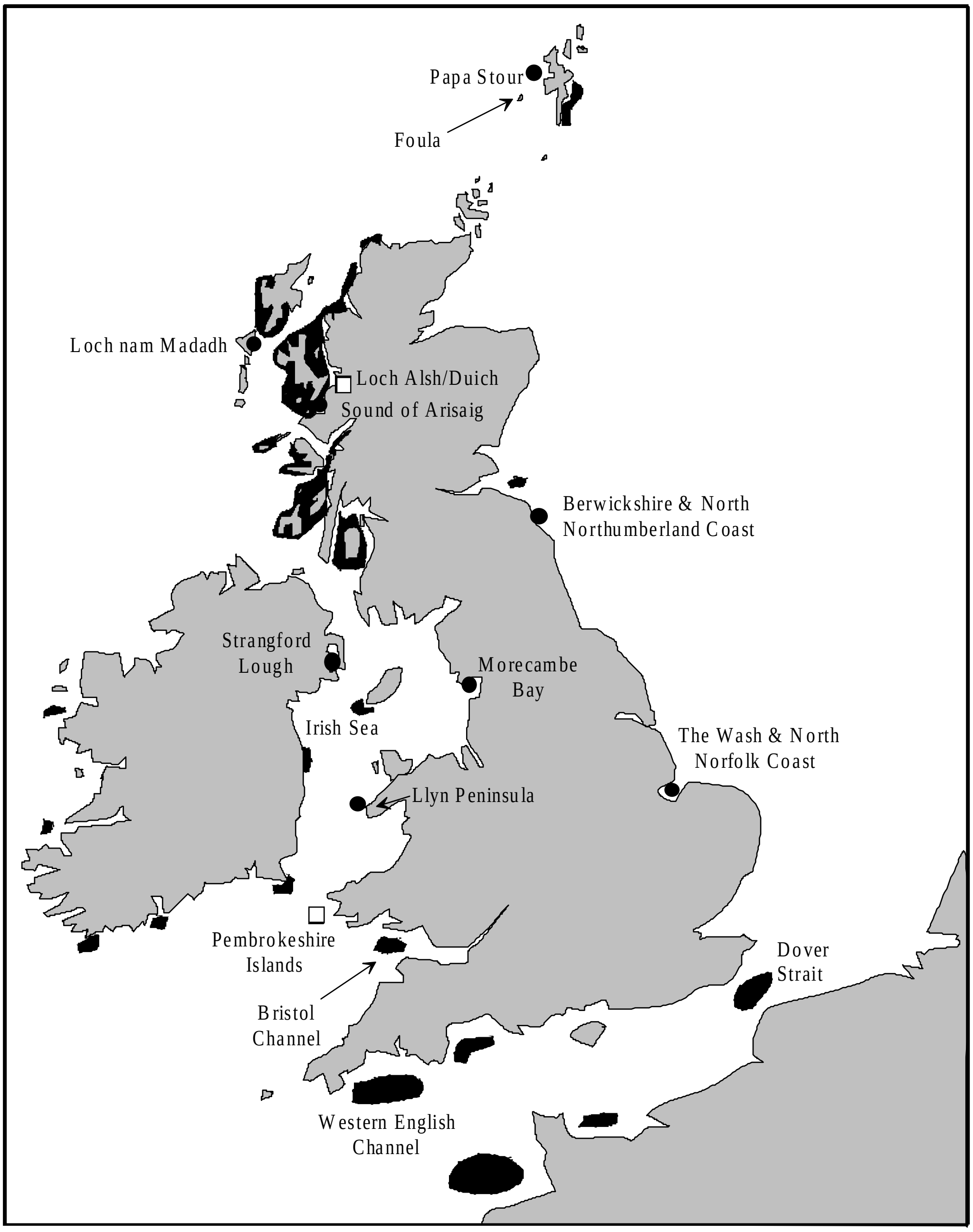

Figure 1. Distribution of brittlestar beds around the British Isles, modified from Aronson (1989). Solid circles indicate ‘demonstration’ candidate SACs in which beds are known to exist. Other candidate or possible SACs supporting these biotopes are shown by open squares. The general location of other, non-SAC areas in which beds have been recorded is indicated by dark patches.

a. SACs probably lacking the biotope complex

The subtidal biotopes of the Solway Firth have been surveyed quite recently, but no brittlestar aggregations have been reported (Covey, 1992; Cutts & Hemingway, 1996). None are known from Cardigan Bay (Mackie et al., 1995). Brittlestar beds are well-known from south-west England but have not been recorded from within the confines of Plymouth Sound (Hiscock & Moore, 1986; Devon Wildlife Trust, 1993) or the Fleet Lagoon (Dyrynda, 1984).

b. SACs containing the biotope complex

The locations of ‘demonstration’ amd other candidate SACs known to support brittlestar beds are shown in Fig. 1. The sites themselves are discussed individually below.

i. Papa Stour

Brittlestar beds are known from several localities around Shetland (Howson, 1988). In the area of the Papa Stour candidate SAC, Howson recorded an *Ophiocomina* bed from coralline algal-encrusted rock ridges at 25m depth in the Sound of Papa, between the island and the Shetland mainland (Fig. 2).

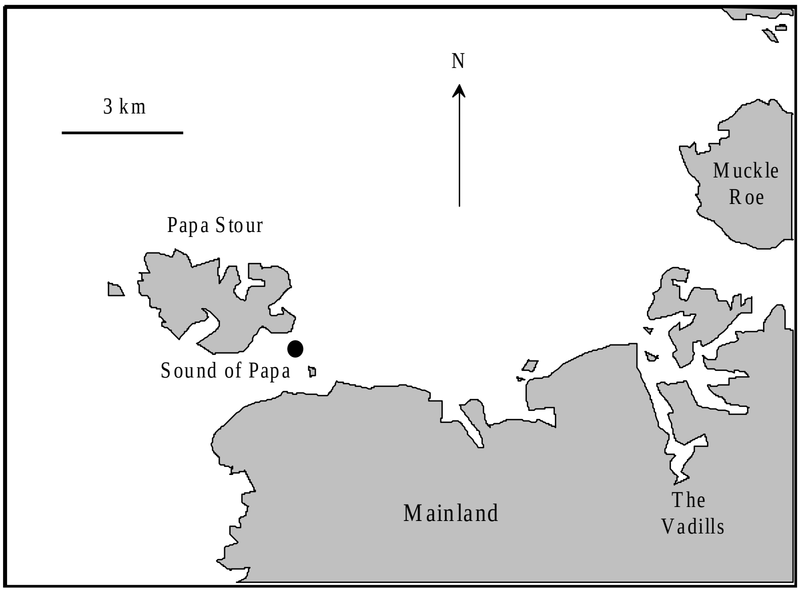

Figure 2. Location of the *Ophiocomina nigra* bed (solid circle) near Papa Stour, Shetland. From Howson (1988).

ii. Loch nam Madadh

The complex system of Loch nam Madadh in North Uist contains a variety of hard and soft substratum biotopes (Entec, 1996). No extensive beds of brittlestars (biotopes MCR.Oph or MCR.Oph.Oacu) have been found, but local aggregations of *Ophiothrix* and *Ophiocomina* occur on rock outcrops, boulders and gravel patches, mainly in the outer parts of the loch (Fig. 3). The absence of extensive aggregations suggests that Loch nam Madadh is probably not an important site for the biotope complex.

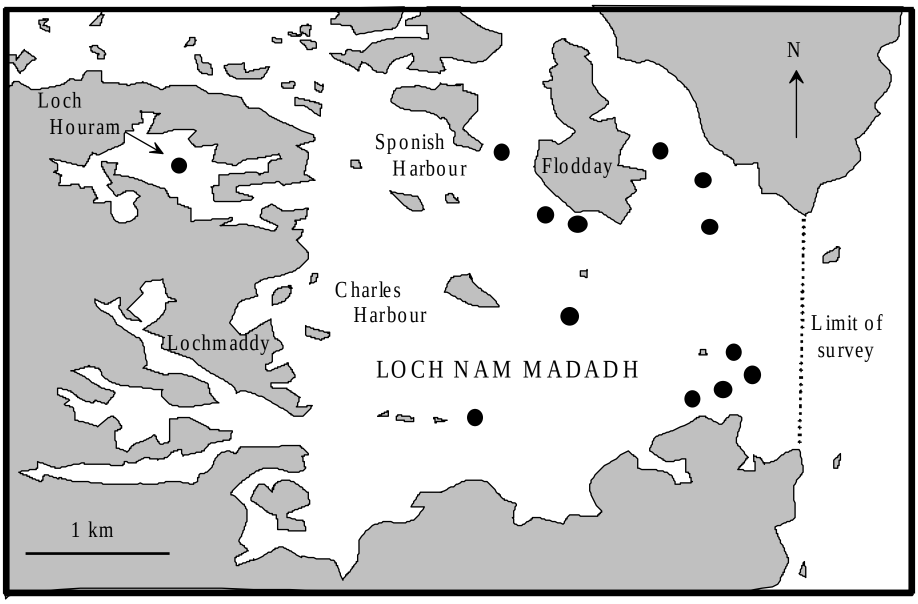

Figure 3. Locations of brittlestar aggregations (solid circles) in Loch nam Madadh. Modified from Entec (1996).

iii. Sound of Arisaig

The benthic biotopes of the Sound of Arisaig candidate SAC have been mapped recently by acoustic methods, towed video and diving (Davies & Hall-Spencer, 1996). Areas of grazed bedrock and boulders with *Ophiothrix* and *Ophiocomina* were found scattered in the entrances to Loch Ailort and the south channel of Loch Moidart. Howson (1990) found the same community on deep (up to 39 m) reefs in the Sound of Arisaig proper and further north in the entrance to Loch nan Uamh, although most of her localities fall outside the northern boundary of the proposed SAC. Both brittlestar species were also found abundantly around bedrock adjacent to a muddy sand plain at 8m depth near the head of Loch Ailort (Howson. 1990).

Brittlestar aggegations thus appear to be quite common within and just outside the Sound of Arisaig SAC (Fig. 4), but are spatially restricted to bedrock outcrops and boulder patches.

iv. Strangford Lough

This large, virtually land-locked marine inlet on the coast of Northern Ireland contains a diverse range of benthic biotopes. Very dense aggregations of brittlestars, mainly *Ophiothrix,* but with some *Ophiocomina,* cover an extensive area of the lower lough (Erwin, 1977). A recent acoustic mapping of benthic biotopes in Strangford Lough (Magorrian et al., 1995) estimated that the *Ophiothrix* beds occupied 0.4 km^2 of the 22.9 km^2 surveyed (Fig. 5).

