

Marine Aggregate Levy
Sustainability Fund (MALSF)

Science Monograph Series: No. 3

Marine
Aggregate Levy
Sustainability Fund
MALSF



Biogenic Reefs and the Marine Aggregate Industry

by Hendrick, V. J., Foster-Smith, R. L. & Davies, A. J.



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Background to the fund

In 2002 the Government imposed a levy on all primary aggregates production (including marine aggregates) to reflect the environmental costs of winning these materials. A proportion of the revenue generated was used to provide a source of funding for research aimed at minimising the effects of aggregate production. This fund, delivered through Defra, is known as the Aggregate Levy Sustainability Fund (ALSF); **marine** is one element of the fund.

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Biogenic Reefs and the Marine Aggregate Industry

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Abstract

Biogenic reefs are hard, compact structures created by the activity of living organisms. These structures create habitats and confer important ecological functions in the areas in which they occur. As a consequence they have been recognised by several legal frameworks which impart requirements for their management. Of the reef-building species in the UK, only three are likely to be of relevance to the marine aggregate industry: the ross worm *Sabellaria spinulosa*, the blue mussel *Mytilus edulis* and the horse mussel *Modiolus modiolus*. This monograph summarises the biology of these widely distributed species, the characteristics of the much rarer colonies that they form and the sensitivities of their reef structures to the potential impacts of aggregate dredging and other disturbances. Some of the management challenges of these habitats are also discussed, including the difficulties in their detection, sampling and mapping.

Keywords:

Biogenic Reef, Annex I Habitat, Ross worm *Sabellaria spinulosa*, Blue mussel *Mytilus edulis*, Horse mussel *Modiolus modiolus*, Habitat mapping.

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Cover Image Acknowledgements

Large image: A blue mussel, *Mytilus edulis*, bed; photo © Elaine Azzopardi, National Facility of Scientific Diving.

Image left bottom: Intertidal ross worm, *Sabellaria spinulosa*, aggregation, The Wash. Photo © Ian Reach.

Images on right in descending order:

The blue mussel, *Mytilus edulis*; photo © Elaine Azzopardi, National Facility of Scientific Diving.

A ross worm, *Sabellaria spinulosa*, aggregation; photo © Envision.

The horse mussel, *Modiolus modiolus*; photo © Elaine Azzopardi, National Facility of Scientific Diving.

The ross worm, *Sabellaria spinulosa*; photo © Vicki Hendrick.

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Section I

Introduction

1.1 Outline of this Report

This monograph is intended as an introductory review of biogenic reefs of relevance to the marine aggregate industry, specifically those of the ross worm *Sabellaria spinulosa*, the blue mussel *Mytilus edulis* and the horse mussel *Modiolus modiolus*. It is intended to serve as a useful starting point to inform the reader of the habitat and its natural value and to summarise the biology and characteristics of these reef-forming species. We also review the evidence regarding the potential impacts of marine aggregate extraction in the context of other threats to the habitat, and summarise the options for detecting, mapping and sampling reefs. The final sections outline some of the challenges for managing biogenic reefs and highlight key gaps in current knowledge.

1.2 Introduction to Biogenic Reefs

Biogenic reefs are hard compact structures created by the activity of living organisms. They do not have a uniform structure and vary in scale and extent, but constitute an important marine habitat that supports a range of other organisms the structure of which is dependent on geographic location and species of reef builder. Dense colonies of several species are widely considered to be reef, though their distributions are such that those of relevance to the UK aggregate industry are limited to the tube-dwelling ross worm *Sabellaria spinulosa*, and bivalves horse mussel *Modiolus modiolus* and blue mussel *Mytilus edulis*.

Other reef builders include the honeycomb worm, *Sabellaria alveolata*, which is typically found intertidally and therefore not generally in areas of interest for aggregate extraction. Many of the studies of this species are, however, of relevance to the closely related ross worm, particularly in regard to life history, and for this reason are referred to in this review.

Lophelia pertusa dominates the majority of cold-water coral reefs in the UK. These are typically restricted to depths of over 100 m and do not extend into English waters. Reefs formed by the serpulid worm *Serpula vermicularis*, are similarly limited to Scottish waters and hence reefs of either species are of limited relevance to the aggregate industry.

The native European oyster *Ostrea edulis* also forms biogenic structures, though in the UK the trend is for small sporadic settlements (Biodiversity Action Reporting System, 2008) which do not occur in the vicinity of licensed aggregate extraction sites. Dense beds of the Pacific oyster, *Crassostrea gigas*, have developed in southern Europe following its introduction for cultivation, and whilst natural spatfall has been found in several UK sites (CABI Bioscience *et al.*, 2005), it is also considered to be outside the scope of this monograph due to its non-native status.

Finally, the tube-building polychaete *Lanice conchilega* (Rabaut *et al.*, 2007; Callaway *et al.*, 2010), the file shell, *Limaria hians* (Hall-Spencer & Moore, 2000), and amphipod crustaceans *Ampelisca spp.* (Dauvin & Zouhiri, 1996), can also form large colonies providing similar ecological functions to accretions of other species more readily categorised as 'biogenic reef'. Whilst several authors have proposed that colonies of the two former species at least may also be considered within this category, their reef-forming status is not universally accepted and they are typically excluded from such classification (e.g. Holt *et al.*, 1998; UKMPA Centre, 2001). *Ampelisca spp.* are also excluded from such classification and all species are therefore considered to be outside the scope of this monograph.

The ross worm, blue mussel and horse mussel can all be found either singly or in colonies of varying density, with a gradation between non-reef and reef biotopes. However, it is the resulting structure of gregarious colonies that is thought to have important implications for the ecological functioning and hence the conservation status of a given colony.

Biogenic reefs are covered by numerous national and international legislations; therefore this review focuses specifically on ‘reef’ in the context of the marine aggregate industry. However the lack of a well-developed reef structure does not imply sub-optimal conditions for the growth of individuals.

1.3 Regulatory Obligations

The conservation importance of biogenic reefs and their role in sustaining marine biodiversity has been recognised by several pieces of legislation which impart requirements for their management (Table 1). It should be noted, however, that the legislative regulations outlined below relate solely to the reef habitats and not to solitary individuals or non-reef communities.

1.3.1 EC Habitats Directive

Council Directive 92/43/EEC on The Conservation of Natural Habitats and of Wild Fauna and Flora (EC Habitats Directive) is the means by which the European Community meets its obligations as a signatory of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention – Bern, 19.IX.1979). Its main aim is to promote the maintenance of biodiversity by requiring Member States to take measures to maintain or restore natural habitats and wild species

at a favourable conservation status, introducing robust protection for those habitats and species of European importance.

‘Reefs’ are one of the many habitats listed in Annex I of the Directive which are to be protected by a network of designated sites. Adopted sites are designated as Special Areas of Conservation (SACs), and together with Special Protection Areas (SPAs) classified under the EC Birds Directive, form a network of protected areas known as Natura 2000 (refer to the Natura 2000 website – www.natura.org for further details). An explanation of the term ‘biogenic reef’ in this context is provided by the Interpretation Manual of European Union Habitats (European Commission, 2003) and its subsequent revision (European Commission, 2007), which together are used for the implementation of the Directive. The revised manual indicates that the definition specifically includes reefs formed by the ross worm as well as the blue and horse mussels.

1.3.2 OSPAR

The Natura 2000 sites are complemented with additional international and regional level Marine Protected Area (MPA) designations under OSPAR, the 1992 Convention for the Protection of the Marine Environment of the North-East Atlantic. This is the current instrument guiding international cooperation on the protection of the marine environment of the

Protection Mechanism	Habitat
EC Habitats Directive	All three habitats are specifically included under the Annex I Reefs (1170) habitat.
OSPAR	The OSPAR list of priority habitats include: <ul style="list-style-type: none"> • Intertidal <i>Mytilus edulis</i> beds on mixed and sandy sediments, • <i>Modiolus modiolus</i> horse mussel beds, and • <i>Sabellaria spinulosa</i> reef.
UK Biodiversity Action Plan	There are specific Habitat Action Plans for <i>Sabellaria spinulosa</i> reefs, horse mussel beds, and blue mussel beds.
Marine Conservation Zones	Habitats of conservation importance include blue mussel beds, horse mussel beds and ross worm reefs.
Scottish MPA	Priority marine features include blue mussel beds and horse mussel beds.

Table 1. The protected status of *Mytilus edulis* (blue mussel) and *Modiolus modiolus* (horse mussel) beds and *Sabellaria spinulosa* (ross worm) reefs.

North-East Atlantic, which combined and updated the 1972 Oslo Convention on dumping waste at sea and the 1974 Paris Convention on land-based sources of marine pollution.

The UK ratified OSPAR in 1998, and in June 2000 a new Annex V on the protection and conservation of the ecosystems and biological diversity of the maritime area, together with a new Appendix 3 with criteria for identifying human activities for the purpose of Annex V. Measures and programmes within the OSPAR Commission's Biodiversity and Ecosystems Strategy include identification of ecological quality objectives of the North Sea, development of lists of species and habitats in need of protection, identification and selection of marine protected areas, and the prevention and control of adverse impacts from human activities.

The OSPAR list (OSPAR Commission 2008) of threatened and/or declining habitats considered to be priorities for protection includes:

- Intertidal *Mytilus edulis* beds on mixed and sandy sediments – this was nominated to the list due to the global and regional importance, rarity, sensitivity, ecological significance and keystone role, with information also provided on threat;
- *Modiolus modiolus* horse mussel beds – nominated due to sensitivity, ecological significance and decline with information also provided on threat; and
- *Sabellaria spinulosa* reefs – nominated due to sensitivity, rarity, ecological significance and decline, with information also provided on threat.

1.3.3 UK Biodiversity Action Plans

The UK Biodiversity Action Plan (BAP) was launched in 1994 as the UK government's response to the 1992 Convention on Biological Diversity (Rio Convention). It describes the UK's biological resources and commits a detailed plan for their protection through national legislation.

Reefs of the ross worm are again listed as a priority habitat and have their own detailed Habitat Action Plan (HAP) in which the emphasis is placed on damage that may be caused by physical disturbance (UK Biodiversity Group, 1999). *Modiolus modiolus* beds were also listed as a priority habitat though the name was subsequently changed to horse

mussel beds to provide a better indication of what the BAP is protecting to a lay audience (Biodiversity Reporting and Information Group 2007). At the same time, blue mussel beds were included as a new priority habitat.

1.3.4 Marine Conservation Zones

The UK Marine and Coastal Access Act (2009) enables the designation and protection of a new type of Marine Protected Area within English and Welsh territorial waters and UK offshore waters adjacent to England, Wales and Northern Ireland. These Marine Conservation Zones (MCZ) will provide a mechanism to protect nationally important (rare, threatened and representative) marine habitats, species, geology and geomorphology, and together with other types of MPAs they will deliver the Government's aim for an 'ecologically coherent network of Marine Protected Areas'. Habitat features of conservation importance to be protected within MCZs include blue mussel beds, horse mussel beds and ross worm reefs. Recommendations for MCZ sites in English territorial waters and UK offshore waters adjacent to England, Wales and Northern Ireland are to be identified through the Marine Conservation Zone Project by 2011, and it is expected that sites will be designated by late 2012. In Welsh inshore waters there will be a small number of Highly Protected Marine Conservation Zones identified through the Marine Conservation Zone Project Wales.

1.3.5 Scottish Marine Protected Areas

The Marine (Scotland) Act (2010) confers powers and duties on Scottish Ministers to develop a network of MPAs in Scottish territorial waters through the Scottish MPA project, whilst the UK Marine and Coastal Act includes equivalent provisions for Scottish Ministers to designate MPAs for biodiversity and geodiversity features in offshore waters adjacent to Scotland. Marine features in Scottish waters which might be protected in MPAs include:

- Blue mussel beds: *Mytilus edulis* beds on littoral sediments; *Mytilus edulis* and *Fabricia sabella* in littoral mixed sediment; and *Mytilus edulis* beds on sublittoral sediment; and

- Horse mussel beds: *Modiolus modiolus* beds with *Chlamys varia*, sponges, hydroids and bryozoans on slightly tide-swept very sheltered circalittoral mixed substrata; *Modiolus modiolus* beds with fine hydroids and large solitary ascidians on very sheltered circalittoral mixed substrata; *Modiolus modiolus* beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata; and *Modiolus modiolus* beds on open coast circalittoral mixed sediment (Marine Scotland, 2010).

Section 2

Ecological Functioning of Biogenic Reefs

Biogenic reefs influence both the physical and biological environments in which they are found, and as a consequence can have a significant ecological and economic role. Some of the most important ecological influences they convey on their environments are summarised below, including their importance as a food source, their competitive interactions, the habitat modifications they can impart, and their consequential influences on biodiversity.