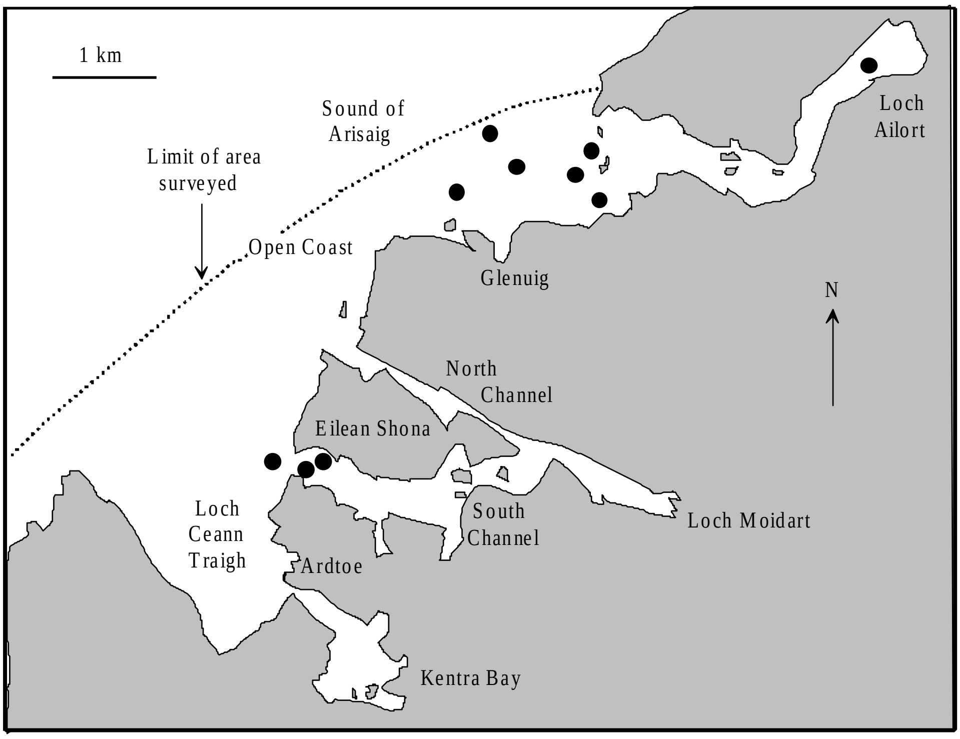

Figure 4. Locations of brittlestar aggregations (solid circles) in the Sound of Arisaig and adjacent sea lochs. Modified from Davies & Hall-Spencer (1996), with additional information from Howson (1990).

v. Morecambe Bay

The Morecambe Bay candidate SAC supports at least one dense *Ophiothrix* bed, at Roa Island at the south end of Walney Channel (C. Lumb, personal communication). The bed extends into the intertidal, covering an area of about 0.1 ha. Its subtidal extent has not yet been determined. The bed appears to be increasing in size.

vi. Llyn Peninsula

Details of the occurrence of brittlestar beds in this area are scarce. Hiscock (1984) recorded a dense *Ophiothrix* bed covering an 'extensive area' at Porth Colmon off the north coast of the peninsula (Fig. 6). *Ophiothrix* aggregations have also been found during surveys associated with exploratory oil drilling at a site 9.5 km north of the headland (Braich y Pwll) at the tip of the peninsula (Mills, 1997). The substratum in this area was composed of tide-swept cobbles and pebbles embedded in a sediment matrix.

vii. The Wash & North Norfolk Coast

No *Ophiothrix* or *Ophiocomina* beds are known from this area. However, a sediment community characterized by *Ophiura albida*, and with *O. ophiura* also present, has been recognized in the Wash (Covey, 1991). Foster-Smith et al. (1997) recorded *Ophiura* spp. on muddy sand, associated with the urchin *Psammechinus miliaris* and the starfish *Asterias rubens*. *Ophiura ophiura* and *O. albida* had overlapping but generally well-defined distributions. Both species were found on a range of substrata, but *O. ophiura* was confined to the south-east Wash and often associated with silty substrata containing a variable shell component. Densities of up to 1500 *O. albida* m^{-2} have been recorded (Dipper et al., 1989).

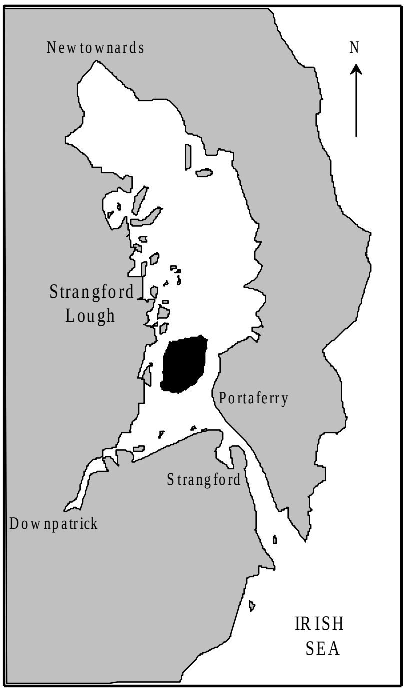

Figure 5. Map of Strangford Lough, showing the area in which brittlestar beds are found (dark patches). Modified from Magorrian et al. (1995).

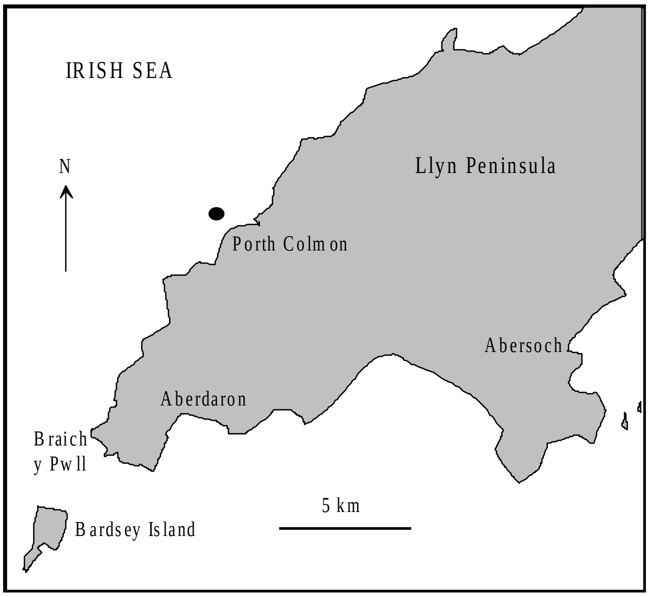

Figure 6. Tip of the Llyn Peninsula, showing the location of the *Ophiothrix fragilis* bed (solid circle) recorded by Hiscock (1984).

viii. Berwickshire & North Northumberland Coast

Foster-Smith et al., (1996) used acoustic methods (see Chapter VII) to map the benthic biotopes of the Berwickshire coast. Extensive *Ophiothrix* (with smaller numbers of *Ophiocomina*) were found on bedrock and boulders from 10 - 20 m depth, occasionally down to 30 m. Beds occurred on urchin-grazed rocks with the tubeworm *Pomatoceros triqueter* and sparse soft corals, *Alcyonium digitatum,* (this species was sometimes absent), and on shallow cobbles with encrusting coralline algae. The beds occurred in a patchy but extensive belt running parallel to the coastline (Fig. 7).

In an earlier survey of the St Abbs area, Pagett (1984) reported beds of three brittlestar species, *Ophiothrix fragilis, Ophiocomina nigra* and *Ophiura albida*. The brittlestars occurred in a variety of species combinations:

- *Ophiothrix* beds occurred on bedrock, boulders or gravel, and usually had some *Ophiocomina,* and sometimes also *Ophiura albida,* mixed in.
- *Ophiura albida* beds occurred on gravel or sand, and frequently contained some *Ophiura robusta.*
- *Ophiocomina* beds occurred on bedrock, gravel or coarse sand. This was the only brittlestar found in monospecific aggregations, but in most beds one or more of the other species were also present.

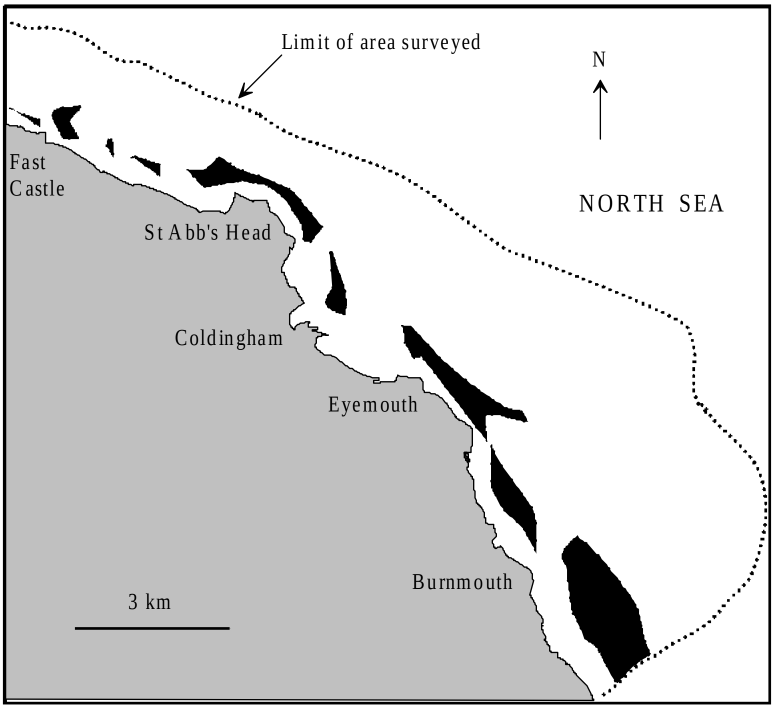

Figure 7. Location of areas supporting brittlestar beds off the Berwickshire/North Northumberland Coast. Modified from Foster-Smith et al. (1996).

3. *Occurrence within other candidate or possible SACs*

Several other candidate or possible SACs are known to support brittlestar beds. *Ophiocomina* - dominated beds are known from around the island of Mousa off the south-east coast of Shetland (Howson, 1988). The upper reaches of Loch Alsh have a cobble and pebble substratum in depths of 11 - 33 m, experiencing moderately strong tidal streams (Connor, 1989). This supports the rare variant biotope MCR.Oph.Oacu, characterized by high densities of the usually cryptic brittlestar *Ophiopholis aculeata* (Fig. 8). *Ophiothrix* and *Ophiocomina* also occur mixed with *Ophiopholis* in these beds. In south-west Britain, *Ophiothrix/Ophiocomina* beds have been recorded from the Pembrokeshire Islands candidate SAC (Bunker & Hiscock, 1987).

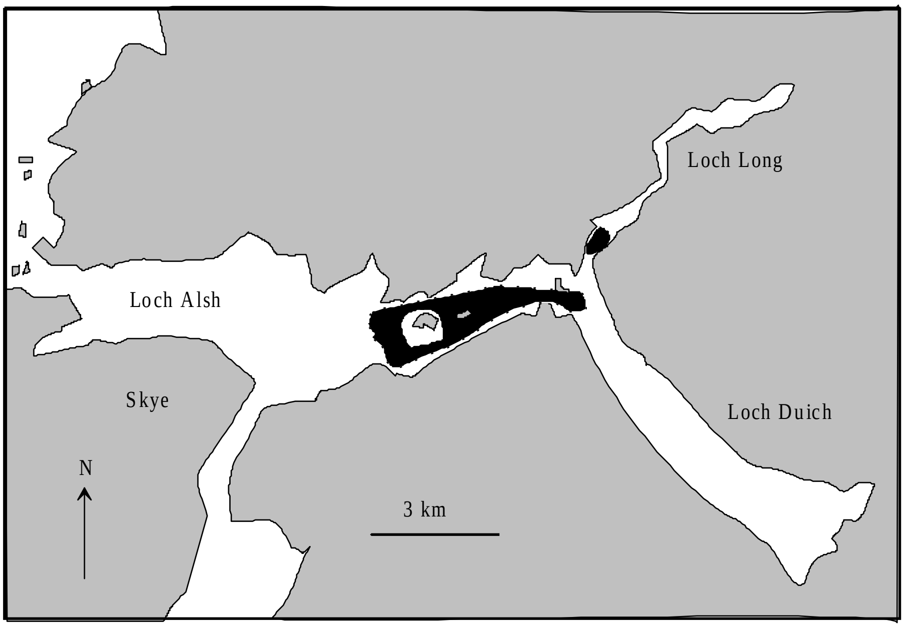

Figure 8. Location of the *Ophiopholis aculeata* - dominated brittlestar beds (dark patches) in the Loch Alsh/Duich/Long system. Modified from Connor (1989).

4. *Assessment of the biotope complex within SACs*

Of the various candidate or possible SACs, those with the most extensive brittlestar beds appear to be Strangford Lough, Berwickshire/North Northumberland and Loch Alsh. Loch Alsh is particularly noteworthy as the sole example of the *Ophiopholis* - dominated biotope within an SAC. Large beds may also be present around the Llyn Peninsula, but their distribution in this area has been less thoroughly mapped.

Brittlestar aggregations in Loch nam Madadh and the Sound of Arisaig appear to be patchy and not very extensive. Good examples of the biotope complex are found in Shetland, but the best recorded there is not located within a proposed SAC. Howson (1988) found a rich bed at 30 m depth off the east coast of the island of Foula. A substratum of rounded, coralline-encrusted cobbles supported very high densities of all three main bed-forming species (*Ophiothrix fragilis, Ophiocomina nigra* and *Ophiopholis aculeata*), while large numbers of *Ophiura albida, O. robusta* and possibly *O. affinis* were found beneath the stones. This is an unusually high species diversity for a single brittlestar bed.