2.1 Food Resource

The high density of worms or mussels within a biogenic reef clearly provides an abundant and often significant food resource for their predators, both in terms of established animals and also their larvae. Blue mussels in particular are important both as a commercial fishery and as a source of food for many benthic predators including invertebrates such as crabs, starfish and gastropods (e.g. *Carcinus maenas*, *Asterias rubens* and *Nucella lapillus* respectively); flatfish (e.g. flounders, plaice and dabs); and birds (including oyster catchers, herring gulls, eider ducks and knot); sometimes to the extent that predation may play a regulatory role for the population (reviewed by Seed & Suchanek, 1992 and Meire, 1993). Predation of horse mussels is thought to be largely by crabs and starfish, although this is generally restricted to juvenile mussels. Adults, meanwhile, are also sometimes collected for human consumption although only on a local scale. Many organisms have been noted to prey on the ross worm including other polychaetes, crabs, the pink shrimp *Pandalus montagui* and fish. However the significance of the ross worm to their diet is not currently clear.

In addition to acting as a food source themselves, mussel beds also act as sites of nutrient regeneration, producing organically enriched biodeposits via faeces and pseudofaeces that provide organic material and other nutrients for a wide range of deposit-feeding invertebrates and suspension feeders both within the mussel beds and over wide areas around them (see Smaal, 1991; Navarro & Thompson, 1997 and

references therein). In this way, the high density of filter-feeding organisms within the biogenic reefs, both in terms of the reef building species and other associated species such as bryozoans, brittlestars and ascidians, are likely to play a significant role in channelling organic material between the plankton and the benthos, a pathway known as 'benthic-pelagic coupling' (see Wildish & Fader, 1998; McCay *et al.*, 2003 and references therein).

2.2 Competitive Interactions

The blue mussel is an extremely efficient filter feeder being capable of filtering particles with 80-100% efficiency over a 2-3 μm size range (Møhlenberg & Riisgård, 1977). If this occurs on a sufficient scale, these mussel beds can deplete the seston available at the bottom of the water column to the extent that they cause a "rain shadow" effect downstream of them (Fréchette & Grant, 1991). Such a capability would have a consequential deleterious impact on other filter feeders in the vicinity, and it has been suggested that blue mussel beds may compete with, for instance, cockle beds in this way (Ramón, 1996). In areas where water flow is low, it has been suggested on the basis of flume experiments that seston concentrations could be similarly depleted directly over dense horse mussel beds (Wildish & Kristmanson, 1984).

On a larger scale, it has been proposed that such competition for food could be important in shaping the structure of benthic communities in the Wadden Sea where food supply is considered to be a main limiting factor for the secondary production of the system (e.g. van der Veer, 1989; Nehls & Thiel, 1993). In support of this suggestion, an area of the Wadden Sea that has a high blue mussel density was found to have lowered phytoplankton biomass and primary productivity in the overlying water (Cadée & Hegeman, 1974). Mussel filtration was thought capable of having a similar basin-scale impact on phytoplankton in San Francisco Bay during a period of drought (Nichols, 1985), although on a

more positive note, the filtration capacity of such a benthic community may serve as a natural control of eutrophication (Officer *et al.*, 1982).

2.3 Habitat Modification

Biogenic reefs also have an important modifying effect on the physical conditions in the areas in which they occur. Several authors, for instance, have reported a range of effects that sabellariids have on sediments and shorelines from the sorting of sediments (Gram, 1968), to stabilisation of beach sands to such a degree that they can provide protection from the effects of wave energy, intercepting the force of waves near the low tide mark (Wells, 1970). This is achieved both through the cementing of sediment grains during tube construction, and also through collection of sand, detritus and finer faecal material between the tubes. Mussel beds also have a strong stabilising effect on the seabed, binding together living mussels, dead shell, and sediments with byssal threads (Meadows *et al.*, 1998; Widdows & Brinsley, 2002). Such coalescence of the substrate can distinguish the biogenic reefs from the surrounding unconsolidated sediments, and may represent the only firm surface in the areas where the biogenic reefs occur. Furthermore, the stabilisation can act over periods varying from a few months to many years, and it is possible that this can lead to large scale changes in areas where a biogenic reef develops or is lost.

Reef growth in turn, alters bottom roughness and small-scale topography (over distances of centimetres to metres and sometimes over kilometres), which changes how the flow in the benthic boundary layer behaves over the reef (Nowell & Church, 1979). This can lead to elevated seston concentrations, faecal deposition and sediment deposition which can then lead to increased density and growth of reef forming organisms and associated fauna (Navarro & Thompson, 1997; Wildish & Fader, 1998). However, in exceptional circumstances, density dependent factors may actually cause limitation in reef extent and abundance by processes such as seston depletion, alteration to water flow and competition for space (Wildish & Kristmanson, 1997).

2.4 Influence on Biodiversity

The habitat modifications created by biogenic reefs have important consequences for the biological communities which they support, and as such reef-building species are often considered to function as keystone species. The complexity of the biogenic reef structure, for instance, can provide protection from biological disturbance (such as predation), or physical disturbance (such as currents and wave action) and stress (such as variations in temperature and desiccation in intertidal communities). One study of rocky, subtidal horse mussel beds, for instance, found they provided a spatial refuge from predation for three members of the mussel bed community assessed as prey – a bivalve, a sea urchin and a brittle star (Witman, 1985). Several generalist predators were observed to consume these prey outside of the mussel beds but not within them. The same study found the beds also offered infaunal invertebrates protection from severe grazing disturbance, predominantly by a sea urchin. In this way the mussel beds proved to be effective refuges because they persisted for many years, resisting the effects of biotic disturbance.

Of similar importance, the shells or tubes of the reef building organisms themselves can provide hard substrata for the attachment of conspecifics and other sessile organisms, particularly epibenthos and crevice fauna, allowing them to become established in predominantly sedimentary areas where they may not otherwise be found (Günther, 1996; Foster-Smith *et al.*, 1997; UK Biodiversity Group, 1999). Juveniles of the commercially important queen scallop, *Aequipecten opercularis*, for instance, may attach to horse mussel clumps prior to becoming completely free-living adults. Thus this habitat may form important nursery grounds for this species (Service & Magorrian, 1997).

Such factors contribute to the generation of oases for benthic communities. As such, the reefs may have a very rich associated fauna and flora that is distinct from other biotopes, and at least in terms of macrofauna is often much richer and more diverse than in surrounding areas (see Figure 1). It is for this reason that reefs are of particular conservation interest. Several studies have found an increased species richness within worm colonies relative to the surrounding area, for both colonies of the honeycomb worm (Kirtley, 1992; Dubois *et al.*, 2005), and of the

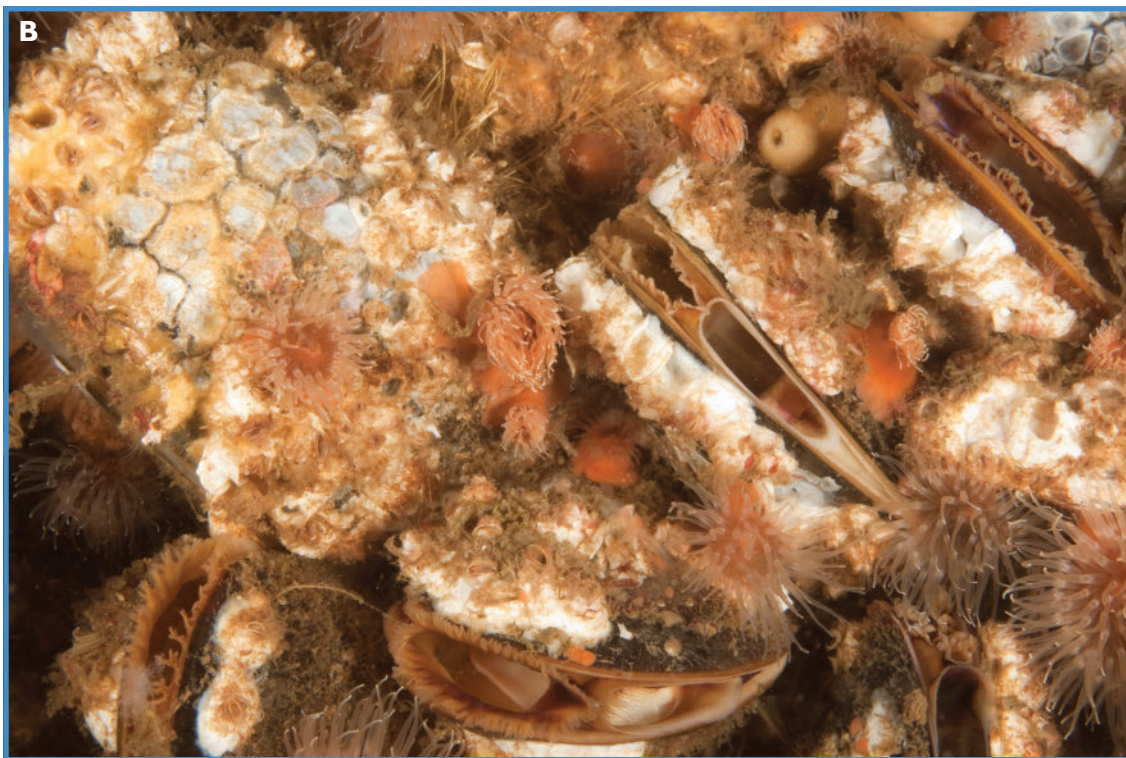
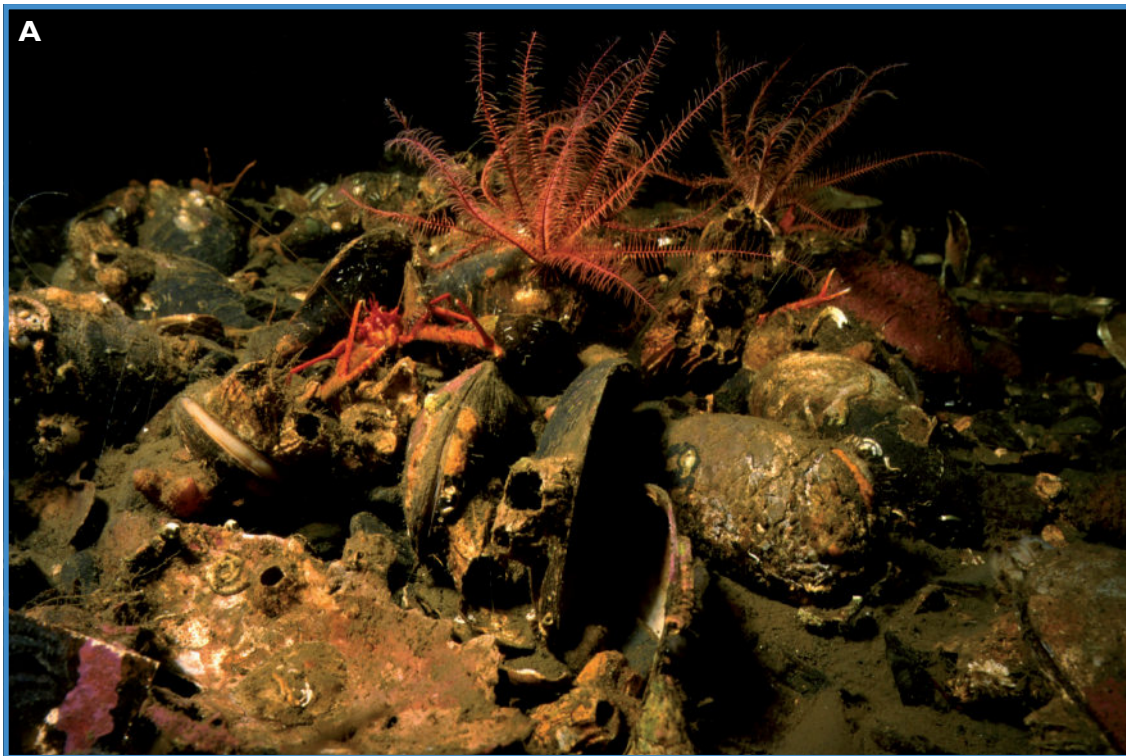


Figure 1. Examples of the biodiversity that might be expected in dense beds of a) Horse mussel – *Modiolus modiolus* (Photograph © T. Wilding), and b) Blue mussel – *Mytilus edulis* (Photograph © E. Azzopardi, National Facility of Scientific Diving).

ross worm (George & Warwick, 1985; Unicomarine Ltd, 1994; Bailey *et al.*, 2001). Ross worm reef was also amongst the most diverse and richest biotopes described in the surveys undertaken in the Wash during the Broadscale Mapping Project (Foster-Smith & Sotheran, 1999).

In their study of a ross worm colony in the Bristol Channel, George and Warwick (1985), reported that the reefs contained a more diverse fauna than nearby areas, whilst the National Rivers Authority (Unicomarine Ltd, 1994; Bailey *et al.*, 2001) found that sites in the Wash associated with the ross worm had more than twice as many species and almost three times as many individuals (excluding the worms themselves) as sites with low or no ross worms. In the latter survey, the distinction between '*S. spinulosa* sites' and 'low or no *S. spinulosa*' was made at only 100 individuals per trio of grab samples (covering 0.3m²), raising the possibility that even relatively sparse ross worms can strongly influence community structure.

As a consequence of these and other such studies it is widely accepted that ross worm reefs function as biodiversity hotspots with increased species richness, leading to the suggestion that a higher species diversity is found amongst the consolidated worm tubes than would occur on sediment or rock alone because species typical of both hard and sedimentary substrata occur within the colonies (Hiscock, 2003; Hendrick, 2007). This may not, however, be true of all colonies.

There is a possibility that reefs may act to reduce diversity. Gregarious distributions can produce almost monospecific frameworks comprising individuals of the same sizes and shapes, for example oyster, vermetid, serpulid, bryozoan and stromatolites (Fagerstrom, 1987). In such cases, the competitive exclusion of other species by the gregarious reef-builder often reduces biodiversity within the area of the reef in comparison to what might have been expected in its absence. Thus younger, dense worm reefs may reduce species richness due to the worms' monopolisation of space and other resources. Even the more established colonies may not increase diversity but merely increase the abundance of species typically found in the general vicinity. One study of the intertidal honeycomb worm, for instance, suggested young colonies may reduce the diversity of shores initially, but as the

colonies age and begin to fragment, space and the range of habitats they provide increases allowing a consequential increase in diversity (Cunningham *et al.*, 1984). Other studies have found that the overall diversity of the community is closely related to the developmental cycle of the reef (Dubois *et al.*, 2002 – honeycomb worm; Pearce *et al.*, 2007 – ross worm), and it may be that a degree of reef maturity is a prerequisite for the establishment of a range of other species but that biodiversity may become suppressed by the predators within the climax community. It should, however, be recognised that measures of biodiversity are scale dependent, and a low measure of biodiversity within the reef complex may still be of importance if it adds to the overall biodiversity of the wider area.

The communities associated with the horse mussel are also known generally to be extremely rich and diverse relative to the other surrounding subtidal habitats, consisting of a range of organisms including a community which seeks shelter in the crevices between mussel shells and byssus threads or which flourishes on its rich sediment (Brown & Seed, 1977; Witman, 1985; Ojeda, 1989). In contrast the associated biota of blue mussel reefs does not, in general, appear to be particularly rich or diverse. However, blue mussels beds often provide the only hard substrate communities in the area and therefore increase local habitat heterogeneity.

Section 3

Biology and Characteristics of Reef-Forming Species

Details of the biology and characteristics of the individual species are briefly reviewed here. The reader is referred to additional sources for further information in the relevant sections.

3.1 The Ross Worm – *Sabellaria spinulosa*

The 'ross worm', *Sabellaria spinulosa* Leuckart, 1849 is a sedentary, epifaunal polychaete that builds rigid tubes from sand or shell fragments binding them together with a mucus cement. It is a suspension feeder that is generally found individually or in small colonies, although it can be gregarious in favourable conditions and large colonies consisting of fused sand-tubes may form thin crusts or extensive reefs (Hartmann-Schröder, 1971). The reefs, commonly known as 'ross', are solid albeit fragile structures which can be many metres across and raised above the sea bed by up to 30cm (Foster-Smith & White, 2001). It is reefs formed by this species that are the most likely to occur within, or adjacent to, sedimentary resources of interest to the marine aggregate industry.

The ross worm is considered to be a subtidal species, although it may also be found intertidally (e.g. Killeen & Light, 2000; Jessop & Stout, 2006). This contrasts with the closely related honeycomb worm *S. alveolata* (Linnaeus, 1767), which is predominantly intertidal. The two can be distinguished by the honeycomb appearance of aggregated tubes of the latter species and the overhanging 'porch' over the tube opening, neither of which are seen in ross worm colonies (Figure 2). The honeycomb worm can also form extensive colonies among which are the French "Les Hermelles" reef in the Bay of Mont-Saint-Michel, and the Sainte-Anne reef which covers over 100 hectares – considered to be the largest reef in Europe (Gruet, 1972; Dubois *et al.*, 2003). This, together with its relative accessibility, has meant that

much of the assumed knowledge of the biology of the ross worm has been extrapolated from research undertaken on the honeycomb worm.

3.1.1 Distribution

The widespread distribution of the ross worm is such that it is considered naturally common around the British Isles, although aggregated reef structures are relatively rare (refer to Holt *et al.*, 1998 for summary descriptions of many reported colonies). The pattern of recorded occurrences of the species is concentrated around the coasts of England and Wales with a more scattered distribution around Scotland and Ireland. However, the pattern follows the observational bias of surveyed locations (Figure 3a) and it is possible that the relative scarcity around Scotland, Ireland and with increasing distance from shore is merely a reflection of lower sampling effort. Interpolation of available records (Figure 3b), incorporating both a spatial and temporal component, indicates that the density of ross worms is typically very low though there are a limited number of high-density hot-spots, most notably in the vicinity of the Wash and along the South Coast. The possibility of more dense, offshore colonies can not be confidently excluded on the basis of this assessment, however, and indeed recent work from the oil and gas industry suggests that this is a real possibility (BMT Cordah Ltd, 2003; BBL Company, 2007). It is believed that there are very few ross worm reefs in other European waters (JNCC & NE, 2010c).

3.1.2 Environmental Requirements

In keeping with other sessile organisms that build reefs in wave swept environments, the ross worm is considered to require stable foundations on which to settle and establish a tube (Jackson, 1977; Wood, 1999; Chisholm & Kelley, 2001). In this regard it is thought to favour substrata which include bedrock; boulders, cobbles, mixed substrata; and mixed sediment (Connor *et al.*, 1997), and



Figure 2. Colonies of a) an intertidal ross worm colony, *Sabellaria spinulosa*, from the Wash (Photographs © V Hendrick), and b) the honeycomb worm, *Sabellaria alveolata* from Llandullas, North Wales. (Photographs © AJ Davies). Photos on the right show individual ross worms and the 'porches' of honeycomb worm tubes.

thus it settles on substrates that are potentially of interest for marine aggregate extraction. Although it is assumed that a firm substratum is required for colony establishment, it has been suggested that the reef can be subsequently increased in extent by addition to the existing colony without the need for hard substratum (Holt *et al.*, 1997). Indeed, several studies have reported extensive ross worm colonies in essentially sandy areas (Warren & Sheldon, 1967; Schäfer, 1972; Warren, 1973). Other evidence from deployment of a sediment profile imagery

(SPI) optical sampler also suggests that reefs can be built on sand without cobble (see Limpenny *et al.*, 2010), whilst firsthand investigation of a colony at Frenchman's Landing in the Wash shows that the reef at that location has, in places, 'seeded' on shell fragments predominantly from blue or horse mussels (pers. comm. Ian Reach, Natural England).

Being sedentary, ross worms rely on wave and current action to bring them a constant supply of food – primarily microplankton, and to wash away

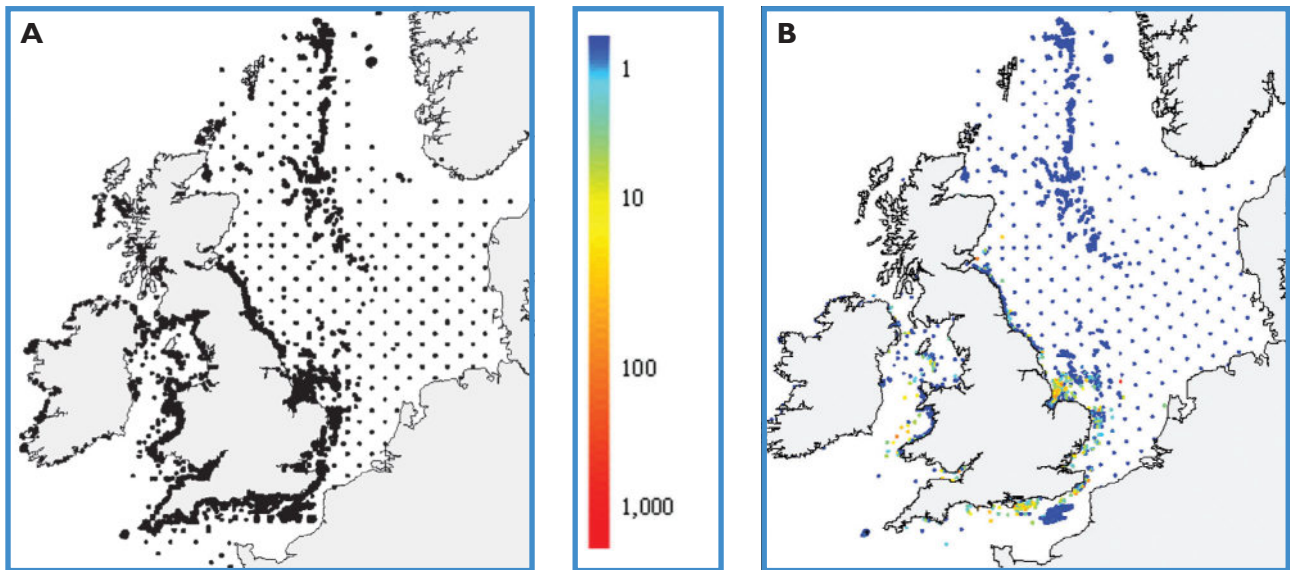


Figure 3. The distribution of the ross worm around Britain and Ireland¹. a) Distribution of collated data points for which an indication of abundance data was available. b) Ross worm density map (*S. spinulosa*/0.1 m²) from spatial interpolation of collated log-transformed density counts using inverse weighting and a search radius of 5 km. Scale bar for numerical abundance map is indicated.

¹ The methodology for density interpolation and details of the available records from which the interpolation map was derived is presented in Hendrick (2007) with a similar interpolation in Limpenny *et al.* (2010). The map is reproduced here merely to give an indication of the relative rarity of high density colonies.

their metabolic wastes (Kirtley, 1992). Although important to dietary provision, strong water movement is perhaps more important to raise sediment into suspension for tube building (Jones, 1999). Thus ross worm colonies are typically associated with weak or moderately strong tidal flows (Jones *et al.*, 2000), although the relative importance of tidal versus wave induced movements is unclear (Connell & Slatyer, 1977). They also appear to favour locations such as the edges of sand banks or areas where there are sand waves (Foster-Smith, 2001a).

Ross worm records typically span depths ranging from a few metres to around 40 m depth (Caspers, 1950; George & Warwick, 1985; Connor *et al.*, 1997; Jessop & Stoutt, 2006) though the vertical distribution extends in to the bathyal at depths of up to 600 m (Hartmann-Schröder, 1971). Reports of large colonies are typically subtidal with a distribution that is likely to be reflective of investigative effort, although a large colony has been reported in the low intertidal (Jessop & Stoutt, 2006).

3.1.3 Reproduction and Development

Numerous observations of ross worm colonies suggest that their fecundity and recruitment may be highly variable (e.g. Linke, 1951; Wilson, 1971; Michaelis, 1978; George & Warwick, 1985). This is unsurprising given the large combination of physical and biological factors all of which can have a bearing on recruitment success.

The family Sabellariidae reproduce sexually via broadcast spawning, resulting in larvae that drift passively in the plankton (Schäfer, 1972; Eckelbarger, 1978), although the reproductive seasonality of the ross worm is unclear given contrasting reports (Hartmann-Schröder, 1971; Romimohtarto, 1980; Wilson, 1981; Garwood, 1982). More recent work in the Outer Thames found ross worm larvae in April 2008, and February, July and November 2009 through sampling with a plankton haul, but not in July 2008, September and March 2009 or April 2010 (pers. comm. Bryony Pearce, Marine Ecological Surveys Ltd). A huge abundance of planktonic larvae was found in the February 2009 survey, consistent with the view that spawning probably occurs largely over winter (Holt *et al.*, 1997; Hendrick, 2007).