C. DISTRIBUTION OUTSIDE THE BRITISH ISLES

As noted previously, brittlestar beds are particularly common around the UK and Ireland, but examples are known from elsewhere. The *Ophiothrix/Ophiocomina* beds of the western English Channel extend to the French side (Allain, 1974; Holme 1984) as far as the Brittany coast (Hily, 1991). Dense populations of *Ophiothrix fragilis* have also been recorded from the Oosterschelde Estuary in the Netherlands (Leewis et al., 1994).

Beds of *Ophiocomina nigra* are known from the coast of Portugal (Saldanha, 1973) and from the Mediterranean of Algeria (Allain et al., 1978). The Mediterranean species *Ophiothrix quinquemaculata* was found at densities of up to 88 m^{-2} at 42 - 70 m depth at Banyuls-sur-Mer on the southern coast of France (Guille, 1964). In the Gulf of Trieste, Adriatic Sea, this species occurs on muddy and sandy substrata at densities of usually 50 - 250 m^{-2}, with local aggregations up to 300 m^{-2} (Fedra et al., 1976). At these densities the brittlestars are the most abundant large epifauna in their communities, but are still relatively sparse compared with some of the populations recorded around the British Isles. Czihak (1954) found the small brittlestar *Ophiactis virens* at a very high density of 10,000 - 13,000 m^{-2} in a submarine cave in the Gulf of Naples.

Outside the north-eastern Atlantic area, the best-known example of a dense epifaunal brittlestar population is that studied by Aronson & Harms (1985) in Sweetings Pond, an inland salt water lake in the Bahamas. Here, the species *Ophiothrix oerstedi* was found at up to 434 individuals m^{-2}, probably because predatory reef fish were absent from the lake. Aggregations of other species are also reported from the Antarctic and sub-Antarctic (Morison, 1979; Fratt & Dearborn, 1984), and from Japan and California (sources quoted in Warner & Woodley, 1975), but little is known of the beds in these areas.

Paleozoic-type epifaunal communities on soft substrata are relatively rare today in shallow, coastal waters but persist to a greater extent in the deep sea, to which groups such as the stalked crinoids are now confined. Brittlestars are an important element of the deep sea fauna (Gage & Tyler, 1991) although populations do not approach the densities recorded in shallower, more productive seas. For example, in Japan, Fujita & Ohta (1990) recorded *Ophiura sarsii* at densities of 30 to several hundred individuals m^{-2} at depths of 100 - 740 m. These beds were thought likely to extend around much of northern Japan in the 200 - 600 m depth range.

D. KEY POINTS FROM CHAPTER II

- Three biotopes within the MNCR classification are characterized by high densities of epifaunal brittlestars.

- Brittlestar beds are numerous and widespread around the coasts of Britain and Ireland, and appear to be rare or absent only along the English North Sea coast south of Northumberland.

- Beds are present in seven of the 12 ‘demonstration’ candidate SACs and probably absent from the remaining five. They also occur in several other candidate or possible SACs.

- Within candidate or possible SACs, brittlestar beds appear to be most extensive in Strangford Lough, along the Berwickshire/North Northumberland coast and in Loch Alsh. Loch Alsh contains the only examples of *Ophiopholis* - dominated beds within an SAC.

- Outside the British Isles and neighbouring seas, shallow-water aggregations of other brittlestar species are known from the Mediterranean and Adriatic Seas, from an isolated locality in the Bahamas, and from the Antarctic, California and Japan. Brittlestars are an important element of the deep-sea epifauna but do not occur at the high densities found in some coastal beds.

III. ENVIRONMENTAL REQUIREMENTS AND PHYSICAL ATTRIBUTES

Like all biological communities, brittlestar beds exist under a particular set of environmental conditions, and are absent where their ecological requirements are not met. This chapter will summarize the physical and biological factors that appear to be necessary for the existence of these biotopes.

A. PHYSICAL ENVIRONMENT

1. Hydrographic conditions

Most brittlestar beds exist in conditions of full marine salinity. However, in the Dutch Oosterschelde Estuary, dense *Ophiothrix* aggregations have been recorded in areas where normal salinity is only 16.5 %o (Wolff, 1968), and the species was found to persist down to 10%o. The usual depth range of bed occurrence is roughly 10 - 50 m, but may exceed 70 m in the western English Channel (Holme, 1984). Aggregations on infralittoral rock in Scottish sea lochs can be found as shallow as 5 m. Rare examples are known of *Ophiothrix* beds extending into the lower intertidal. Beds may have very abrupt upper or lower depth limits. Off the Isle of Man, the *Ophiothrix* bed studied by Brun (1969) had a sharp upper boundary at 26 m. The lower limit was not determined, but the bed extended to at least 37 m depth.

Beds are usually sheltered from strong wave action, but examples in moderately exposed situations are known (Ball et al., 1995). They can be found in a variety of current regimes. Many sea loch examples experience only weak tidal streams, but on more open coastlines brittlestar beds are generally associated with higher-energy environments. In the Dover Strait, *Ophiothrix* beds experience current speeds of up to 1.5 $m\ s^{-1}$ during average spring tides (Davoult & Gounin, 1995). Similarly strong tidal streams (1.0 - 1.2 $m\ s^{-1}$) were also recorded over beds in the Isle of Man (Brun, 1969). In both locations, *Ophiothrix* densities of up to 2000 individuals m^{-2} were recorded. Such high densities can probably only be maintained where strong currents can supply enough suspended food. Food requirements probably set a lower limit on the current regime of areas able to support brittlestar beds, but this has not yet been determined. The behavioural responses of brittlestars to changes in current speed will be discussed in Chapter IV.

2. Substratum type

Brittlestar beds have been recorded on a wide variety of substrata, ranging from bedrock through boulders and cobbles to gravel, sand and mud. Beds on cobbles, gravel and mixed coarse sediments are probably the most common, and these substrata will obviously predominate where strong currents are experienced. In the Bristol Channel, *Ophiothrix* was recorded at high density (up to 838 m^{-2}) on reefs formed by tubes of the polychaete worm *Sabellaria spinulosa* (George & Warwick, 1985). The brittlestars clustered on the reefs and rock outcrops rather than in the gravel-filled hollows between them, probably because the elevated sites offered a more favourable position for suspension-feeding. In Strangford Lough, dense *Ophiothrix* beds overly shells of the horse mussel *Modiolus modiolus* (Magorrian et al., 1995).

Brittlestars lie on or cling to the substratum, but are not attached to it. Beds therefore usually occur on upward-facing, level or gently-sloping bottoms, rather than vertical cliff faces or overhangs. In strong currents, the mutual support provided by the interlinked arms of densely-packed brittlestars enhances the stability of the beds and reduces the chance of individuals being swept away (Warner, 1971).

3. Temperature

Brittlestar beds exist across virtually the entire geographic extent of the UK and Ireland (Fig. 1). Within the British Isles their distribution is therefore not obviously limited by temperature, although individual species such as *Ophiopholis aculeata* and *Ophiura robusta* do show a latitudinal distribution pattern. In the Oosterschelde Estuary, *Ophiothrix fragilis* was common in areas regularly experiencing winter temperatures down to 3^{o}C, but was eliminated when temperatures fell to 0^{o}C (Wolff, 1968). Such extremes are only likely to be found in enclosed situations with very shallow water depths, and will not be experienced by the majority of open-coast brittlestar beds.

4. Sedimentation

High rates of sedimentation are probably unfavourable to brittlestar beds due to the fouling of the animals' feeding organs (tube feet and arm spines), and in extreme cases suffocation (Aronson, 1992). Beds in current-swept situations will not experience this problem, but it may be a factor in limiting the distribution of beds in semi-enclosed areas such as sea lochs.

B. BIOTIC ENVIRONMENT

Bed-forming brittlestars may use sessile organisms as convenient supports for elevated suspension-feeding, but they are not dependent on them. Predation is the component of the biotic environment that has been most frequently implicated as a factor limiting the occurrence of brittlestar aggregations. The influence of predation over geological time has been discussed in Chapter I. However, it may also operate at a smaller scale to limit the spatial distribution of beds in modern benthic environments.

1. Predation

Aronson (1987a,b, 1989, 1992) has been the chief proponent of the hypothesis that low predation pressure is a necessary condition for the existence of present-day brittlestar beds. The hypothesis has been tested by field experiments in the Isle of Man and the Clyde Sea, involving measurement of the mortality rates of tethered brittlestars in natural aggregations, and others transported to nearby rocky reefs where beds are absent. In both the Isle of Man and the Clyde, mortality of tethered brittlestars was much higher on rocky reefs than in the brittlestar beds. Predators attacked almost four times as many tethered brittlestars in the reef habitats as they did in the beds. Fish (mainly wrasse) and crabs were the main predators on reefs, whereas starfish (*Asterias rubens*) were the main agents of mortality in the beds. Starfish were common both on reefs and in brittlestar beds, while fish and crabs were rare outside the reef habitats. The differences in predation pressure between the two habitats were therefore due largely to differences in fish and crab abundance. Aronson noted that in situations where an *Ophiothrix* bed adjoins a rocky reef, the two are often separated by a 'halo' of several metres of bare substratum. This may represent the foraging radius of rock-dwelling fish and crabs, which are inhibited by their own predators (larger fish such as cod, *Gadus morhua*) from moving more than a short distance from shelter.

Similar experiments carried out in the Bahamas provided further evidence in support of the predator-limitation hypothesis (Aronson & Harms, 1985). Specimens of *Ophiothrix oerstedi* transplanted from the Sweetings Pond population to nearby coastal reefs were rapidly eaten by fish. Brittlestars occurred naturally in the reef habitat but at much lower densities than in Sweetings Pond, and lived cryptically among corals rather than out in the open. Predatory fish were absent from the pond, where the only potential brittlestar predators were slow-moving invertebrates.

There is evidence that fluctuations in *Ophiothrix fragilis* populations in the western English Channel over a scale of decades may be related to changes in the abundance of the large predatory starfish *Luidia ciliaris* (Holme, 1984, Aronson, 1992). This phenomenon, and other natural events affecting brittlestar beds, will be reviewed in Chapter V.

Predation is less likely to be a controlling factor in the distribution of *Ophiocomina nigra* beds, as this species appears to secrete a distasteful mucus which offers at least partial protection from predators (Fontaine, 1964; Wilson et al., 1977). *Ophiocomina* is absent from the stomachs of most fish species caught in the vicinity of brittlestar beds (B. Ball, personal communication).

C. KEY POINTS FROM CHAPTER III

- Brittlestar beds are usually found in conditions of full marine salinity, but examples are known from brackish water bodies. Depth range is roughly 10 - 70 m. Beds may have abrupt upper or lower depth boundaries.

- Beds occur in a variety of hydrodynamic regimes. Wave exposure can be weak to moderately strong. Tidal streams may be very weak over beds in semi-enclosed water bodies, but those on open coasts are usually found in current-swept areas.

- Beds can be found on a wide range of substrata, from bedrock to sand and mud. Boulders, cobbles, gravel or coarse sand are probably the most common types. Beds are generally on level or gently-sloping substrata.

- The occurrence of brittlestar beds is not limited by temperature, except in very shallow, enclosed areas where temperature extremes may be encountered. Beds are probably inhibited by heavy sedimentation.

- There is experimental evidence that predation by fish and crabs may limit the occurrence of brittlestar beds in present-day ecosystems, as well as over geological time-scales.

IV. BIOLOGY AND ECOLOGICAL FUNCTIONING

In the coastal waters of the British Isles, dense brittlestar aggregations are a widespread and prominent feature of the benthic environment and have attracted the attention of marine ecologists since their existence was first recognized at the turn of the century (Allen, 1899). The most detailed studies of the ecology of bed-forming brittlestars have been carried out in the English Channel, but there is no reason to believe that those in other regions will behave differently. This chapter will review what is known of the ecology, behaviour and life cycles of brittlestars in subtidal aggregations, the non-brittlestar fauna associated with these beds, and the effects of brittlestar beds on the local marine environment.