The larvae then appear to spend between a few weeks and several months in the plankton (Wilson, 1929) before using their tentacles to seek appropriate conditions for settlement (Wilson, 1968; Eckelbarger, 1978). If these are not found, the larvae are able to postpone metamorphosis for several weeks. Purely physical factors have only minor influences on settlement (Wilson, 1968), but sabellariids are strongly stimulated to settle and metamorphose in response to the presence of the tube cement of other sabellariids (Wilson, 1968; 1970b; Eckelbarger, 1978; Jensen, 1992). This helps to ensure the suitability of settlement site and facilitates massive colonisation in areas previously only colonised by scattered individuals.

Although few studies have focused on the rates at which the ross worm can extend their dwelling tubes (Hendrick, 2007 and Davies *et al.*, 2009 being exceptions), it appears that the capacity for tube growth is such that sabellariid reefs may be expected to develop quickly following successful settlement (Linke, 1951; Vorberg, 2000; Stewart *et al.*, 2004; Braithwaite *et al.*, 2006). Personal observations have indicated that tube extension rates of adult ross worms can be highly variable, and up to 6mm a day for several days when provided with an adequate sediment supply. A more rigorous assessment of tube growth rates under different sedimentation conditions is currently under investigation (Last *et al.*, In preparation). Provided that the organisms are not killed or dislodged from their tubes, the natural growth and aptitude for repair is such that they can be expected to rebuild parts of their dwellings within a few days following any damage (Hendrick, 2007).

To date there have been no specific studies of the longevity of individual ross worms or of their colonies although estimates for sabellariids are typically in the region of 1-2 years (Kirtley, 1966; McCarthy, 2001; McCarthy *et al.*, 2003), with a few reports suggesting longer life spans (Wilson, 1974; George & Warwick, 1985). It is possible that the age of a colony, meanwhile, may greatly exceed the age of the oldest individuals present particularly since sabellariid larvae are strongly stimulated to metamorphose by conspecific secretions, encouraging continuous succession of generations.

3.1.4 Colony Characteristics

As indicated previously, the ross worm can be found in colonies of varying size and density, though there are few clear descriptions of the colony characteristics in the literature. It seems, however, that reefs often have a relatively substantial core which becomes increasingly patchy towards its margins. The characteristics of the whole structure can thus vary throughout its extent.

Colony heights start at a few millimetres for encrusting tubes which tend to adhere to the substrate along their length. For colonies with an upright morphology, where the tube openings turn away from the substrate and run upwards more or less parallel to one another, tube heights of up to 50cm have been reported (Hartmann-Schröder, 1971; Schäfer, 1972). Such heights appear uncommon, and most reports of ross worm colonies in UK waters are rarely more than a few centimetres thick (Holt *et al.*, 1998), with heights of the more substantial colonies being in the region of 10-30 cm high (Foster-Smith & White, 2001; BMT Cordah Ltd, 2003; Woo, 2008; JNCC & NE, 2010a).

Spatial extent is typically poorly described, a reflection of the difficulty in detecting the colonies and also because the colony boundaries are rarely distinct. Some exceptions to this include three areas of reef within the Inner Dowsing, Race Bank and North Ridge candidate SAC (cSAC) which together are estimated to cover approximately 1500 hectares (JNCC & NE, 2010c); and Saturn reef, just south of Swarte Bank, which was estimated to cover an area approximately 750m by 500m when it was first discovered (BMT Cordah Ltd, 2003). Two examples exceeding 1 km² have been also been reported off Thanet (Marine Ecological Surveys Limited, 2005) and Hastings (Marine Ecological Surveys Limited, 2006). Less specific descriptions refer to 'huge colonies' (Hartmann-Schröder, 1971), which occasionally cover several square kilometres (Schäfer, 1972).

Video assessments indicate the spatial patchiness of ross worm colonies can also vary greatly (e.g. JNCC & NE, 2010a). In some areas, video tows have shown well developed reefs extending for many metres interspersed with occasional small patches of sand. In contrast, colonies in other areas form small patches of only a few metres extent or

less, dominated by surrounding sand. Such spatial variability influences the distinctiveness of the reef habitat relative to the surrounding area. It also complicates the determination of spatial extent of a reef if the positions of the boundaries are consequently unclear.

Recorded densities of ross worm colonies are also highly variable with only moderate numbers recorded on some surveys/sites and very dense worms recorded on others. In denser colonies, over 3,000 *S. spinulosa* individuals/m² were reported for a reef in the Bristol Channel (George & Warwick, 1985), and densities of over 4,500/m² were reported for a reef in the Wash (Unicomarine Ltd, 1994).

Assuming limited longevity of individual worms, the continued existence of a colony becomes dependent on successful recruitment of new individuals. Although continuous succession of generations is promoted by the settlement-inducing properties of the tube cement (Eckelbarger, 1978; Jensen, 1992), the multitude of factors which have a bearing on recruitment success mean that this is not guaranteed. Thus the longevity of a colony may match that of the individuals, it may repeatedly develop and decline in a regular progression after each successive generation has died, or it may remain relatively stable if the loss of individuals is matched by new recruitment.

To date there have been few studies on the persistence of ross worm colonies and most information is somewhat anecdotal, although dense colonies have been consistently recorded in the environs of The Wash and its approaches (Foster-Smith & Hendrick, 2003). Many ross worm colonies, however, have appeared fairly short-lived surviving for one or two years only (Schäfer, 1972). Such transience is particularly associated with encrusting colonies (e.g. UK Biodiversity Group, 1999), with their vulnerability often being attributed to winter storms (Holt *et al.*, 1998), although the evidence for this is weak. It has also been proposed, although again evidence is lacking, that the stability of ross worm colonies maybe a function of stability of the substratum with the more transient reefs occurring principally on relatively unstable substrata, and with longer lasting reefs being a product of more stable substrata (Connor *et al.*, 1997; Holt *et al.*, 1997). Elsewhere temporal stability has been inferred from the presence of long lived species within the colony matrix (George & Warwick, 1985).

In addition to the decline of short-lived colonies, there are many instances reported in the literature of the apparent loss of dense colonies that have previously appeared relatively stable, or of fluctuations within them indicating that population declines are not necessarily irreversible (Michaelis, 1978; Reise, 1982; Riesen & Reise, 1982; Reise & Schubert, 1987; Dörjes, 1992). A reef just north of Docking Shoal bank, meanwhile, appears to have changed cyclically since 1999 due to natural processes (see references in JNCC & NE, 2010c). The reason(s) behind such fluctuations are rarely evident though there have been many, generally speculative suggestions to account for their apparent loss. Many of these attribute the loss to a source of disturbance, but it is also possible that apparent declines are an artefact of the difficulty in sampling colonies with a naturally patchy distribution.

3.1.5 Associated Species

The Marine Habitat Classification system recognises a number of biotopes in which ross worms are considered to be common or abundant, and has identified a number of other species which are considered to be characteristic of each (Connor *et al.*, 2004; see also Foster-Smith *et al.*, 2000; JNCC, 2010; JNCC & NE, 2010c and Limpenny *et al.*, 2010). Although not all of these biotopes will constitute reef habitat, the list is indicative of the wide range of species that can be found amongst ross worm colonies, and shows no species are known to be restricted only to them in distribution. Specific studies have noted an association with the pink shrimp *Pandalus montagui* (Warren & Sheldon, 1967), or of the porcelain crab *Pisidia longicornis* and the squat lobster *Galathea intermedia* (Pearce *et al.*, 2007), but it seems likely that the faunal community associated with a given ross worm colony is likely to be reflective of the geographic location.

3.1.6 Further Information

There is a relative paucity of recent work on the ross worm reported in peer-reviewed journals which is likely to be a reflection of the difficulty in studying its habitats rather than due to lack of interest. As a consequence of the limited evidence, many of the numerous reviews relating to ross worms and their reef formations (e.g. Rees & Dare, 1993; Holt *et al.*, 1995; 1997; 1998; UK Biodiversity Group, 1999;

Jones *et al.*, 2000; UKMPA Centre, 2001; Foster-Smith & Hendrick, 2003; Jackson, 2008; OSPAR Commission, 2008; and Limpenny *et al.*, 2010) have repeated the same information to the extent that some suggestions and propositions have been perpetuated and have gained a wider acceptance than is perhaps justified by the evidence. Further work is, therefore, needed on many aspects of the species and its reef habitats.

In addition to the reviews listed, the reader is referred to work by David Kirtley and Stanislas Dubois for further information on the general ecology of sabellariids, and to work by Douglas Wilson(b) and Kevin Eckelbeger in particular for further information regarding their reproductive biology – see bibliography for further details.

3.2 The Blue Mussel – *Mytilus edulis*

The common or blue mussel, *Mytilus edulis* Linnaeus, 1758 is a gregarious mussel that has a widespread distribution including much of the European coast from the high intertidal to shallow subtidal. It is common on rocky shores of open coasts and attaches to hard substrates by the protein fibres that it secretes called byssus threads. These threads are planted in such a manner that the animals are able to withstand water movements in any direction, although they are generally aligned parallel to the predominant direction of water flow (Yonge, 1976). On softer sediments, the individuals are usually semi-infaunal, projecting above the sediment where they also create an irregular surface topography. The shell shape is roughly triangular though can vary considerably with environmental conditions, and is usually purple or blue in colour (Figure 4).

Over some of its range, the blue mussel hybridizes with the Mediterranean mussel *M. galloprovincialis*, particularly in the south west of England, leading some authors to refer to the '*Mytilus edulis* species complex', or to '*Mytilus* spp.' in the literature. *Mytilus edulis* is, however, the more dominant form in British waters (National Biodiversity Network, 2010), and thus it is the focus of this review.

At high densities, blue mussels forms dense beds of numerous layers with individuals bound together by byssus threads. Spatial complexity increases



Figure 4. The blue mussel, *Mytilus edulis* and associated fauna (Photograph © Elaine Azzopardi, National Facility of Scientific Diving).

with colonisation by new individuals within the bed until overcrowding results in mortality as underlying mussels are starved or suffocated by the accumulation of particulate matter, especially in rapidly growing populations (Richardson & Seed, 1990). The resulting matrix of living and dead shells can accumulate substantial amounts of sediment, faeces and pseudo-faeces, particularly in areas with a degree of shelter from wave action, but still with sufficient water transport to allow good mussel growth. The resulting biomediated structures can reach tens of centimetres thickness, leading to classification as 'biogenic reef'.

3.2.1 Distribution

The blue mussel is a morphologically variable species that is widely distributed in the northern hemisphere (Seed, 1976) and is capable of forming dense beds over much of its range. It is considered very common in British coastal waters (Figure 5), and significant beds of blue mussels on soft sea beds are found in scattered locations within this broad range (Natural England Undated-a). There are large commercial beds in the Wash, Morecambe Bay, Conway Bay and the estuaries of south-west England, north Wales, and west Scotland (Tyler-Walters, 2008). The reader is referred to MarLIN (2010) for distribution maps of the various *Mytilus* biotopes, and to Holt *et al.* (1998) for a review

of the distribution of natural beds within the UK marine cSACs. The latter includes descriptions from all over Britain and led the authors to consider the occurrence of dense colonies to be particularly likely in estuarine areas.

3.2.2 Environmental Requirements

The broad distribution of the blue mussel is a reflection of its tolerance of a wide range of environmental variables. Natural reefs are typically found on mixed, firm sediments in relatively wave sheltered bays and estuaries where there are strong currents (Holt *et al.*, 1998). In wave exposed areas, it requires a hard and stable substratum such as rock or large boulders for the development of larger colonies (Seed, 1969), although in more sheltered areas the beds may develop on more sandy substrates (Roberts & McKenzie, 1983).

The mussel is also tolerant of a wide range of exposures to both wave action and tidal currents. The byssal threads provide sufficient anchorage for all but the most exposed shores, but they do require some degree of water flow to provide a sufficient supply of particulate matter or 'seston' for growth and removal of waste. Dense beds have a heightened requirement in relation to water flow in order to provide sufficient food and oxygen for the density of mussels, and to prevent a rapid build-up of particulate matter within the bed that may result in the smothering of underlying layers. In general, it has been considered that this water movement is best provided by tidal currents rather than wave action, though the latter may also contribute in some areas (Holt *et al.*, 1998).

The blue mussel can be found in salinities ranging from fully marine to highly estuarine, although larger colonies usually occur low on the shore and in the mid to lower reaches of the estuary (Holt *et al.*, 1998). Its upper limits in the high intertidal zone are thought to be a reflection of its tolerance limit to high temperatures and desiccation (Seed & Suchanek, 1992), though reduced feeding due to aerial exposure may also be a factor (Widdows & Shick, 1985). In contrast, the lower zonal limits, are thought to be controlled primarily by biological factors such as predation, with physical factors playing a secondary role (Holt *et al.*, 1998). In general, reef development is typically within the lower third

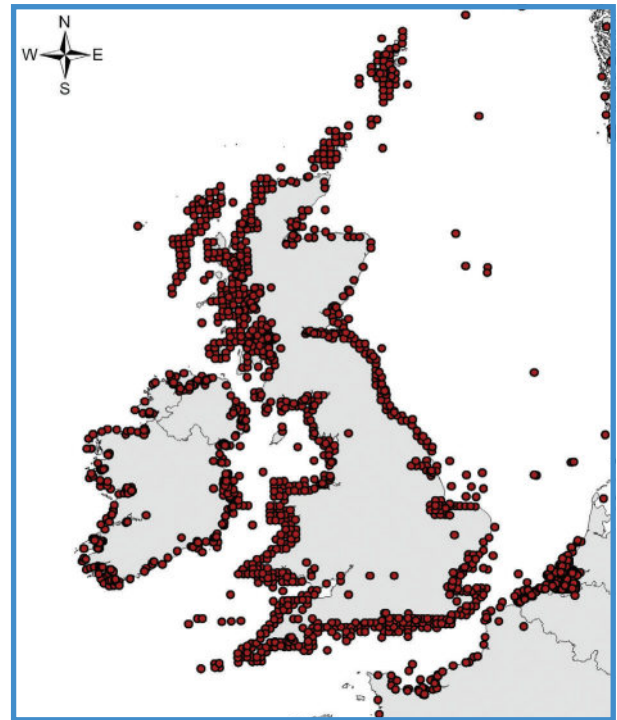


Figure 5. Distribution map of the blue mussel, *Mytilus edulis*, in Britain and Ireland plotted from iOBIS records (assessed 29/09/2010).

of the intertidal or shallow subtidal, but has been reported down to depths of approximately 30m (pers. comm. Ian Reach, Natural England).

3.2.3 Reproduction and Development

As with the ross worm, the fecundity and recruitment success of the blue mussel may be very variable both spatially and over time due to the wealth of influential factors all of which undergo a degree of variation. The mussel can reproduce in its first year (Seed, 1969), and populations generally undergo some spawning all year round but with a major peak in spring. Larval growth to metamorphosis typically takes two to four weeks, though may be up to six months depending on factors such as temperature, food supply and availability of suitable substrate (reviewed by Holt *et al.*, 1988).

Whilst the larvae may settle directly onto adult beds (McGrath *et al.*, 1988), at which point they are known as 'spat', the blue mussel may also undergo a two-stage extended dispersal strategy in which a primary settlement occurs onto sublittoral filamentous substrata such as hydroids and algae (Bayne, 1964; Pulfrich, 1996). This may be a mechanism for reducing competition between very young and adult mussels,

and/or to prevent filtration of the larvae by the adult mussels. The spat then detach after reaching a size of ca. 1-2 mm in length, drifting in the water column with the aid of byssus threads to a secondary, firmer settlement site which affords sufficient stability for further development (Lane *et al.*, 1985). The density of the resulting spatfall can be variable with reports of over 80 cm⁻² in a study at Ballynahown, Ireland (McGrath *et al.*, 1988), although relatively modest recruitment levels into the shelter provided by crevices between adult byssal threads are sufficient to maintain persistent beds (Holt *et al.*, 1998). Conversely, heavy juvenile recruitment may not necessarily lead to the formation or maintenance of a dense bed or reef if predation or losses due to wave action are high.

Growth and production rates within blue mussel colonies can also be extremely high, particularly in estuarine and other enclosed areas (Holt *et al.*, 1998). Beukema (1983) for instance, determined that blue mussel beds in the Wadden Sea account for up to 25% of the total macrobenthic production, whilst a study by Dare (1976), calculated the production by two year classes to be 2.5-3 times their maximum standing crop, with few mussels surviving beyond their third year. Such a turnover may not be unusual for dense colonies due to the self-thinning of multiple-layers as a result of resource limitation and smothering, and the consequential detachment by water movement if the colonies become well developed. Thus although the majority of mussels within a reef are likely to be fairly young – up to two or three years of age (Seed, 1976), there are reports of individual mussels living over fifteen years (Sukhotin *et al.*, 2007).

3.2.4 Colony Characteristics

Blue mussel colonies vary in size and extent over a continuum from small, patchy clumps, through thin veneers where mussels merely cover the substratum to well-developed reefs. The density and biomass of the reefs can be similarly variable from hundreds to tens of thousands of mussels/m² (see review by Smaal, 1991), and can extend for several hectares (Dankers *et al.*, 2001), though they are more often in the form of small clumps.

It is possible that a successful recruitment event may result in a bed of only a single year class. At first the spat may be almost hidden within the substrate, but if the biomass of the mussels is high, sufficient mud may build-up amongst the growing mussels so that they emerge as a thin carpet overlaying a layer of mussel mud which may accumulate to a depth of 0.75 m in four to five months (Dare, 1976). Such single-year class colonies tend to be more transient than those comprising a number of year classes, and are often dislodged by water movement, particularly during storms (McKay & Fowler, 1997). The mussel mud, however, is highly cohesive once it has consolidated, and the deposits themselves may last for years after the mussels have largely gone (Holt *et al.*, 1998). Mussel colonies of multiple year classes may also vary in relief and there are reports of layers of high density, living and dead mussels forming beds of up to 10 cm thickness in the intertidal (Nixon *et al.*, 1971), and of subtidal beds as thick as ca. 120 cm (Simpson, 1977). Well developed reefs in most UK sites rarely exceed 30-50 cm, however (Holt *et al.*, 1998).

Large, raised reef areas often take a hummock or ribbon-like form usually up to a few metres across, and often with patches of sediments or cobbles and boulders in between (Holt *et al.*, 1998). It is possible that the shape of the whole bed will be aligned with the predominant direction of water flow, although a cross-tide wave form akin to mega-ripples overlaying a sand bank may be superimposed upon this. More commonly the beds exhibit a more irregular shape as a consequence of the patchy and variable growth of competing mussels, and their irregular attachment to each other with byssal threads. In such cases, the lower areas comprising only one or two layers of mussels may be very extensive and continuous, particularly where they form on more solid substrata. The latter may usually be regarded as beds rather than reefs, and can be over 50 ha in extent (Holt *et al.*, 1998).

As has already been indicated, individuals within a blue mussel reef are typically only a few years old at most since the reefs have a tendency to grow rapidly and then be detached by water movement as they become well developed. Such detachment can then leave the bed vulnerable to tidal scour and wave action (Seed & Suchanek, 1992). Nevertheless, the beds themselves may be relatively stable, particularly

in more sheltered areas, if recruitment to the bed is such that a regular turnover of individuals is maintained. Studies undertaken within the Wadden Sea, for example, suggest that the distribution and extent of some of the mussel beds investigated remained fairly constant over a period of decades, although the abundance of mussels within them varied considerably over that time as a consequence, at least in part, of irregular mass spatfalls, variable predation and ice winters (Dankers & Koelemaj, 1989; Nehls & Thiel, 1993; Beukema & Dekker, 2007).

3.2.5 Associated Species

The associated biota of blue mussel reefs does not generally appear to be particularly rich or diverse in comparison with what has been reported for the ross worm or horse mussel. A survey in the Wadden Sea, for instance, recorded a total of 52 macrofaunal species and 44 meiobenthic plathelminth species in association with blue mussel beds (Dittman, 1990; see also Asmus, 1987; Seed, 1996 and review by Holt *et al.*, 1998). However, as is the case with ross worm colonies, blue mussel beds often provide the only hard substrate communities in the area and can therefore increase habitat heterogeneity. This, and other factors discussed previously in the section on ecological functioning, can lead to a higher diversity within such beds than in the surrounding areas, as has been reported by many studies (Dittmann, 1990; Günther, 1996; Ragnarsson & Raffaelli, 1999). For the reasons outlined previously, the more stable beds are likely to build up a much more diverse associated community, but it is possible that a build-up of dense epifauna may in turn promote the decline of the reef if it promotes its physical break up, particularly on less stable substrata.

3.2.6 Further Information

As a consequence of its widespread distribution, abundance, intertidal habitat and its ecological and commercial importance, the blue mussel has been extensively studied giving rise to a wealth of scientific literature. For a more detailed overview, and general information on its biology, ecology and physiology the reader is referred to reviews by Field (1922); Gosling (ed.) (1992); Bayne (1976) and Holt *et al.* (1998). More specific information on the reproductive biology and larval ecology can be

found in Seed & Suchanek (1992) and Lutz & Kennish (1992) respectively, whilst the reader is referred to Hawkins & Bayne (1992) for more information on blue mussel physiology and feeding ecology. Predation on the blue mussel has been reviewed by Seed (1993) – invertebrates, and Seed & Suchanek (1992) and Meire (1993) – birds, whilst a range of known diseases and parasites of the mussel have been reviewed by Bower (1992).

3.3 The Horse Mussel – *Modiolus modiolus*

The horse mussel, *Modiolus modiolus* (Linnaeus, 1758) is the largest British marine mussel that is found fully or partially buried in sediments (both soft and coarse), or attached to hard substrata using byssus threads. It has a wide depth range from shallow occurrences in intertidal low shore rock pools, but is more common subtidally down to depths of around 280m. Individuals commonly aggregate into clumps and are capable, under suitable conditions, of forming extensive beds or reefs. Whilst individual horse mussels are found throughout most British coasts, extensive reef formations are rarer (defined as having a coverage of 30% or more, OSPAR, 2008). They occur through the accumulation of shell and faecal mud deposits and have been shown to support elevated local biodiversity (Holt *et al.*, 1998). Adults are usually more than 10cm in length, with a shell colouration of dark blue or purple. However, the outermost layer usually gives adults a yellow or dark brown appearance (Figure 6). This species can be distinguished from the blue mussel by a blunter hinge area which is not quite anterior due to the extension of the shell margin in the horse mussel (Tyler-Walters, 2007).

3.3.1 Distribution

The horse mussel is an Arctic-boreal species that is limited in distribution by warmer temperatures to the south but occasional specimens have been reported as far south as north west Africa. Around the north west Atlantic, it occurs from the Bay of Biscay to northern Norway, with occurrences off Iceland and the Faeroes (Tebble, 1966; Poppe & Gotö, 1993). It is found throughout British waters, but has most frequently been reported in northern and western areas (Figure 7).



Figure 6. A horse mussel, *Modiolus modiolus* from Loch Creran Scotland. (Photograph © Elaine Azzopardi, National Facility of Scientific Diving).

Extensive horse mussel beds are found only in parts of north and western Scotland, the Ards Peninsula, Strangford Lough, the Isle of Man, north-west Anglesey and north of the Llŷn Peninsula. Dense beds of young horse mussels have been found in the Bristol Channel, but beds of adults are not known to occur there (Natural England Undated-b).

Descriptions of the horse mussel usually state the presence of aggregated clumps on mud or muddy-gravel sediments although the vast majority of these will not fall into the definition of biogenic reef, due to low density and coverage. However, several areas do contain large beds definable as biogenic reef including beds in Strangford Lough (Roberts, 1975), the Isle of Man (Jones, 1951; unpublished references in Holt *et al.*, 1998), Scottish waters (Comely, 1978; Howson *et al.*, 1994) and within the Llŷn Peninsula (Lindenbaum *et al.*, 2008). One notable area of horse mussel beds that has received significant research focus have been those within the Bay of Fundy on the Scotian Shelf, Canada (see Wildish *et al.*, 2009). The results of these studies are valid for application to beds found in Britain.

3.3.2 Environmental Requirements

Horse mussels have been reported from the low intertidal (Davenport & Kjosvik, 1982) through to 280m (references in Schweinitz & Lutz, 1976). However, aerial exposure may cause erratic heart rates and significant water loss, and this coupled with their limited tolerance of low salinity and

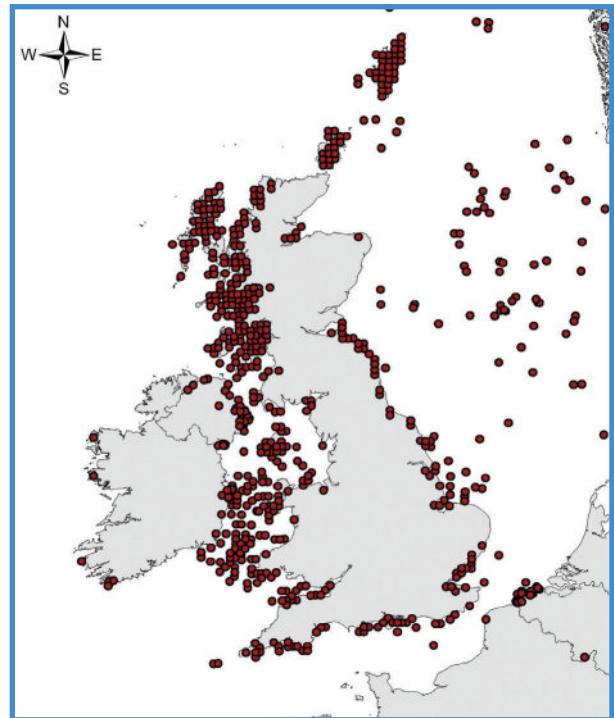


Figure 7. Distribution map of the horse mussel, *Modiolus modiolus* in Britain and Ireland plotted from iOBIS (assessed 29/09/2010).

temperature change mean that intertidal horse mussels are at the edge of this species' tolerance limits (Coleman, 1976; Davenport & Kjosvik, 1982). The densest populations that are known as reef are found between 5 and 50m in British waters (Holt *et al.*, 1998), whilst infaunal reefs have been found at over 80m in the Bay of Fundy (Wildish *et al.*, 2009).