A. ECOLOGY OF BED-FORMING BRITTLESTARS

1. Causes and consequences of aggregation

Brittlestars are not the only echinoderm group known to occur in dense populations: aggregations of crinoids, sea urchins and sea cucumbers have also been recorded (Warner, 1979). The relatively simple nervous and sensory systems of echinoderms have been thought incapable of producing true social behaviour, ie. the intentional association of individuals with others of their own species. Reese (1966) suggested that aggregations arose from the individual responses of echinoderms to features of the physical environment, so for example, brittlestars might congregate in areas where strong currents bring an abundant supply of food. Broom (1975) investigated this question on an *Ophiothrix* bed in Torbay, Devon, by removing individual brittlestars from the bed, placing them on bare substratum and observing their responses. Isolated animals began ‘walking’ across the prevailing current, pausing and changing direction at intervals until other brittlestars were encountered. The animals rejoined the beds and resumed feeding. Movement across the bottom was only terminated by contact with conspecifics, and not by contact with stones, weed, hydroids or *Alcyonium* colonies. These experiments demonstrate that *Ophiothrix* can recognize and respond to conspecifics, and that this social response is important for the maintenance of aggregations. The abrupt boundaries frequently shown by *Ophiothrix* beds (Brun, 1969; Warner, 1971) are also strong evidence of social behaviour, as it unlikely that discontinuities in substratum type or water flow could be sharp enough to account for them.

Broom’s (1975) experiments also demonstrated the advantages of social aggregation for individual *Ophiothrix*. In the prevailing current speeds at the site, isolated brittlestars could not maintain their position on the substratum and were swept away. The minimum group size seen to persist for one day was 35 individuals. Broom estimated that at least 100 would be necessary for long-term group survival. The enhanced stability of aggregations in fast currents was also observed by Warner (1971). At current speeds above 0.25 m s^{-1}, aggregated *Ophiothrix* ceased feeding, flattened themselves against the substratum and linked arms, this mutual support allowing the bed to maintain its position on the sea floor. At slower current speeds, the support provided by neighbouring brittlestars will allow each animal to extend more feeding arms than would otherwise be possible.

Bed formation also has reproductive advantages for the animals involved. Brittlestars reproduce by external fertilization (see below), and the success of this will be enhanced by the close proximity of large numbers of individuals.

The presence of such dense concentrations of suspension-feeding brittlestars might be thought to cause serious competition for food, but in fact the density of animals may actually increase the supply of suspended food to them. The dense forest of arms raised into the current will have a baffle effect, slowing down the rate of water flow over the bed and producing an increased deposition of food particles. Dense aggregations would be expected to provide optimum conditions for the spread of parasites or disease, but nothing is known of this aspect of brittlestar ecology.

2. Feeding

Ophiothrix fragilis feeds on plankton and suspended detritus intercepted by the tube feet of arms extended into the water column (Warner & Woodley, 1975). While feeding, the animal's disc is held just off the bottom, supported by several flexed arms, the remaining arms being raised into the passing current (Warner, 1971). More arms can be used in feeding in dense aggregations where support is provided by neighbouring animals. Material trapped on the tube feet is collected into a bolus and passed down the arm to the animal's mouth. Warner & Woodley found that the diet of *Ophiothrix* in Torbay consisted mostly of silt and detritus particles, but Brun (1969) found that diatoms were the main food on Isle of Man beds.

In the Dover Strait, Davoult & Gounin (1995a) found that current speeds below 0.2 m s^{-1} were optimal for suspension-feeding, and that feeding activity ceased if velocity exceeded 0.3 m s^{-1}. These values agree with those found by Warner (1971). In the Dover Strait, currents exceed 1.5 m s^{-1} during average spring tides, and the time available for feeding therefore varies according to the tidal cycle. Suspension-feeding by *Ophiothrix* is more or less continuous during neap tides, but the flux of particles is small because the slow current speed inhibits resuspension of material from the sea bottom. During spring tides, current speeds increase rapidly, bringing about a large resuspension of particles. Feeding bouts at these times are very brief, but more profitable to the brittlestars owing to the increased concentration of suspended matter. Growth rate of *Ophiothrix* in the Dover Strait is maximal in April/May, coincident with the spring phytoplankton bloom (Davoult & Gounin, 1995).

Ophiocomina nigra is a highly versatile feeder, able to exploit almost any available food source (Fontaine, 1965). Like *Ophiothrix*, it can capture small suspended particles, but in this case using a net of mucus strands secreted between the arm spines. Slightly larger particles are captured by the tube feet. Large particles or invertebrate prey can be actively grasped by the arms. *Ophiocomina* will also deposit-feed on benthic detritus or algal films, and will scavenge from carcasses on the sea floor. Individuals living intertidally will also use the arms to graze the detrital film at the air-water interface.

Ophiopholis aculeata has been recorded suspension-feeding on phytoplankton (Roushdy & Hansen, 1960). Brittlestars of the genus *Ophiura* are omnivorous, feeding on organic detritus, microalgae and small sediment-dwelling organisms. In Denmark, Feder (1981) found the large *Ophiura ophiura* to be quite predatory in its feeding habits, eating a wide variety of small bivalves, polychaetes and crustaceans. Tyler (1977) recorded a similar diet for specimens from the Bristol Channel, whereas the smaller *O. albida* was found to rely more on microalgae and detritus.

3. Structure of brittlestar beds

Although they may have sharply-defined boundaries, brittlestar beds do not usually comprise a uniform carpet of animals of unvarying density. Off the southern Isle of Man, the brittlestar bed studied by Brun (1969) had a mean density of 1347 animals m^{-2}, with local concentrations up to 2196 m^{-2}. Approximately 90% of these were *Ophiothrix fragilis,* the remainder being *Ophiocomina nigra* and *Ophiopholis aculeata.* In Torbay, the bed studied by Warner (1971) and Broom (1975) measured at least 1 km long by 200 m wide. Boundaries were sharp, but brittlestar distribution within the bed was very patchy. Mean density was 309 individuals m^{-2}, but denser patches of up to 1864 m^{-2} were present. Within the bed, only about 23% of the sea floor was actually covered by brittlestars. The denser patches were up to 30 m across, irregular in shape, and variable in position over time. The bed was largely composed of *Ophiothrix fragilis,* but small numbers of *Ophiocomina nigra* also occurred in discrete aggregations of their own. A third brittlestar species, *Amphipholis squamata,* was also found among small *Ophiothrix* on rock outcrops. The *Ophiothrix* population in the bed showed a bimodal size distribution (Warner, 1971), being composed of large adult animals (disc diameter 8 - 12 mm) and tiny juveniles (disc diameter < 2 mm). Animals of intermediate size were absent from the gravel plain supporting the dense bed, but occurred on rock outcrops among *Alcyonium* colonies, and in crevices on nearby vertical rock faces. In the brittlestar bed, the tiny juveniles were found clinging to the arms of the adults, where they were probably feeding semi-parasitically on material captured by the adult tube feet. At slightly larger sizes, the juvenile *Ophiothrix* apparently migrated to rock outcrops and clumps of sessile epifauna. The factors leading to this movement, and the eventual reverse migration back to the level plain environment have not been determined.

In Kinsale Harbour, southern Ireland, Ball (1991) found that *Ophiothrix* of intermediate size could be found within the genital bursae (slits on the underside of the disc) of larger adult individuals. Between 9 and 22% of adult *Ophiothrix* were found to be carrying smaller animals in this way. This phenomenon of ‘pseudo-brooding’ was also recorded by Smith (1938). Its significance is unknown.

In the Gulf of St Malo, *Ophiothrix* beds were composed entirely of two-year old animals (Allain, 1974). Animals in the centre of the beds had a larger disc diameter than those at the periphery. This difference in growth rate may reflect the suitability of conditions for suspension-feeding in different parts of the bed. In the centre, individuals can raise more arms to capture food because of the greater support provided by neighbours.

In Strangford Lough, brittlestar beds are composed overwhelmingly of *Ophiothrix fragilis*, mixed with smaller numbers of *Ophiocomina nigra* (Erwin, 1977). At the fringes of the community, the *Ophiothrix* population often ends abruptly, but *Ophiocomina* continues for some distance at about the same density as in the *Ophiothrix* bed. This phenomenon arises from a difference in the social behaviour of the two species. The highly aggregative tendencies of *Ophiothrix* have already been described. *Ophiocomina* appears to be less fond of close contact with others of its species and does not occur in such dense aggregations as *Ophiothrix*. *Ophiocomina* often adopts a regularly-spaced distribution, in which individuals with arms spread horizontally do not quite touch each other (Warner, 1979). In the western English Channel, *Ophiocomina* aggregations up to 300 m across were observed using towed underwater televison on extensive offshore plains of rippled gravel and on the smooth tops of massive rock outcrops (Wilson et al., 1977). Within these patches, individual *Ophiocomina* showed a dispersed, non-random distribution on the sea bed. The regular spacing-out of individuals was confirmed by laboratory experiments, in which animals never came to rest in close proximity to one another, and sometimes showed antagonistic arm movements when encountering conspecifics. The regular spacing of individual *Ophiocomina* broke down only at very high population densities (200 m^{-2}). Observations suggested that when mixed with

Ophiothrix, Ophiocomina individuals maintain the same type of spacing among themselves as when they occur alone.

4. Reproduction and recruitment

Ophiothrix fragilis has an extended breeding season running roughly from April to October (Smith, 1940; Ball et al., 1995). Eggs and sperm are shed into the water column and fertilization is external. Larvae are planktonic. In the Dover Strait, the main period of larval settlement is in September/October, but some settlement also occurs in February, April and June (Davoult et al., 1990). Maximum population densities (approximately 2000 individuals m^{-2}) are found during the main recruitment period in September (Davoult, 1990). A similar seasonal pattern was found by Brun (1969) in the Isle of Man, where newly-settled juveniles were found in August and September. Peak juvenile numbers occurred in November in a Bristol Channel population (George & Warwick, 1985). In Kinsale Harbour, Ireland, post-settlement juveniles could be found throughout the year, with maximum numbers (up to 1000 juveniles m^{-2}) in October (Ball et al., 1995). Mortality was high, leading to low levels of recruitment into the adult population. All studies agree that recruits initially settle on the arms of adults.

There is some disagreement concerning the life span of *Ophiothrix fragilis*. Davoult et al. (1990) suggested a life span of 9 - 20 months. Taylor (1958, quoted in Gorzula, 1977) recorded that *Ophiothrix* reached a disc diameter of about 14 mm in two years, and that most individuals died after spawning in their second summer. However, other researchers have considered the animals to be much longer-lived. Gorzula (1977) quotes evidence that Swedish *Ophiothrix* can live for up to eight years. A life span of over nine years has been suggested from counts of growth bands in the skeletal arm plates of *Ophiothrix* (Gage, 1990). It is possible that growth rates may vary widely in different areas, or that the different varieties of *Ophiothrix fragilis* recognized by French workers may have contrasting population dynamics. These inconsistencies show that even in a species as well-known as this, many basic questions still remain to be resolved.

The breeding system of *Ophiocomina nigra* appears to be somewhat more complex than that of *Ophiothrix fragilis* (Gorzula, 1979). Male and female individuals grow to about the same size, but in the spring, large female brittlestars (disc diameter 10 - 20 mm) are often found in close association with small males (mostly 5 - 10 mm diameter). The small males cling to the upper or lower disc surface of the females. In the Clyde, spawning took place over a limited period in late June. Spawning was not confined to the paired males and females, but it is possible that these acted as a ‘trigger’ for synchronized spawning of the whole population (Gorzula, 1979). *Ophiocomina nigra* appears to be a slow-growing, long-lived species spawning annually after reaching an age of 3 - 4 years, and living for up to 14 years (Gorzula, 1977). In contrast to the pattern in *Ophiothrix*, juvenile *Ophiocomina* appear not to settle among adults. The Clyde populations studied by Gorzula (1977) were each dominated by a single size-class of animals, suggesting that each *Ophiocomina* bed is formed by a single settlement of juveniles which thereafter receives little or no recruitment.

There is no detailed information available on the life cycle or population dynamics of *Ophiopholis aculeata*. Tyler (1977) found that populations of *Ophiura albida* in the Bristol Channel had a well-marked annual reproductive cycle, with spawning taking place in May and early June. Spent adults and planktonic larvae were found up to early October. This short annual reproductive period led to the occurrence of distinct size cohorts in the adult population. In contrast, the larger *Ophiura ophiura* had a more protracted breeding season, and adult size classes were less distinct. Gage (1990) suggested a life span of 5 - 6 years for

O. ophiura from the west of Scotland. Studies of growth bands in the arm plates suggested that the animals enter a phase of rapid growth in early spring, continuing until late autumn/early winter. Skeletal growth ceases during the winter (Wilding & Gage, 1995). Further details of growth rates in *Ophiura ophiura* and *O. albida* are given by Dahm (1993).