The horse mussel reaches its southern limit around the Bay of Biscay, and has only rare occurrences further south. This indicates that there is an upper thermal limit which probably controls distribution. It has been suggested that temperatures greater than 23°C for a month is the upper temperature limitation (Read & Cumming, 1967), with short-term observations of exceptionally high temperatures (30-32°C) showing significant mortality (Read, 1969). Fairly restricted tolerance is also evident for salinity as, with the exception of young mussels, there are only limited occurrences in estuaries. Salinity tolerance has been established between 27 and 41 on the practical salinity scale (Pierce, 1970).

Several other studies have investigated other environmental requirements. This species is also able to physiologically compensate for a variable food supply by reducing feeding rate when food

availability is low, usually in autumn and winter (Navarro & Thompson, 1996). The species is as tolerant of oxygen deficiency as the blue mussel, with both species being exceptionally tolerant when compared to other common species such as crustaceans, echinoderms and gastropods (Theede *et al.*, 1969).

3.3.3 Reproduction and Development

Horse mussels are long-lived reaching sexual maturity at around three to six years of age. This delay in maturity is likely to be an adaptation to the high predation pressure on small individuals, enabling energetic resources to be channelled towards growth over reproduction in early life. Thus horse mussels show rapid growth over the early years followed by much slower growth post-sexual maturation and once they have reached lengths less vulnerable to predation (Anwar *et al.*, 1990).

Spawning of horse mussels is erratic and differs between populations. For example, in Strangford Lough, limited spawning occurs throughout the year with no pronounced annual maxima (Seed & Brown, 1977; Brown, 1984). In contrast, reproduction in Scandinavia shows a clearly defined spawning in June, followed by a period of gonad redevelopment and possibly a further release. Spawning has been reported to occur during a narrow range of temperatures (7-10°C), which appears to be relatively stable in Strangford Lough (but not at other sites) and this probably allows the constant spawning that occurs in the Lough (Brown, 1984). Off the south east of the Isle of Man, spawning also shows a pronounced annual cycle of gonad development and recruitment, with maximum spawns likely in the spring and summer, but trickle spawning also occurs throughout the year (Jasim & Brand, 1989). The horse mussel life cycle starts with small fertilised eggs, and under laboratory observations, first settlement after 19 days (de Schweinitz & Lutz, 1976). Settlement usually occurs on hard substrate including shell and stone but is more likely amongst the byssal threads of established horse mussel colonies (Roberts, 1975).

3.3.4 Colony Characteristics

The aggregative behaviour of horse mussels is commonly reported in occurrence records. It arises from the interaction of environmental, recruitment and predation pressures (e.g. Bertness & Grosholz, 1985), diminishing predation risk through safety in numbers and provision of refugia for juveniles amongst the byssal threads of adults (Roberts *et al.*, 2004). Colonies have also been shown to support recruitment, as spat have been found to settle on the shells of adult animals. (Comely, 1978).

Development of a horse mussel reef takes many generations of recruitment to build up sufficient density of individuals, coverage and biogenic structure. The most common reef-form is semi-infaunal, which develops as the accumulation of dead shells over multiple generations. The shells increase bottom friction and reduce flow velocity, resulting in the trapping of fine sediment and faecal muds, which in turn contributes to engineered conditions that support other species. In this reef-form, living horse mussels are not immediately obvious as they are part buried and may be difficult to distinguish from dead shell, but they are likely to be patchily distributed. Such colonies range in scale from small clumps which are not currently described as biogenic reef to continuous raised biogenic-reefs that can be several metres high, although the threshold at which a horse mussel colony becomes reef is still unclear. Horse mussel colonies may also be infaunal amongst coarse grounds such as gravel. These are much rarer than semi-infaunal reefs and occur in areas of high current velocity where individuals are found as infauna bound amongst gravels and cobbles. They form a unique biogenic reef, which are usually wave like in structure and extend up to 3m high (Wildish & Fader, 1998).

The spatial extent of horse mussel colonies is rarely described though they can cover many hectares. An exception is an acoustic survey in the Bay of Fundy which described patches of seabed bioherms ~20m wide and up to 1.2km long, evenly spaced at distances of tens to hundreds of meters. Video and stills imagery confirmed at least some of the bioherms to be horse mussel reefs (Wildish *et al.*, 1998), whilst grab samples in the area indicated densities of up to 158 mussels/m² (Wildish & Fader, 1998). A similar survey off the Llyn Peninsula indicated that the reef there covered an area of approximately 0.5km by

3 km, exhibiting variable coverage within this range (Lindenbaum *et al.*, 2008). The same study reported only minor differences in area estimates and reef shape over several years and considered the North Wales biogenic reef was likely to have persisted for over 150 years. Such longevity may not be unusual. A study of horse mussels from multiple sites in the North and Irish Seas by Anwar *et al.* (1990), for instance, found most individuals to be in excess of 35 years old, whilst oldest studied was 48 years. This is indicative of a high degree of temporal reef stability.

3.3.5 Associated Species

Several studies have investigated the fauna associated with horse mussel reefs (e.g. Roberts, 1975; Rees *et al.*, 2008; Sanderson *et al.*, 2008). An indication of the diversity that they can support is shown by a study of horse mussel clumps in Strangford Lough which recorded 90 associated invertebrate taxa (Brown & Seed, 1977) and a widely cited but unpublished report which found 270 invertebrate taxa associated with horse mussel reef around the Isle of Man (Holt & Shalla, 1997). On some, but not all reefs, sponges, hydroids, red seaweeds, ascidians and brittlestars are abundant, whilst echinoderms such as urchins and starfish, as well as molluscs such as whelks are commonly found (Holt *et al.*, 1998). There is evidently much variability in associated communities of horse mussel reef around the UK, but no species are known to be restricted to them in their distribution.

3.3.6 Further Information

Much of the key literature regarding the horse mussel were produced in the 1970s and 80s by authors such as Seed and Brown, largely focusing on reproduction and growth (e.g. Seed & Brown, 1977; 1978; Anwar *et al.*, 1990). This work is being continued by the *Modiolus* Restoration Research Group (MRRG) based at the Queen's University Laboratory in Northern Ireland. The reader is also referred to work by DJ Wildish and colleagues for work undertaken in the Bay of Fundy on the hydrodynamics of horse mussel reefs and their wider effects on the environment, and to this and work undertaken in the Irish Sea for mapping surveys (Chivers *et al.*, 1990; Lindenbaum *et al.*, 2008).

Section 4

Sensitivities to Disturbance

The presence and scale of biogenic reefs are governed by the complex interplay of factors that on one hand allows them to build up and develop, and on the other to break down. Whilst the potential for development of reefs is largely determined by the environmental requirements and biology of the reef building species as outlined in the previous section, their decline is principally a result of disturbance. 'Disturbance' is used here to mean a process which removes biomass (Grime, 1977), that can act on both the reef building species and the communities which they support. It is a key mechanism in the determination of species abundance, distribution and diversity in many marine communities (Sousa, 1979; 1984; Witman, 1985; Connell *et al.*, 1997), and thus understanding its role is one of the greatest challenges to understanding the dynamics of natural populations (Alvarado *et al.*, 2001).

There are many potential sources of disturbance to biogenic reefs, both natural and anthropogenic in origin. Whilst reference is made to a range of biological, chemical and physical disturbances in order to give better context to the impacts of aggregate extraction, only the most severe are described here. Further details of the sensitivity of these reefs to disturbance, can be found in other reviews (e.g. Holt *et al.*, 1995; 1997; 1998). In keeping with these, sensitivity is defined here as the likelihood that an organism or community will suffer damage or death when exposed to an external factor beyond the range of environmental parameters normally experienced, and vulnerability as the likelihood of exposure of an organism to an external factor to which it is sensitive. They have both been taken into consideration under the general heading of 'sensitivity' here. Both concepts, together with representativeness and uniqueness, have been commonly used as criteria in the identification of areas or habitats requiring special management or protection (Zacharias & Gregr, 2005).

4.1 Predation

An association between the pink shrimp, *Pandalus montagui*, and ross worm reefs has long been accepted (Mistakidis, 1957; Warren & Sheldon, 1967), although it is not clear whether the association is due to the worms as a food source, or possibly more likely, as a function of the often prolific nature of the benthic food supply associated with the colonies (Warren, 1973). Other polychaetes, crabs and fish have also been noted to prey on the ross worm, though little attempt has been made to quantify the extent to which this occurs. The often high densities of *Asterias rubens* starfish that have often been noted in the vicinity of ross worm colonies may also be acting in a predatory capability on the reef structure.

Blue mussels are an important source of food for many benthic predators including invertebrates, flatfish and birds (reviewed by Seed & Suchanek, 1992 and Meire, 1993). Bird predation is largely restricted to intertidal mussels, which in some areas may be responsible for a yearly mortality of 25-40% (McGrorty *et al.*, 1990; Dankers *et al.*, 2001). Predation by fish and invertebrates is of greatest importance on the lower shore where it often prevents the subtidal extension of blue mussel beds, with predation by the starfish *A. rubens* having the potential to be particularly devastating (Dare, 1982; Kristensen & Lassen, 1997; Saier, 2001).

Predation of horse mussels, largely by crabs and starfish, is of great importance in determining the survival of juveniles (Brown & Seed, 1977; Anwar *et al.*, 1990; Tyler-Walters, 2007). It appears to wane dramatically as the mussels grow and become more difficult to open, however, to the extent that it may become negligible for adult mussels (Seed & Brown, 1978).

4.2 Competition

Competitive interactions between the reef building species and with other species is likely to be predominantly in the guise either of competition for space, or competition for food as a result of the filtration capabilities of large densities of the reef building species or other filter feeders. High densities of the brittle star, *Ophiothrix fragilis*, for instance, an efficient filter feeder, are thought capable of having a detrimental effect on both ross worm reefs and horse mussel beds not only through its filtration of food particles from the water column, but also as a result of filtration of their larvae (George & Warwick, 1985; Holt *et al.*, 1998).

Although the filtration efficiency of blue mussels is such that it may limit the food availability of a ross worm colony nearby, in areas where the sediment regime favours the worms, it is possible that they may out-compete mussels. Such a supposition was proposed to explain the population shift from one dominated by blue mussels to one dominated by the honeycomb worm in Heysham following changes in the sediment regime resulting from a number of sea defence developments (Holt *et al.*, 1998). It is possible that the ross worm may have a similar competitive edge in such conditions.

4.3 Invasive Species

Following its introduction in Europe for cultivation purposes, the Pacific oyster *Crassostrea gigas*, has spread to the extent that it has established a solid place in the Wadden Sea ecosystem where it competes for space with blue mussels (Fey *et al.*, 2010). Here it has taken over several mussel beds in the Dutch Wadden Sea, and almost all mussel beds are now considered to be oyster reefs in the German Wadden Sea. This species shift is, however, considered to be primarily a consequence of recent climatic conditions rather than a causative decline in the native species as a consequence of the exotic oyster (Nehls *et al.*, 2006). Reefs of the honeycomb worm in France are also becoming increasingly colonised by the Pacific oyster where it is thought that their high filtration rates may enable it to outcompete the worms for food (Dubois *et al.*, 2006). These and other such studies suggest the Pacific oyster has the potential to compete with biogenic reef species in UK waters, but although it is distributed throughout the UK

following an initial introduction in 1926 (Utting & Spencer, 1992), it does not currently appear to be giving great cause for concern here (Eno *et al.*, 1997).

4.4 Physical Impact

Although healthy colonies are durable and fairly robust, biogenic reefs are nevertheless relatively fragile structures that are consequentially vulnerable to physical damage. Such damage may arise from many sources – fishing activities, construction of offshore structures and aggregate extraction being examples – and this is considered to be the greatest vulnerability of ross worm reefs (Rees & Dare, 1993; Jones, 1999). Indeed trawling for shrimp or finfish, dredging for oysters and mussels, net fishing and potting are all believed to cause physical damage to erect ross worm reef communities. The impact of mobile gear is thought to break the reefs down into small chunks, thus changing the habitat for the rich infauna and epifauna associated with it (Jones, 1999). Shrimp fisheries in particular have been specifically implicated in the loss of several ross worm colonies from the Wadden Sea – attributed to the grinding of reefs with heavy gear (Reise, 1982; Riesen & Reise, 1982; Reise & Schubert, 1987), and in the approach channels to Morecambe Bay (Mistakidis, 1956). In the latter case, subsequent surveys suggest recovery of ross worms has not occurred despite the cessation of fishing many years ago (Sankey, 1987), although this seems most likely to be due either to lack of larval supply, or to permanent or ongoing alterations to the habitat (Holt *et al.*, 1998).

Following these and other similar reports, Vorberg (2000) undertook experimental and observational studies which indicated that the relatively light trawls used in brown shrimp (*Crangon*) fisheries would not cause serious damage to sabellariid reef constructions. Instead he proposed that the decline in the Wadden Sea reefs may have been due to natural disturbance such as storm tides, or anthropogenic measures such as dyking or construction of coastal-protection structures, changing the currents affecting larval distribution and the supply of tube-building material and nutrition. Although the natural growth and repair capacity of the ross worm is such that they can rebuild damaged parts of their dwellings within a few days provided they are not killed or removed from their tubes (Davies *et al.*, 2009), Vorberg's conclusions were

based on limited field experiments using single pass trawls with no nets. The possibility of impairment by shrimp fisheries in the medium to long-term cannot be ruled out in the event of intensive fishing, despite the relatively light gear. Trawling with heavier gear, such as those used by flatfish fisheries for example, is likely to have greater destructive potential. Indeed numerous studies have found significant evidence of trawl scars from unspecified fisheries through ross worm colonies (Collins, 2003; Pearce *et al.*, 2007 and references therein), indicating that damage from fishing gear is a real possibility.

Blue and horse mussels are also considered to have an intermediate to high intolerance to physical disturbance (Tyler-Walters, 2008 and 2007 respectively). A study on the Oregon coast of trampling on the California mussel *Mytilus californianus* beds, for instance, suggests this genus is susceptible to anthropogenic physical damage in this way (Brosnan & Crumrine, 1994), although intertidal colonies are likely to have limited exposure to physical disturbance as a consequence of fishing activities by virtue of their distribution. Subtidal beds in contrast, are likely to suffer damage from fishing activities as has been documented for horse mussel beds in Strangford Lough, not only by disruption to larger colonies reducing the value of the habitat, but also by damage, and presumably mortality, to individual mussels through scallop dredging (Service & Magorrian, 1997; Magorrian & Service, 1998). In the Wadden Sea, blue mussel beds are also considered under pressure from the extensive and heavily exploited mussel fisheries, especially from spat collection for aquaculture. This was attributed with the removal of close to the entire stock of blue mussels in this region between 1988 and 1990 (Dankers *et al.*, 1999).

4.5 Storms and Climate Change

Biogenic reefs require a degree of robustness to withstand sufficiently strong water currents for the provision of food and for ross worms, tube building material. However, it is possible that their stability is to some degree a function of stability of the substratum such that on less stable surfaces increased wave movement through storm events, for example, may reduce the stability of attachment. This may be especially true of thicker mussel beds where the byssal threads of the uppermost layers are attached

to the mussels beneath rather than directly to the substrate, although other studies have suggested that the beds develop a more stable structure as they mature (see Dankers *et al.*, 2001 and references therein). Heightened water movement could result in increased scouring and mortality of individuals (Jackson & Hiscock, 2008), or to the breakup of the biogenic structure altogether (Holt *et al.*, 1998). Such vulnerability to storms and tidal surges has been suggested for ross worm colonies (Holt *et al.*, 1998), and has been reported for mussel beds in the Wash, Morecambe Bay and the Wadden Sea (Nehls & Thiel, 1993; Holt *et al.*, 1998). Thus whilst a mussel bed may be destroyed in this manner, it has been suggested that individual mussels may survive such a disturbance with the possibility of initiating new beds (Reusch & Chapman, 1995). Elsewhere, however, it has been reported that displaced mussels rarely survive since they either become buried in sand or mud or are predated upon by birds (Dare, 1976).

As a consequence of their susceptibility to storms, increased storminess was considered to be the impact to which ross worms are most vulnerable in the event of climate change (Viles, 2001). Blue mussel beds may additionally be at risk from a reduction in salinity as a consequence of increased storm runoff, particularly in the intertidal, or to cold winters which have been blamed for the loss of intertidal mussel beds in the Wash and Wadden Sea (e.g. Dankers *et al.*, 2001). In contrast the aspect of climate change to which horse mussels were thought to be most susceptible is higher summer temperatures, potentially giving rise to changes in its distribution pattern (Viles, 2001).

4.6 Pollution and Water Quality

Anthropogenic chemical threats are primarily those associated with pollution. Hoare and Hiscock (1974) reported other workers had described the ross worm as a pollution indicator, but unfortunately did not include the relevant references in their manuscript. However, their own study and several by others suggest that it is unlikely the ross worm shows any special sensitivity to chemical contaminants or to changes in water quality (Jones, 1972; Walker & Rees, 1980; Holt *et al.*, 1997; Holt *et al.*, 1998) although direct evidence is limited. This may not be the case for associated biota, however (Connor *et al.*, 1997). Despite this, pollution is nevertheless listed

as one of the major threats to this species in the Wadden Sea. The reefs lost from this area, possibly as a consequence of fishing activities, were replaced by blue mussel beds and sand-dwelling amphipods *Bathyporeia* spp. This has been partly attributed to an increase in coastal eutrophication, favouring the mussels (Jones, 1999).

Mussels process large volumes of water and seston during feeding and bioaccumulate the contaminants which they absorb directly from the water and via suspended particulate matter (reviewed by Livingstone & Pipe, 1992 and Widdows & Donkin, 1992). Thus it has been suggested that blue mussel beds could have intermediate sensitivity to anti-fouling substances and heavy metal contaminants (Jones *et al.*, 2000), and that phytoplankton blooms, produced by nutrient enrichment (e.g., industrial and residential sewage discharge, agriculture), may also pose a threat (de Jong *et al.*, 1999). Elsewhere it has been suggested that blue mussels are generally tolerant of a wide range of contaminants (Tyler-Walters, 2008), although it is noted that generalisations about sensitivity to chemical pollutants are often too simplistic (Holt *et al.*, 1995; Holt *et al.*, 1997). Little information was found regarding the sensitivity of horse mussels to water contaminants, but it is thought likely to have a similar metabolism to that of the blue mussel and hence, possibly, a similar tolerance to chemical contaminants (Tyler-Walters, 2007).

4.7 Changes in Turbidity or Burial

Physical disturbances to the sea bed through trawling, installation of structures such as offshore renewable energy devices, laying or trenching in of cables or pipelines, beach nourishment and aggregate dredging for instance, all have the potential to increase water turbidity, at least in the short term. However, sabellariid organisms live in dynamic sedimentary environments and their populations can certainly persevere in turbid conditions, despite 'typical' natural levels of burial. Indeed some degree of sediment transport is essential for their tube-building, although an increase in siltation may clog feeding apparatus (Jackson & Hiscock, 2008). The physiology of blue mussels enables this species too to exist in areas of high turbidity, possessing efficient mechanisms both to reduce the influx of sand and to eliminate excess sand from the mantle cavity (de

Vooy, 1987). As a consequence of such abilities both blue (Tyler-Walters, 2008) and horse mussels (Tyler-Walters, 2007) are considered to have a 'low intolerance' to turbidity and siltation, thriving in areas that would be harmful to other suspension feeders, although high levels of suspended sediment may interrupt feeding, or result in the production of pseudofaeces at energetic cost (Navarro & Widdows, 1997). Increasing the inorganic particle load may also reduce the organic 'food' ingested through dilution as the blue mussel is non-selective in what it ingests and rejects as pseudofaeces (Foster-Smith, 1975).

In addition to increasing water turbidity, such offshore activities may also disturb the seabed to the extent that they result in burial of nearby habitats, although this is perhaps more likely to result from beach nourishment or spoil dumping (Miller, 2002). In such circumstances, both the honeycomb worm (Jackson, 2006) and ross worm (Jackson & Hiscock, 2008) are considered to have a low intolerance to smothering. The honeycomb worm for instance, was reported to survive short-term burial for days and even weeks in North Cornwall, Devon where sand depth may change one or two meters following storms. They were, however killed by longer-term burial (Wilson, 1970a). Similarly, current research on the burial tolerance of the ross worm has found that this species too can survive short term, episodic sand burial of at least several centimetres for up to 32 days, in some cases extending their tubes to such an extent whilst buried that they can re-surface (Last *et al.*, In preparation). Nevertheless, losses of some sabellarid reefs have been attributed to burial (Zale & Merrifield, 1989; Porras *et al.*, 1995), though no indications of the maximum tolerance could be found. A ross worm reef off the coast of Dorset, for example, appears to be periodically overwhelmed by large mobile sand waves (Collins 2003; Hiscock, 2004). Similarly transport of sand resulted in the burial of some ross worm colonies that had colonized a gas pipeline off the coast of Aberdeen such that the innermost limit of living colonies was displaced over 1.5km offshore (Braithwaite *et al.*, 2006). In Jade Bay, North Sea, the loss of a 2km² ross worm reef previously described by Schuster (1952), was attributed by Dörjes (1992) to burial as a consequence of mud deposition, although he pointed out that fishing could not be ruled out as having contributed to the decline. Evidence for rapid

burial of colonies has also been detailed by Schäfer (1972) in his descriptions of the paleoecology of worm reefs. He pointed out that rapid sedimentation kills the animals but can preserve the tubes as fossils, and attributed the normal cause of such rapid sedimentation to sudden bad weather. Perhaps such examples of colony loss as a consequence of burial suggest that sensitivity of ross worms to burial should not be dismissed too lightly, particularly in the event of activities which are likely to increase vulnerability to burial.

Current experimental work indicates that the blue mussel also has a degree of tolerance to burial, with some specimens surviving up to 32 days burial under several centimetres of sand (Last *et al.*, In preparation), and many other individual specimens being able to emerge from a shallow (2 cm depth) covering of sand following a single episodic burial. Whilst this capability would undoubtedly lessen the impact of sudden burial, it is unclear to what extent individual mussels might be able to resurface given attachment by the byssal threads of other individuals within a reef network. Indeed excessive levels of silt and inorganic detritus are thought to be damaging to blue mussels once they accumulate too heavily within the reef matrix (Seed & Suchanek, 1992), although the degree to which this might be influenced directly by water quality rather than production of faeces and pseudofaeces is unclear (OSPAR Commission, 2008). Sand burial has also been shown to limit lower regions of blue mussel zonation patterns in New Hampshire, USA (Daly & Mathieson, 1977) and this is probably important in some British locations, particularly in areas of shifting sands such as in Morecambe Bay and the Solway Firth (Holt *et al.*, 1998). Certainly burial of mussel beds by large-scale movements of sand, and resultant mortalities has been reported from Morecambe Bay (Dare pers. comm. reported in Holt *et al.*, 1998).

There is little evidence of the sensitivity of horse mussel to burial although they too have the potential to move up through gradually accreting mud in order to maintain their relative position within a growing reef network (Tyler-Walters, 2007), though the rate of accretion that they can tolerate is not known. A study into the long-term changes in contaminant loads associated with spoil disposal in the Humber, however, did detect contaminants in the shells of these long-lived animals indicating their survival

within the dispersal zone. But, the study did not indicate whether this was associated with a loss of condition (Holt *et al.*, 1998).

Although the ross worm can be regarded as being relatively insensitive to changes in water quality induced by man's activities, the exception to this will be situations in which sediment loadings are reduced to the extent that the supply of suitable material for tube construction and repair is restricted, perhaps due to changes in the hydrological regime as a result of a construction or coastal engineering (Nehring, 1999). It is unlikely ross worms will be unduly sensitive to increased sediment loadings (Holt *et al.*, 1997). A decrease in suspended sediment, especially organic particulates, could potentially reduce the food available to blue or horse mussels and hence their growth rates, but they are generally considered to have high intolerance to such an impact (Tyler-Walters, 2007; 2008).