B. ASSOCIATED FAUNA

Brittlestar beds may appear at first glance to support few animals besides the brittlestars themselves. Where dense *Ophiothrix* aggregations are found on bedrock surfaces they may monopolize the substratum, virtually to the exclusion of other epifauna (Ball et al., 1995). However, beds on softer substrata may contain a rich associated fauna (Warner, 1971; Allain, 1974; Davoult & Gounin, 1995). Allain (1974) provides a list of the species found by various authors in brittlestar beds in the English Channel and Irish Sea. Large suspension-feeders such as the octocoral *Alcyonium digitatum,* the anemone *Metridium senile* and the hydroid *Nemertesia antennina* are present mainly on rock outcrops or boulders protruding above the brittlestar-covered substratum. The large anemone *Urticina felina* may be quite common. This species lives half-buried in the substratum but is not smothered by the brittlestars, usually being surrounded by a ‘halo’ of clear space (Brun, 1969; Warner, 1971). *Urticina* will eat brittlestars, hence their avoidance of it.

Large mobile animals commonly found on *Ophiothrix* beds include the starfish *Asterias rubens, Crossaster papposus* and *Luidia ciliaris*, the urchins *Echinus esculentus* and *Psammechinus miliaris*, edible crabs *Cancer pagurus*, swimming crabs *Necora puber, Liocarcinus* spp., and hermit crabs *Pagurus bernhardus*. Brittlestar beds are not a major habitat for fish, although Warner (1971) recorded poor cod *Trisopterus minutus* shoaling over the beds in Torbay. Warner found that *Ophiothrix* was preyed upon by crabs, dragonets *Callionymus lyra* and plaice *Pleuronectes platessa*, but did not seem to be a major food item for any of them. The large starfish *Asterias rubens* and (especially) *Luidia ciliaris* are also brittlestar predators, and are usually actively avoided by them. A starfish moving through an *Ophiothrix* bed is preceded by a ‘bow-wave’ of brittlestars moving out of the way.

Brittlestars of the genus *Ophiura* are known to be a common prey for flatfish such as plaice (eg. Downie, 1990).

Where brittlestar beds exist on muddy gravel or sandy substrata, the underlying sediments may contain a diverse infauna. Warner (1971) found that numbers and biomass of sediment-dwelling animals were not significantly reduced under dense brittlestar patches. Shell length of the commonest animal, the bivalve *Abra alba,* showed no correlation with the presence of brittlestars. There was thus no evidence that brittlestar beds restricted the occurrence or growth of other benthic animals. Deposit-feeding animals might even find conditions more favourable under beds as a result of the increased deposition of organic matter (from brittlestar faeces) in those areas. Similar conclusions were drawn by Allain (1974), and by Davoult & Gounin (1995), who noted that the epifaunal animal community on brittlestar-covered pebble bottoms in the Dover Strait was more diverse than nearby communities in fine sediments experiencing lower current speeds.

The larger animals found in and around brittlestar beds are all found in other coastal benthic biotopes, and there are no known examples of species dependent on the beds or obligately associated with brittlestars. However, it is not impossible that some specialist brittlestar commensals may eventually be recognized amongst the smaller fauna.

C. INTERACTION WITH THE LOCAL MARINE ENVIRONMENT

Dense beds of suspension-feeding brittlestars, in some cases extending over hundreds of square metres of sea floor and containing millions of individuals, represent significant concentrations of biomass on the sea floor. The removal of large amounts of suspended particulate matter from the water column, combined with the output of nitrogenous excretory products, can make an important contribution to the cycling of nutrients in the areas where beds occur. In the Bay of Brest, Brittany, benthic suspension-feeders, numerically dominated by *Ophiothrix fragilis* (local aggregations over 400 individuals m^{-2}) can filter the equivalent of 30% of the total water volume of the bay daily (Hily, 1991). The inflow of nutrient-rich stream water into the bay leads to very high primary productivity, but eutrophication does not occur, apparently because of the removal of particulate matter by the benthic community. Davoult et al. (1991) estimated the quantities of ammonium excreted by *Ophiothrix* beds in the Dover Strait and concluded that the beds made an important contribution to the total flux of ammonium into the water column in the area. This nutrient regeneration is a necessary component of the cycle of phytoplankton production on which most marine life ultimately depends. Further work (Davoult & Gounin, 1995b) showed that rates of ammonium release vary over the year in parallel with changes in the brittlestar biomass and feeding rate. All these parameters increase over the spring to a peak in May/June before declining again.

The possible role of brittlestar beds in other important biogeochemical cycles has been little-studied (Hutchins et al., 1996). Gounin et al. (1995) studied the transfer of heavy metals (iron, manganese, lead, copper and cadmium) through *Ophiothrix* beds. They concluded that heavy metals ingested or absorbed by the animals transited rapidly through the body and were expelled in the faeces. The brittlestars did not appear to accumulate metals in the tissues and so would not act to decontaminate the near-bottom water mass.

D. KEY POINTS FROM CHAPTER IV.

- Aggregations of *Ophiothrix fragilis* result from the active association of animals with their conspecifics, not simply from individual responses to environmental conditions.

- The advantages of living in dense aggregations include increased stability in strong currents, enhanced feeding success and ease of fertilization.

- *Ophiothrix* is primarily a suspension-feeder, trapping phytoplankton and detritus on the tube feet of arms extended into the current. *Ophiocomina* is a highly versatile feeder, able to suspension-feed, graze benthic detritus or scavenge on carrion.

- Brittlestar beds usually have a patchy internal structure, with localized concentrations of higher animal density.

- *Ophiothrix* beds may consist of large adults and tiny, newly-settled juveniles, with animals of intermediate size living in nearby rock habitats or among sessile epifauna.

- *Ophiocomina* is less tolerant than *Ophiothrix* of close contact with conspecifics. Individuals often show a dispersed, non-random distribution, this pattern only breaking down at very high population densities.

- *Ophiothrix* has a lengthy breeding season. Maximal settlement usually occurs in September/October, but some recruitment may take place at other times of year. New recruits settle on the arms of adult individuals. Life-span may be up to nine years.

- *Ophiocomina* grows slowly and lives for up to 14 years. Spawning appears to take place over a limited period during the summer. Recruits do not settle in association with adult aggregations.

- A variety of large mobile crustaceans and echinoderms can be found in brittlestar beds and the underlying substratum may support a rich fauna of smaller animals. The sediment fauna does not appear to be restricted in numbers or growth by the carpet of brittlestars, and probably benefits from the enhanced deposition of organic matter in the beds. There are no known obligate associates of brittlestar beds.

- Brittlestar beds represent major concentrations of biomass on the sea floor and may play an important role in local nutrient cycles by filtration of suspended particulate matter and excretion of nitrogenous waste.

V. SENSITIVITY TO NATURAL EVENTS

Several authors have noted that brittlestar beds are long-lasting features of the benthic environment. Brun (1969) concluded from the results of repeated sampling off the southern Isle of Man that the beds there were stable structures, and quoted local fishermens'opinion that their spatial extent had increased (the time-scale over which this increase had occurred was not given). Garner (1878) and Chadwick (1886) also provide early records of brittlestar beds from the Isle of Man. Davoult & Gounin (1995) stated that the *Ophiothrix* population in the Dover Strait had remained stable, dense, and with a precise and unchanged location for 'several years'. Cabioch (quoted in Holme, 1984) stated that beds in the eastern Channel and near Roscoff were sufficiently constant features to be given names by local fishermen. However, in most areas the lack of long-term records prevents any more precise estimation of the longevity of brittlestar aggregations. Long-term data are available only for the western English Channel. These indicate a cycle of bed expansion and contraction over a scale of decades, possibly driven by oceanographic factors and consequent changes in predator populations. In a few other locations, authors have recorded the disappearance of previously extensive brittlestar aggregations, demonstrating their sensitivity to particular forms of environmental change.

This chapter will describe the known case studies of naturally-driven fluctuations in brittlestar beds, and list the agents of change that appear to underlie them. On general biological principles, several other factors can be identified that one would expect to have the potential to affect brittlestar beds. These will also be briefly summarized.

A. RECORDED EXAMPLES OF FLUCTUATIONS IN BRITTLESTAR BEDS

1. The western English Channel: changes in predation intensity

Fluctuations in the extent of *Ophiothrix fragilis* beds in the western Channel were reviewed by Holme (1984), using records made by various workers over a period of almost a century. Dense beds were first recorded in the Eddystone area by Allen (1899), but records from the 1920s and 30s suggest that *Ophiothrix* had become much less common by that time. In the early 1950s, beds were once more recorded in the western Channel using sea-floor photography (Vevers, 1952), and these persisted until the late 1960s. From about 1970 onwards, there was a marked decline in *Ophiothrix* populations in the Plymouth area, and the formerly dense aggregations disappeared. This situation prevailed at the time of Holme's review (1984). The 1970s decrease in *Ophiothrix* populations was apparently confined to the English side of the western Channel, and no comparable decline occurred off the French coast, or in the eastern Channel.

Holme considered that the most likely factor underlying these cyclical changes was the intensity of predation by the large starfish *Luidia ciliaris*. Records of this species in the Plymouth area show a roughly inverse relationship to the abundance of *Ophiothrix fragilis* (Aronson, 1992). *Luidia ciliaris*, and the related *L. sarsi*, showed a marked increase in abundance near Plymouth during the early 1970s, the period during which the *Ophiothrix* beds were declining. Records from earlier decades are more fragmentary, but there are suggestions that the starfish were rare or absent at the times when the brittlestar beds were flourishing. The increase in *Luidia* numbers from 1970 onwards was apparently confined to the English side of the western Channel, so that *Ophiothrix* populations outside this area were not affected.

Luidia ciliaris is known to prey upon *Ophiothrix fragilis* and other echinoderms (Brun, 1972). It is uncertain whether the observed rate of feeding of *Luidia* upon *Ophiothrix* (2.4 individuals day^{-1} in Brun's laboratory study) is high enough to directly account for the disappearance of the beds, but it is likely that brittlestar mortality rates would be increased by the disruptive effect of the starfish in addition to direct predation. By breaking up the dense aggregations of *Ophiothrix*, *Luidia* would render the beds less stable and more likely to be dislodged by strong currents.

The increase in *Luidia* populations during the 1970s may have been driven by the 'Russell Cycle', a multidecadal oceanographic cycle affecting the western Channel (Russell, 1935; Southward, 1980), and expressed by changes in sea surface temperature, circulation patterns, nutrient levels and plankton communities. A change in sea conditions and plankton composition occurred off Plymouth in 1968 (Southward, 1980), probably due to the inflow of water from the Celtic Sea, and this may have brought an influx of *Luidia* larvae and created the conditions necessary for their successful development.

Ball et al. (1995) found that the stomachs of *Luidia ciliaris* specimens from Kinsale Harbour, Ireland, contained up to 13 *Ophiothrix*, but considered that the starfish had little effect on the density of the brittlestar aggregations owing to the continuous presence of juveniles able to colonize newly cleared surfaces. It is possible therefore that the cyclical changes in the western Channel might have a more complex causal mechanism, involving a failure of *Ophiothrix* recruitment as well as increased predation by *Luidia.*

2. The Gulf of Trieste: oxygen depletion

Stachowitsch (1984) observed a mass mortality of benthic organisms in the Gulf of Trieste, northern Adriatic Sea, apparently caused by the onset of severe hypoxia (oxygen depletion) in the near-bottom water. A wide variety of organisms were affected, including burrowing invertebrates, sponges, and the brittlestar *Ophiothrix quinquemaculata*, a dominant component of the local epifaunal community (Fedra et al., 1976). The area affected by hypoxia covered several hundred km^2. The mass mortality proceeded very rapidly. On September 10, 1983, no abnormal signs were visible, but by September 12 conditions had deteriorated severely. All brittlestars and sponges were dead within 2 - 3 days of the onset of hypoxia.

This event appears to have been caused by a combination of unfavourable weather and tidal conditions, coinciding with a period of maximal organic input from coastal pollution and sedimenting phytoplankton. The 1983 summer was unusually hot, and a strong thermocline had developed only 2 - 3 m above the sea bottom in the Gulf of Trieste. Water exchange in the gulf is poor, and the area tends to accumulate sediment and suspended organic material. Very high productivity in the water column, combined with sewage input throughout the summer tourist season, probably led to the consumption of most of the dissolved oxygen by microbial activity. Mortality occurred when the oxygen-deficient water mass extended to the sea floor.

3. The Oosterschelde Estuary: temperature

Leewis et al. (1994) described fluctuations in the abundance of *Ophiothrix fragilis* in the Dutch Oosterschelde Estuary over the period 1979-90. These changes appeared to be driven by winter temperatures. Following the mild winters of 1979-80 and 1987-88, populations of brittlestars increased enormously, the animals occupying 60 - 90% of the available hard substratum in layers up to 5 cm deep. Populations were greatly reduced (to less than 10% spatial coverage) following cold winters in 1978-79, 1984-85 and 1985-86. The populations undergoing these changes were living in very shallow water (5 - 7 m depth) and were therefore vulnerable to spells of unusually cold weather.

4. Relevance of these examples to beds in other areas

The cyclical changes in the western English Channel show that dense populations of brittlestars can persist for several decades, but may also decline sharply in the space of a few years and remain at low levels for a decade or more if conditions remain unfavourable. These changes appear to be natural in origin, and associated with large-scale oceanographic cycles (mediated through changes in predator populations). It is possible that analogous processes operate in other areas, but have not been detected due to the absence of comparable long-term records.

The examples from the Gulf of Trieste and the Oosterschelde Estuary are probably of more limited general relevance. Hypoxia of the severity described in the Adriatic is extremely unlikely to occur in the current-swept environments typical of most brittlestar beds around the UK and Ireland, although the necessary combination of environmental conditions (poor water circulation, high organic input) can be found in sea lochs or other semi-enclosed localities. The majority of brittlestar beds are found in much deeper waters than those of the Oosterschelde, and are therefore better insulated from exposure to extremes of temperature.

B. OTHER POTENTIAL AGENTS OF CHANGE

1. Physical disturbance by storms

It is conceivable that severe storms could break up and scatter individual brittlestar beds. However, the decadal persistence of beds in areas such as the western Channel shows that at this geographic scale, populations can withstand the annual extremes of weather.

2. Pathogens or parasites

Dense aggregations of brittlestars would seem to offer ideal conditions for the rapid spread of pathogenic organisms or parasites, but so far no examples of this have been recorded. However, several examples are known of echinoderm populations that have been massively reduced by sudden oubreaks of epidemic disease. Cases include the mass mortality of the sea urchin *Diadema antillarum* throughout the Caribbean as a result of infection by a water-borne pathogen (Lessios, 1988), and the decimation of urchin populations in the North Atlantic by parasitic amoebae and nematodes (Hagen, 1995). Epidemic disease should therefore be considered as having the potential to significantly affect populations of bed-forming brittlestars.

C. KEY POINTS FROM CHAPTER V

- Reports from several areas suggest that brittlestar beds can persist over periods of years, but longer-term cycles of change have been detected only in the western English Channel.
- Populations of *Ophiothrix fragilis* in the Plymouth area appear to vary inversely with the abundance of the predatory starfish *Luidia ciliaris*. The abundance of *Luidia* in its turn may be determined by decadal-scale oceanographic changes in the western Channel.
- Examples are known of the rapid destruction of *Ophiothrix* aggregations by water column oxygen depletion and unusually severe winter temperatures. These factors are likely to operate only in shallow, semi-enclosed water bodies with poor circulation, and will not be found in deeper or better-flushed environments.
- Epidemic disease is a factor that can sharply reduce populations of echinoderm species over wide geographic areas, but so far no instances have been recorded among brittlestars.

VI. SENSITIVITY TO HUMAN ACTIVITIES

There are very few recorded examples of brittlestar beds being directly affected by human activities. Most of this chapter therefore consists of a summary of the factors that could be expected to have an influence on these biotopes. There are no detailed case studies but the few relevant observations are mentioned where appropriate.

A. HUMAN ACTIVITIES POTENTIALLY AFFECTING BRITTLESTAR BEDS

1. Fishing

Brittlestars themselves are of no economic value, and their aggregations are not significant habitats for any commercially-important fish or shellfish. Fishermen tend to avoid areas with dense brittlestar populations because the animals foul their nets (Aronson, 1989). There is consequently little likelihood of damage to brittlestar beds by fishing activities. Aronson & Harms (1985) speculated that human overexploitation of fish resources could favour the spread of brittlestar aggregations by reducing predation pressure on the animals. The seas around the British Isles, in which brittlestar beds are common, have certainly been the sites of intensive fishing activity for many decades. There is no evidence of any causal connection between these two aspects, but it is not impossible that human activities may be changing the ecology of the British seas in ways that favour particular benthic communities. Lindley et al. (1995) described changes in the zooplankton of the North Sea over the past few decades, specifically a marked increase in the proportion of echinoderm larvae (brittlestars and sea urchins) relative to copepods. The increased dominance of echinoderms was apparent from the early 1980s onwards, beginning over the Dogger Bank and extending northwards to the level of southern Scotland. The sediment-dwelling brittlestar *Amphiura filiformis* accounted for most of the larval echinoderm increase over the Dogger Bank. Suggested human-induced causes of this phenomenon were increased eutrophication of the North Sea, and a reduction in predation pressure caused by overfishing. Demonstration of a cause-and-effect relationship in cases such as this is difficult, but both processes might conceivably have similar effects on the abundance of epifaunal brittlestars such as *Ophiothrix* and *Ophiocomina.*

2. Organic pollution and eutrophication

The input of dissolved nutrients or particulate organic matter (eg. from sewage or aquaculture waste) to coastal areas may in some cases favour the proliferation of brittlestar beds by increasing the supply of suspended food (Hily, 1991). Raymont (1950) recorded an increase in *Ophiocomina nigra* populations following the addition of fertilizers to the waters of an enclosed basin of Loch Sween, Argyll. However, high levels of organic enrichment would be expected to have deleterious effects on brittlestars and other suspension feeders by excessive sedimentation and hypoxia. Organic pollution may well have contributed to the environmental oxygen depletion causing mass mortality of brittlestars in the Gulf of Trieste (Stachowitsch, 1984). The imprecision of these statements regarding the levels of organic input having beneficial or harmful consequences for brittlestar beds reflects the lack of any quantitative study of the question. Logically, the tolerance of beds to organic pollution should depend on the local geography and hydrodynamic regime, with highest tolerance in open-coast, well-flushed areas.

The expansion of cage aquaculture of Atlantic salmon along the fiordic coastlines of western Scotland and Ireland over the past few decades has led to increased local inputs of organic material into many semi-enclosed water bodies (sea lochs/loughs) (Black, 1996). The effects of this on brittlestar beds have not been studied in detail, but some relevant observations have been made in Killary Harbour, western Ireland (Keegan & Mercer 1986). A dense aggregation of *Ophiothrix* and *Ophiocomina* was recorded in 1974 from a site at the mouth of the harbour, mainly on rocky outcrops but extending out onto adjacent sandy silt areas. A salmon farm was established at the site in the late 1980s, within 100 m of the main beds. Despite the presence of this farm for the past ten years, the extent and density of the brittlestar beds appear not to have changed (B. Ball, personal communication), although an increase in siltation has taken place.

3. Other pollutants

It is logical to suppose that brittlestar beds would be adversely affected by major pollution incidents such as oil spills, or by continuous exposure to toxic metals, pesticides, or the anti-parasite chemicals used in cage aquaculture. The water-accumulated fraction of diesel oil has been found to be acutely toxic to *Ophiothrix fragilis* and *Ophiocomina nigra* (Newton, 1995). So far, however, there are no field observations of epifaunal brittlestar beds being damaged by any of these forms of pollution.

4. Coastal alteration

Aronson (1989) refers to the demise of Warner's (1971) *Ophiothrix* bed in Torbay, and tentatively attributes this to increased sedimentation caused by the localized dumping of construction materials. There appear to be no published details of this, but human alteration of the coastal environment clearly has the potential to affect brittlestar beds and other benthic communities, particularly if this involves changes to important parameters such as current regime and sedimentation rate. The potential effects of dredging and other forms of coastal engineering on benthic biotopes is an area requiring more detailed study.

5. 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). No biological invasions of relevance to brittlestar beds have been detected, but the possibility that such an event might occur in the future cannot be discounted. As an example of what can occur, the mass mortality of the sea urchin *Diadema antillarum* throughout the Caribbean during the period 1983-84 may have been caused by an exotic pathogen introduced in ballast water by a ship transiting the Panama Canal (Lessios, 1988).

B. KEY POINTS FROM CHAPTER VI

- There are very few recorded instances of brittlestar beds being directly affected by human activities.

- Brittlestar beds are not exposed to damage by fishing activities. It has been suggested that human overfishing might promote the spread of these communities by reducing predation pressure, but so far there is no firm evidence for this.

- Moderate levels of organic input to the sea may be beneficial to suspension-feeding brittlestars but excessive enrichment is likely to be harmful. The threshold levels of organic input causing these effects have not been determined, and are likely to depend on local hydrography.

- Other forms of marine pollution can be expected to harm brittlestar beds, but so far there are no recorded examples of this occurring. Coastal alteration could affect local brittlestar populations, either positively or negatively (eg. increased sedimentation from dredging), depending on the nature of the changes.

- Introduced organisms (especially pathogens or parasites) are a potential threat in all coastal communities. So far, brittlestar beds have not been affected, but the example of Caribbean *Diadema* suggests that even abundant and widespread species can be vulnerable.

VII. MONITORING AND SURVEILLANCE OPTIONS

A variety of techniques exists for surveying subtidal 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 study of brittlestar beds.

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, then towed over, or dropped to, the sea bottom before being hauled back aboard with a sample of the substratum and associated fauna. Brittlestar beds tend to occur on fairly hard grounds consisting of pebbles, gravel or coarse sediments, often strewn with boulders or rock outcrops. For this type of substratum, the Naturalist’s dredge (Holme, 1971) is the most commonly-used sampling device. This takes a superficial scrape from the sea bottom, and will not penetrate the substratum unless this is very soft. If towed over a dense brittlestar bed, the dredge will bring up enough animals to demonstrate the general nature of the community, but accurate estimation of densities is not possible. Quantitative sampling can be achieved using one of several types of grab (Holme, 1971), which sample a known area of substratum and its biota. Grab sampling will not generally be possible where the sea floor consists of anything firmer than shell gravel (eg. large cobbles, boulders or bedrock).

Remote sampling is useful for demonstrating the existence of a brittlestar bed if the presence of such a community is suspected. Much of the data reviewed by Holme (1984) was collected by grab and dredge sampling in the western English Channel. The spatial extent of an aggregation could be established by sampling at points along one or more transects, but this is likely to be very time-consuming. The use of a towed dredge also has the disadvantage that its passage may be highly destructive to the structural integrity of the brittlestar bed and may lead to the displacement of animals by water currents.

Advantages and disadvantages of remote sampling

Advantages

- Grab sampling allows precise measurement of faunal densities
- No depth or time limitations on sampling
- Field operation relatively simple
- Standard equipment widely available from marine laboratories and research institutes

Disadvantages

- Use may be limited by bottom type (too hard) or topography (too irregular)
- Establishment of the spatial extent of beds may be very time-consuming. Abrupt boundaries will be very difficult to detect.
- Dredges may be destructive to brittlestar beds

2. Diving

SCUBA diving has been used increasingly since the 1970s for field studies of subtidal biotopes. Diving has also been the mainstay of the MNCR biotope surveys around the UK. The overwhelming advantage of the technique as applied to brittlestar beds is that it allows close-up observations and field experiments (eg. Warner, 1971; Broom, 1975; Aronson, 1989). 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 30m, and most field studies of brittlestar beds 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 such as 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 hundreds of metres. Many brittlestar beds are in areas swept by strong tidal currents, which will severely constrain the time divers can spend on a site. The use of suction-samplers (air-lifts) by divers offers another method for sampling the benthos from brittlestar beds, particularly on rocky substrata where ship-borne grabs cannot be used. Suction samplers provide a fast and efficient means of collecting a quantitative sample of brittlestars and associated fauna. They can also be used in gravel, cobble and sandy areas.

Advantages and disadvantages of diving

Advantages

- Allows first-hand behavioural observations and field experiments
- Allows quadrat measurements of animal densities
- Allows repeated monitoring of fixed study sites
- Equipment widely available, relatively inexpensive compared with ROVs or towed video
- Can be carried out from small boats or from shore

Disadvantages

- Strict depth and time constraints. Also prevented by strong currents
- Has potential physical hazards (eg. decompression sickness)
- Operations subject to strict legislative controls
- Only possible to cover small areas on individual dives

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 sledge 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. 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 sled within view of the camera. Analysis of the resulting videotapes usually consists of counting the features of interest within a strip of known width traversed by the moving camera sled. 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). A time-lapse still photographic camera is often mounted on a video sledge to provide an additional record (usually with better resolution than the video images) at intervals along the tow path.

Although the equipment required for towed video surveys is relatively simple, it is expensive and generally confined to large marine laboratories or academic institutions. The technique has been used to survey brittlestar aggregations in Strangford Lough (Magorrian et al., 1995) and the western English Channel (Wilson et al., 1977), but its application is limited to areas of level sea bottom without too many boulders or rock outcrops. Many brittlestar beds occur on grounds where towed video could not be used without serious risk to the equipment.

Advantages and disadvantages of towed video

Advantages

- Able to survey large expanses of sea floor quickly
- Allows precise density measurements of features of interest
- No depth or time constraints (in coastal waters)

Disadvantages

- Equipment needs hard boat to operate. May be unable to access very shallow waters or enclosed inlets
- Equipment readily available but expensive
- Deployment may be constrained by sea bed topography

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 acheived 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 slightly more difficult than from a towed video recording, as an ROV will not always remain at a fixed distance from the substratum, and the field of view may therefore change. Some models of ROV have mechanical ‘arms’ controlled by the surface operator and so have some capacity to take benthic samples. ROV deployment may be restricted by strong water currents.

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
- Deployment areas less restricted than towed video. Can be used 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 and not widely available
- May be difficult to employ in areas with strong water currents
- Sampling is non-random, ie. areas for observation are selected by the operator, with consequent potential for bias in density estimations

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 analyze 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. The technique therefore clearly has enormous potential for rapid mapping of marine benthic habitats.

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 frequent 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, brittlestar aggregations were identified and mapped. Acoustic survey is a rapidly-evolving field of marine technology and alternative systems with enhanced capabilities are likely to appear in the 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

Disadvantages

- Equipment needs a hard boat to operate. May be unable to access very shallow waters or enclosed inlets
- Equipment expensive and not widely available
- 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 following table summarizes the capabilities of the various monitoring techniques, with respect to the study of brittlestar beds.

	Remote sampling	**Diving**	**Towed video**	**ROV**	**RoxAnn™**
Equipment widely available	Yes	Yes	Yes	No	No
Hard boat required	Yes	No	Yes	Yes	Yes
Physical hazards	No	Yes	No	No	No
Depth/time limitations[1]	No	Yes	No	No	No
Geographic constraints[2]	Yes	No	Yes	Yes	Yes
Seabed topographic constraints[3]	Yes	No	Yes	No	No
Sample collection	Yes	Yes	No	Yes (some models)	No
Close-up observation	No	Yes	No	Yes	No
Areal coverage	Very low (per grab sample)	Low	Very high	High	Very high
Faunal density measurement	Yes	Yes	Yes	Yes	No

1. Refers to depths likely to be encountered in UK coastal waters (ie. < 200m)
2. Access to very shallow water or narrowly enclosed inlets
3. Deployment constrained by submarine obstructions

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 extent and composition of brittlestar aggregations 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, DO/NI) from the JNCC, and ideally also from co-workers in academic institutions or public sector marine laboratories.

Establishment of the existence of brittlestar beds within an SAC or any other defined coastal area is likely to be fairly easy. Initial information can come from historical records, local fishermen, diving surveys, remote sampling or camera observations. This stage has been achieved for the candidate SACs covered here. The basic composition of the community is also easily established, as the major bed-forming brittlestars are distinctive and unlikely to be confused with each other. Other large epifauna such as crab and starfish species can be readily identified first-hand in the field or on videotape. If the beds are to form part of an overall SAC biotope monitoring programme, the most important parameters to measure will be the spatial location and extent of these features and the population density of brittlestars within them. The occurrence of potential agents of change (eg. predators such as *Luidia ciliaris*) and the scale of human activities in or near the SAC (eg. sewage outfalls, salmon farms) will also form part of the programme.

1. Monitoring techniques

Measurement of the spatial extent of beds over large areas could be achieved using RoxAnn^{TM}, towed video or ROV. In practice, many beds will be located on grounds where the use of towed video is difficult or impossible, and RoxAnn^{TM} may prove to be the most effective method. For ground-truthing of RoxAnn^{TM} findings, ROV observations are probably advisable as a standard method, since many beds are in waters beyond effective diving range. Even where depth allows, diving is probably unnecessary for routine monitoring unless is it desired to collect brittlestars or to sample the fauna underlying the beds. Brittlestar densities can be estimated from ROV recordings, unless the beds are extremely dense (ie. with multiple layers of animals), in which case grab sampling could be carried out at selected points (where substratum type allows) across the extent of the aggregation.

RoxAnn^{TM} can clearly distinguish dense *Ophiothrix fragilis* aggregations (Magorrian et al., 1995), but is less likely to detect relatively low-density beds such as those commonly formed by *Ophiocomina nigra*. Where these are present, visual surveys using methods appropriate to the depth and substratum type (towed video, ROV or diving) will be the best techniques to use.

2. Monitoring objectives

Quantitative measurement of the extent and density of a brittlestar bed on a yearly or twice-yearly basis, over a period of several years, would be a relatively simple undertaking, but is one that has seldom been carried out. Data of this kind would reveal whether any changes are taking place that can be related to coastal modifications, predator abundance, nearby inputs of organic matter, or other pollutant sources. On *Ophiothrix* beds, monitoring of recruitment would also be valuable and could be achieved quite easily by counting juveniles on the arms of adult brittlestars collected during the peak settlement period (September/October).

The basic elements of a monitoring programme for a brittlestar bed should be (with appropriate techniques indicated):

a. Spatial location and extent of beds (RoxAnn^{TM}, ROV)

There are no quantitative records of long-term changes in the size and location of individual brittlestar beds (as opposed to broader-scale observations of their presence in a particular geographic area). Previous mapping exercises have not been sufficiently detailed to determine whether beds show subtle changes in location over time. RoxAnn^{TM} mapping will be the most appropriate method to use for dense *Ophiothrix* beds with a strong acoustic ‘signature’. Lower-density aggregations such as those typical of *Ophiocomina* or *Ophiura* will require visual observation, for which an ROV is probably the tool most useful in the likely range of environmental circumstances.

b. Brittlestar population density (Grab-sampling, diving, ROV)

ROV observations will often allow the measurement of brittlestar densities, but the non-random selection of counting areas may introduce some bias in the results. Grab-sampling at randomly-selected points (or, better still, at regularly-spaced points along one or more transects) within the mapped extent of a brittlestar bed will eliminate this source of bias, and allow estimation of the degree of patchiness within the bed. If the substratum is unsuitable for the use of a grab, diver counts (or suction-sampling, in very dense aggregations) in quadrats at points along a transect could be made if water depth allows. If water depth is too great for diving and the substratum too hard for grab-sampling, densities will have to be estimated from ROV recordings, with care taken to avoid bias in the areas of sea bottom used for counting.

The various bed-forming brittlestar species are easily recognized and the species composition of a mixed bed can therefore be determined from visual observations or grab samples.

The same methods and qualifications will apply if it is intended to record the densities of large epifauna such as crabs and starfish within the brittlestar bed. In this case, measurements of densities in areas outside the brittlestar bed could be made for comparative purposes.

c. Brittlestar population structure and recruitment (Grab- or diver sampling)

For *Ophiothrix fragilis*, rates of recruitment could be quite easily monitored by counting the numbers of newly-settled juveniles found on the arms of a sample of adult brittlestars collected using a grab or by divers (depending on the substratum). The best time to carry out such a survey would be in September/October, the period of peak recruitment indicated in most studies.

Regular monitoring of population structure in any species would involve measurement and analysis of body size (represented by disc diameter) in samples of animals collected at intervals throughout the year (eg. Ball et al., 1995). This would probably be too time-consuming to be included within a routine SAC monitoring programme, and is more within the capabilities of a marine research laboratory or other academic institution.

3. Interpretation of change

Care will be needed when monitoring spatial extent and population density of beds. Due to the patchy distribution of brittlestars within many beds, and the fact that patch sizes and locations will change over time, there may be a danger of confusing natural changes with those caused by human activities. It would be advisable to monitor for a number of years to establish a baseline, prior to any attempt to interpret changes.

The limited information available suggests that the abundance of predators (particularly *Luidia ciliaris*) will be the most important naturally-occurring agent of change to be included within a monitoring programme. Starfish abundance can be easily estimated by diving or ROV surveys. With respect to monitoring human-induced effects, the activities with the greatest potential to cause change in bed location and extent are probably organic pollution (eg. from sewage disposal or aquaculture) and coastal alteration processes such as dredging or breakwater construction. The extent of these activities in and around a marine SAC will presumably be routinely monitored at each site, and their effects can be assessed against simultaneous records of the location and extent of brittlestar beds in the area.

C. KEY POINTS FROM CHAPTER VII

- Several techniques are available for determining the extent and composition of brittlestar beds. Towed video surveys are likely to be limited by sea bed topography, and diving surveys by depth and currents. ROVs are not subject to these constraints. RoxAnn^{TM} is an effective means of mapping the extent of dense *Ophiothrix* beds, but must be 'ground-truthed' using other methods.
- For basic mapping of the biotope complex within an SAC, a RoxAnn^{TM} survey backed up by ROV observations is recommended.
- For monitoring purposes, measurements of the spatial extent and density of brittlestar aggregations can be made relatively easily using RoxAnn^{TM}, visual surveys and/or grab sampling. Apprropriate methods will be determined by the type of bed, water depth and substratum.
- In addition to brittlestar densities, the numbers of other epifauna, especially predators, should be recorded, and human activities having the potential to cause changes (eg. coastal modification, organic pollution) also monitored.

VIII. GAPS AND REQUIREMENTS FOR FURTHER RESEARCH

The ecological functioning of brittlestar beds, and the biology of the main bed-forming species, are quite well-known in comparison with many other subtidal communities. The major gaps in knowledge relate to the temporal persistence of beds (long-term data exist only for the western English Channel) and to the effects of human activities on them. Brittlestar beds have a number of characteristics that would make them useful indicators of change in the coastal environment of the British Isles, and the monitoring of beds could potentially be included in the management schemes of several candidate SACs.

A. BRITTLESTAR BEDS AS COASTAL INDICATORS

Useful characteristics include the following:

- They are easily-defined biotopes, dominated by one or a few species, whose biology and ecological requirements are relatively well-known.
- Beds are large, conspicuous and relatively easy to detect and monitor.
- They are widespread around the British Isles (with the same dominant species), making regional comparisons possible.
- They are known to persist for long periods (years to decades), but can also decline and disappear rapidly if conditions change.
- Fluctuations have been shown to be related both to large-scale hydrographic processes (western English Channel), and to short-term, localized events (hypoxia in the Gulf of Trieste). They can therefore indicate environmental change at a range of scales.

The potential of brittlestar beds as indicators could be most effectively fulfilled by monitoring the size and composition of beds at a range of localities around the UK, supplemented by information on local hydrography and degree of exposure to relevant human impacts (eg. pollution sources). In addition to the large-scale biotope characteristics considered in this report, other features of brittlestars may make them useful indicators of water quality in the coastal environment. Some species of brittlestars (and many other echinoderms) harbour symbiotic bacteria in their skin tissue (Kelly & McKenzie, 1995). There is evidence that exposure to hydrocarbon contaminants derived from oil-based drilling muds causes a decrease in the numbers of these sub-cuticular bacteria (Newton 1995; Newton & McKenzie, 1995), making this a potential assay for environmental stress in brittlestars.

The suitability of the various candidate SACs for monitoring purposes will be considered in the next chapter.

B. SIGNIFICANCE OF BEDS IN COASTAL ECOSYSTEMS

It would be valuable and instructive to have more information on the role of brittlestar beds in the coastal environment, in particular on the quantities of carbon and nutrients that are cycled through this component of the ecosystem. This aspect of brittlestar ecology has been little-studied, but the existing data suggest that beds may make an important contribution to local ecosystem functioning (Ott & Fedra, 1977; Davoult et al., 1991; Hily, 1991). An evaluation of their role would require measurements of parameters such as local primary productivity, bed biomass and productivity, feeding and excretion rates and assimilation efficiency. A study of this kind would be too complex to be included in a routine SAC monitoring programme, but could be usefully carried out by academic researchers at a suitable SAC.

IX. SYNTHESIS AND APPLICATION TO MARINE SAC MANAGEMENT

The preceding chapters have reviewed the available information on the distribution and ecology of brittlestar beds, 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 these biotope occur, 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 the 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 brittlestar beds. 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 is the *Ophiopholis*-dominated variant MCR.Oph.Oacu, which is found at a small number of sites in Scotland and Ireland. *Ophiopholis aculeata* itself is more widespread and cannot be considered a rare species. There are no other rare species known from these biotopes.

b. In decline or have been

Brittlestar beds as a whole are not known to be currently declining. Fluctuations have been recorded in the past, but these appear to be cyclical, and purely natural events.

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

The UK and Ireland are undoubtedly areas of global importance for shallow-water epifaunal brittlestar beds, a relatively rare biotope on a world scale (Aronson, 1989).

d. Particularly good or extensive examples of their type

The frequency and extent of brittlestar beds around the British Isles, compared with their relative rarity in other parts of the world, means that they can be considered the ‘classic’ examples of their type.

e. Keystone species providing a habitat for other species

Brittlestars are clearly the ‘keystone’ species of these biotopes, but this is true only in a trivial sense, given that the biotopes themselves are specifically defined on the basis of mass brittlestar occurrence. The beds do provide a habitat for other species, but none are known to be unique to this community.

f. Biotopes with a particularly high species richness

Beds on sedimentary substrata may support a higher density and species richness of infauna than nearby brittlestar-free substrata, but this is probably not a feature of major conservation importance. The unique and important features of brittlestar beds relate to the brittlestars themselves rather than the associated fauna.

g. Biotopes important for the efficient functioning of regional ecosystems

There are indications that brittlestar beds may be important components of the carbon and nutrient cycles in their local ecosystems, but there are not yet sufficient data to evaluate this role fully.

h. Of high aesthetic, symbolic or recreational importance

Brittlestar beds do not possess any features within this category.

This assessment leads to the overall conclusion that the conservation importance of subtidal brittlestar beds lies in:

- The restricted distribution of the biotope MCR.Oph.Oacu
- The British Isles contain a large proportion of the known shallow-water epifaunal brittlestar beds, and these are the best-known examples of their type.
- Large beds may be locally important elements in ecosystem functioning.

The scientific importance of brittlestar beds and their potential usefulness as biological indicators have been discussed in Chapters I and VIII.

2. Sensitivity

The cyclical fluctuations in the extent of beds in the western Channel, and the mass mortality of brittlestars in the Gulf of Trieste show that these aggregations are sensitive to environmental changes at a range of scales. Sensitivity to pollutants such as oil, pesticides or heavy organic enrichment has not been demonstrated in the field but can be considered likely.

3. Feasibility of management

It is unlikely that active steps could be taken to manage brittlestar beds in large, open-coast areas such as the western English Channel, other than through generic measures designed to maintain the overall quality of the marine environment. In geographically more restricted areas such as sea lochs, local controls could be considered on activities such as the use of anti-parasite chemicals in fish farms, if these were specifically shown to be affecting brittlestar beds or other benthic biotopes.

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

In the following sections, ‘status and monitoring value’ summarizes the extent of our current knowledge of the biotope complex in each SAC, makes a provisional assessment of the relative importance of the site from a conservation-related perspective, and assesses its usefulness to a brittlestar bed monitoring scheme of the type outlined in Chapter VIII.

1. Papa Stour

a. Status and monitoring value

The presence of an *Ophiocomina* bed has been noted. This was recorded on algal-crusted rock ridges at about 25 m depth (Howson, 1988). The substratum, depth, and the strong tidal streams in the Sound of Papa indicate that use of an ROV would be the most appropriate means of gaining further information on the extent and density of brittlestar aggregations here. This might be a good site to include in a monitoring programme, as it occupies a near-pristine environment close to the northern geographic limits of the UK. The diverse bed off the island of Foula (Howson, 1988) should also be investigated further, owing to the unsusually high diversity of brittlestar species recorded in it.

b. Potential management concerns

There are probably no likely human impacts in this area, other than those associated with unpredictable major pollution events such as the *Braer* oil spillage.

2. Loch nam Madadh

a. Status and monitoring value

Brittlestar aggregations here appear to be localized and not very extensive. Their conservation importance in this area (and value for monitoring purposes) is therefore probably low.

b. Potential management concerns

The density of human habitation in the Loch nam Madadh 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. Significant human impacts on brittlestar aggregations in the area appear unlikely.

3. 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. The brittlestar aggregations appear to be confined to rock and boulder patches, and occupy only a small proportion of the benthic environment. This site is therefore not of major importance for these biotopes.

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. As in Loch nam Madadh, there are probably no current management concerns relevant to brittlestar beds.

4. Strangford Lough

a. Status and monitoring value

The biological diversity and recognized conservation importance of Strangford Lough have led to its major biotopes being mapped in some detail (Erwin, 1977; Magorrian et al., 1995). *Ophiothrix* and *Ophiocomina* aggregations are extensive, occupying a large area towards the mouth of the lough. Strangford Lough is therefore a potentially useful site for monitoring of these features. The work of Magorrian et al. (1995) shows that RoxAnn ^{TM} is an effective tool for mapping the extent of these dense beds.

b. Potential management concerns

Strangford Lough supports a much larger human population than any 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. It would be interesting to monitor the extent and density of the brittlestar beds in relation to any future changes in the volume of organic effluent discharged into the lough.

Some parts of Strangford Lough have been heavily impacted by trawling for the queen scallop *Aequipecten opercularis* (Service & Magorrian, 1997). The greater part of the area showing the physical effects of trawl activity lies to the north of the lough's brittlestar beds, and so far these appear not to have been damaged.

5. Morecambe Bay

Little has been recorded concerning the extent and history of the *Ophiothrix* beds in this area. The observation that the bed on Roa Island appears to be expanding is interesting and deserves further investigation, particularly with respect to the effect that this may have on the existing benthic communities. The Irish Sea coasts in this area experience a variety of significant human impacts, including sewage pollution, and monitoring of brittlestar beds here could usefully add to our presently limited knowledge of the effects of human-induced environmental change on this biotope.

6. Llyn Peninsula

a. Status and monitoring value

There is no detailed information available on the extent of brittlestar beds around the Llyn Peninsula. This situation could be rectified using a combination of RoxAnn^{TM}, diving and ROV surveys. The relative importance of the area for the biotope and its potential as a monitoring site cannot therefore be assessed at present.

b. Potential management concerns

The overall human impact on brittlestar beds around the peninsula is likely to be very low at present. Expansion in oil or gas extraction in the Irish Sea may be the most likely future source of concern, if any developments take place in this particular area.

7. The Wash & North Norfolk Coast

a. Status and monitoring value

The *Ophiura* aggregations in the Wash are well-documented but have not been subjected to detailed scientific study. Little is known of their dynamics but they could form part of a monitoring programme for the site. Visual observations or remote sampling would be the required methods, as beds of this kind are unlikely to be detected by acoustic surveys.

b. Potential management concerns

The Wash is subjected to a wide variety of human influences. The lack of detailed information on the ecology of the *Ophiura* aggregations precludes any current assessment of the likely impact of human activities upon them.

8. Berwickshire & North Northumberland Coast

a. Status and monitoring value

Brittlestar beds have been shown to be very extensive along this coast, occurring on a variety of substrata, and to include examples dominated by *Ophiothrix fragilis, Ophiocomina nigra* and *Ophiura albida* (Pagett, 1984; Foster-Smith et al., 1996). This candidate SAC probably contains some the best examples of such beds in any of the 'demonstration' sites, and should therefore be included in any planned monitoring programme.

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. Overall, however, the North Sea is heavily influenced by human activities, and it would be valuable to have long-term data on the response of brittlestar beds to future trends in water quality and pollutant concentrations along this coast.

C. OTHER CANDIDATE OR POSSIBLE SACs

Of the localities designated as candidate or possible SACs, the Loch Alsh/Duich/Long system contains the only examples of *Ophiopholis*-dominated beds (biotope MCR.Oph.Oacu). This enhances the conservation importance of the site. It would be interesting to know more of the dynamics of these beds, for comparison with the more common and better-studied *Ophiothrix*-dominated examples. At the time of Connor's (1989) report there appeared to be little threat to the biotopes of this loch system, although he noted that leases for salmon farms had been granted in Lochs Alsh and Duich. An expansion of fish farming in the area might have some adverse effects on the benthic communities due to the highly-enclosed situation of the lochs. Monitoring the effects of any new aquaculture developments should therefore be the highest managment priority if the site is designated as an SAC.

D. SUMMARY TABLE

The table below summarizes 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 eight 'demonstration' candidate SACs, and one possible SAC (Loch Alsh/Duich/Long system).

Papa Stour	**Status:** Possibly a good example of an *Ophiocomina* bed in a near-pristine environment. **Monitoring value:** High, owing to nature of environment and geographic location. **Potential management concerns:** Probably none at present.
Loch nam Madadh	**Status:** Localized *Ophiothrix* aggregations. Better examples known

	elsewhere. **Monitoring value:** Low **Potential management concerns:** Probably none at present
Loch Alsh etc.	**Status:** Good examples in a near-pristine environment. Contains biotope (*Ophiopholis* beds) of national conservation importance. **Monitoring value**: High, owing to rarity of biotope and nature of environment. **Potential management concerns:** Probably none at present, but expansion of aquaculture should be monitored.
Sound of Arisaig	**Status:** Localized *Ophiothrix* and *Ophiocomina* aggregations. Better examples known elsewhere. **Monitoring value:** Low **Potential management concerns:** Probably none at present.
Strangford Lough	**Status:** Extensive and dense *Ophiothrix* beds (with *Ophiocomina*). Good examples of the biotope. **Monitoring value:** High, owing to extent of biotope and range of human activities in the area. **Potential management concerns:** Scallop dredging
Morecambe Bay	**Status:** At least one sizeable *Ophiothrix* bed known. Little detailed information. **Monitoring value:** High, may give valuable information on response to human-induced change in coastal waters. **Potential management concerns:** Unknown. Area heavily influenced by human activity.
Llyn Peninsula	**Status:** *Ophiothrix* beds known to occur, but extent and relative importance poorly-known. Monitoring value uncertain. **Monitoring value:** Unknown, but further information highly desirable. **Potential management concerns:** Probably none at present.
The Wash & North Norfolk Coast	**Status:** Extensive *Ophiura* beds, ecology poorly-known. **Monitoring value:** May be useful for monitoring quality of the site. Not readily comparable with *Ophiothrix*-dominated beds owing to differnces in the ecology of these genera. **Potential management concerns:** Unknown, possibly none at present.

Berwickshire & N. Northumberland Coast	**Status:** Extensive beds on a variety of substrata. *Ophiothrix, Ophiocomina* and *Ophiura*-dominated examples present. **Monitoring value:** High, owing to extent of biotope and geographic location (sea area subject to strong human influence). **Potential management concerns:** Probably none at present.

It can be seen from the table that the most important SACs for representation of the biotope complex, and value for future monitoring purposes, are Papa Stour, the Loch Alsh system, Strangford Lough, Morecambe Bay, the Berwickshire/North Northumberland Coast, and possibly the Llyn Peninsula. Loch nam Madadh and the Sound of Arisaig are of much lower importance. The *Ophiura* beds in the Wash are directly comparable only with the *Ophiura*-dominated examples from Berwickshire, but could play a part in the monitoring scheme for this SAC and deserve further study.

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