4.8 Marine Aggregate Extraction

Marine aggregate extraction removes the substrate together with associated benthic fauna (see Boyd & Rees, 2003; Cooper *et al.*, 2007 and references therein). This will inflict severe, direct damage to any biogenic reef within the immediate vicinity (see Table 2). The distribution of ross worm colonies is such that co-occurrence is a strong possibility, as confirmed by dredging scars reported in close proximity to ross worm colonies (Foster-Smith, 2001a; Pearce *et al.*, 2007). Mussel beds, however, are likely to be much less vulnerable since there is currently little overlap between their distribution and licensed extraction sites.

In areas adjacent to aggregate extraction, the impacts on biogenic reefs from sediment plumes and sediment deposition derived from mechanical disturbance of the seabed by the drag head, or from the screening and overflowing processes are much less clear. This material comprises a large inorganic particulate load together with significant quantities of organic matter (Newell *et al.*, 1999), and may be carried for significant distances along the seabed as a benthic plume. However given that all three species commonly inhabit areas of high natural turbidity, their tolerance to the suspension and/or settlement of fine material during adjacent dredging activity may be high (Tyler-Walters, 2007; Jackson & Hiscock,

2008; Tyler-Walters, 2008). Though this has yet to be demonstrated conclusively, evidence from recent laboratory studies referred to in the previous section support this view, indicating furthermore, that tolerance to burial by coarser material may be even greater (Last *et al.*, In preparation). Deposition of such fractions is likely to result from the process of screening extracted material. Nevertheless, the tolerance of the biotic communities associated with these reefs may be much less and many studies have reported impacts on benthic community structure in the vicinity of dredging activity (e.g. Newell *et al.*, 1999; Cooper *et al.*, 2007), with variable predictions as to their recovery times.

In the field, a study of the recoverability of the ross worm reported colonisation of a site within a matter of months following the cessation of aggregate extraction (Pearce *et al.*, 2007). They concluded that the dredging activities had not, therefore, altered the seabed in a way that is detrimental to recolonisation, and further suggested that dredging may even be instrumental in improving recolonisation conditions given the high recruitment levels observed in this area. Large numbers of juvenile ross worms were also recorded a year after aggregate extraction at a similar site by a second study that suggested they may have benefited from a shift in sediment composition to a gravelly/sandy habitat (Cooper *et al.*, 2007). It should be noted, however, that both studies were undertaken at Hasting Shingle Bank where the screening of unwanted sediment fractions is not permitted (Cooper *et al.*, 2007). Thus these results relate solely to the process of aggregate extraction and not to associated screening. The benthic plumes generated by the latter process will have additional impacts that may hamper recovery, although the effects of suspended sediment on planktonic larvae, for instance, or on newly recruited juveniles through scouring, are unclear. Nevertheless, the prediction that development of ross worm colonies, to a stage equivalent to the oldest colonies observed in the area, was likely to be complete within three years following cessation of dredging is reassuring, despite high levels of trawling in the area. Similarly, in a study in the Wash, Foster-Smith (2001a) found that the best ross worm reefs seen in the area were associated with ground clearly scarred by dredging activity, and suggested that this may be a result of a

reduction in the overburden of sand having resulted in a cobble/sand habitat more suitable for ross worm colonisation.

4.9 Recoverability

The acceptability of many activities in the marine environment will depend, at least in part, on the persistence of any impacts after the activity has ceased. Thus an indication of expected recovery times will aid the management of the marine environment and of biogenic reefs in particular.

For the ross worm, there is inconsistency in the literature between estimates and reports of the speed of colony recovery following disturbance. Most pessimistic is that of the Wadden Sea Red List (Ssymank & Dankers, 1996) which classifies regeneration of this habitat as 'difficult' (15-150 years). A reflection, perhaps, of the apparent lack of recovery of ross worm colonies in the Wadden Sea following their dramatic decline over recent decades (Vorberg, 2005; Vorberg *et al.*, 2009). This is likely to be a consequence, at least in part, of the fundamental changes that have occurred in the Wadden Sea ecosystem (Reise & Schubert, 1987; van der Veer, 1989; Lotze, 2005), although fishing pressures, to which much of the losses have been attributed, still continue (Reise, 1982; Riesen & Reise, 1982). Similarly no recovery has been seen from the losses in Morecambe Bay for which there is no overriding explanation, although potential causes are discussed by Holt *et al.* (1997). Other reports, such as the studies undertaken at Hastings Shingle Bank (Cooper *et al.*, 2007; Pearce *et al.*, 2007), indicate recovery might be much more rapid (<5 years).

The latter studies, together with observations of apparently natural fluctuations in the structures of some populations (see Limpenny *et al.*, 2010), have led to the ross worm being considered as an '*r*-strategist'¹ (Holt *et al.*, 1998; Hiscock, 2004; Jackson & Hiscock, 2008). Such species typically exist well below the carrying capacity of their

¹ The ross worm has also been described as having the contrasting life-history strategy – a '*k*-strategist' (George & Warwick, 1985; Rees & Dare, 1993) – due to the persistence of some colonies and the belief that individuals are slow-growing and may live for several years (Wilson, 1974). This view is not widely held, however.

Factors	Sp.	Intolerance	Recoverability	Sensitivity	Confidence
Substratum loss	Ss	High	High	Moderate	High
	Me	High	High	Moderate	High
	Mm	High	Low	High	Moderate
Smothering	Ss	Low	Immediate	Not sensitive	Moderate
	Me	Intermediate	High	Low	Low
	Mm	Intermediate	Low	High	Very low
Increase in suspended sediment	Ss	Low	Immediate	Not sensitive	Moderate
	Me	Low	Immediate	Not sensitive	High
	Mm	Low	Immediate	Not sensitive	Low
Decrease in suspended sediment	Ss	Intermediate	High	Low	Moderate
	Me	Low	Immediate	Not sensitive	Very low
	Mm	Low	Immediate	Not sensitive	Low
Increase in turbidity	Ss	Tolerant	Not relevant	Not sensitive	High
	Me	Tolerant	Not relevant	Not sensitive	Not relevant
	Mm	Low	Very high	Very low	Moderate
Decrease in turbidity	Ss	Intermediate	High	Low	Low
	Me	Tolerant	Not relevant	Not sensitive	Not relevant
	Mm	Tolerant*	Not relevant	Not sensitive*	Very low
Abrasion & physical disturbance	Ss	Intermediate	High	Low	Low
	Me	Intermediate	High	Low	Moderate
	Mm	High	Low	High	Low
Displacement	Ss	High	High	Moderate	Low
	Me	Intermediate	High	Low	Moderate
	Mm	Low	Very high	Very low	Very low

Table 2. Sensitivity assessment of (Ss) *Sabellaria spinulosa* (Jackson & Hiscock 2008), (Me) *Mytilus edulis* (Tyler-Walters 2008) and (Mm) *Modiolus modiolus* (Tyler-Walters 2007) to the potential impacts of marine aggregate dredging, adapted from the MarLIN sensitivity assessment to which the reader is referred for further details (www.Marlin.ac.uk/sensitivityrationale.php). * The species may benefit from the change in external factor (intolerance has been assessed as “tolerant”).

environments (MacArthur & Wilson, 1967), and have life history strategies which enable them to exist in variable or unpredictable environments, responding to suitable conditions with a high rate of reproduction and rapid development (Krebs, 1985). Catastrophic declines and a high recovery rate are to be expected from such populations, although recovery will be subject to continued suitability of environmental conditions and larval supply. The impact of various disturbances on these aspects are

poorly understood, and hence limit predictions on recovery that requires further investigation. The inherent variability in recruitment success adds a further element of unpredictability to recovery rates

Blue mussels too may be considered to have an ‘r’-life history strategy, acting as an opportunistic species by colonizing quickly and growing rapidly to reproductive size (Suchanek, 1978). Recruitment is favoured by cold preceding winters due to

decreases in predator populations and delays in the arrival of newly settled predators allowing maximum time for growth to reproductive size before the onslaught of heavy predation. Blue mussels appear to spawn at a time which is best for maximizing settlement opportunities and/or maximizing growth before being preyed upon (Suchanek, 1978). Good annual recruitment is possible and juvenile beds can develop regularly, but spatfall and recruitment in some beds of blue mussels is very variable year on year, and the survival rate of juvenile beds is low (Dankers *et al.*, 2001). Recovery of beds from disturbance may, therefore, take several years (at least five – Tyler-Walters, 2008), on cessation of the disturbance and given continued suitability of environmental conditions. Such natural recovery has been observed in many areas of the Wadden Sea where newly formed mussel beds are protected from fisheries (Dankers *et al.*, 2001).

The horse mussel, in comparison, does not become sexually mature until it is several years old (Anwar *et al.*, 1990), and these large but slower growing mussels then enjoy enhanced longevity (Seed & Brown, 1978), potentially compensating for poor annual recruitment. Recruitment appears sporadic and generally low, though varies with season, location and hydrographic regime (Seed & Brown, 1978; Brown, 1984). Newly settled larvae and juveniles require the protection of adults to avoid intense predation pressure and hence any population reduced in extent or damaged through disturbance is likely to take many years to recover if at all (Tyler-Walters, 2007). Such appears to be the case following the severe decline in horse mussel beds in Strangford Lough, attributed to habitat disturbance by mobile fishing gear (Roberts *et al.*, 2004).

Section 5

Detecting, Mapping and Sampling Reefs

Surveys designed to map the distribution of biotopes, such as biogenic reefs, usually combine acoustic remote sensing with sampling or observation using video/camera systems. Although biogenic reefs can sometimes be 'seen' on remotely sensed images, experience has shown that this is not sufficiently reliable for remote sensing alone to be used for detection and mapping for two reasons: Firstly, there can be confusion between reef structures and some other habitats, such as cobble and irregular sand waves. Secondly, although the detection of well-developed reefs might be definitive, less well developed structures (still qualifying as reef) may not produce a strongly characteristic image. The general advice to surveyors is to 'ground truth' areas that remote sensing indicates might support reef and to sample at least some adjacent areas where reef is not predicted to support any inference about the distribution of reef. Acoustic remote sensing, therefore, is used to detect likely reef structures and, once confirmed by sampling or observation, to assist in the process of delineating the areas of reef.

5.1 Acoustic Remote Sensing

Most surveyors, particularly with a background in hydrography rather than biology, favour the direct interpretation of images, and sidescan can provide high resolution images showing reef-like structures from the acoustic 'shadows' thrown by small topographic features. Patterns in the backscatter strength also can reveal areas of high rugosity often associated with reefs. Figure 8 is typical of sidescan from an aggregate extraction area. The features marked as '3' would be associated with reef, but would need ground truthing to establish this with certainty. This signature may also be found with coarse sand waves.

Multibeam systems are also strongly favoured by geoscientists because the detailed bathymetric data acquired can be used to create a digital elevation model (DEM) (Figure 9). This can then be manipulated (through false illumination from varying directions and angles, and also by careful selection of

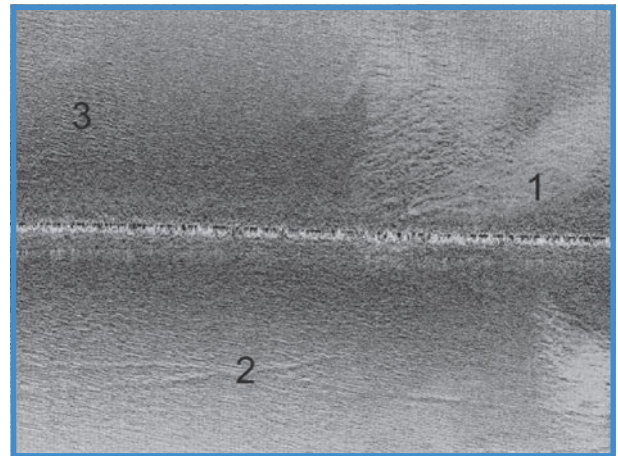


Figure 8. Sidescan image from licensed extraction site Area 107 using a GeoAcoustics SS941; 1 – low backscatter area of sand waves; 2 – dredge furrows; 3 – strong backscatter with heterogeneous texture/small features, often a signature of ross worm reef (Limpenny *et al.*, 2010).

colour scales) to show features of interest. Profiles can also be calculated across any feature from the DEM which has the potential to show fine scale relief such as those of biogenic structures. Multibeam also provides backscatter, similar to sidescan though not of the same resolution. Because multibeam systems are hull-mounted rather than deep towed, the backscatter does not show shadows generated by small objects.

Single beam acoustic ground discrimination systems (AGDS) record hardness and roughness properties of the sea floor and a given combination of values can provide a 'signature' that indicates particular habitats (Figure 10). These systems are relatively inexpensive and are often used by the fishing industry, particularly prawn fishers. However, they have lost favour with many surveyors primarily because the data recorded usually require some processing with reference to ground truth data before they can be properly interpreted, whereas it is assumed (probably incorrectly) that sidescan images do not require inferential interpretation. Nevertheless AGDS

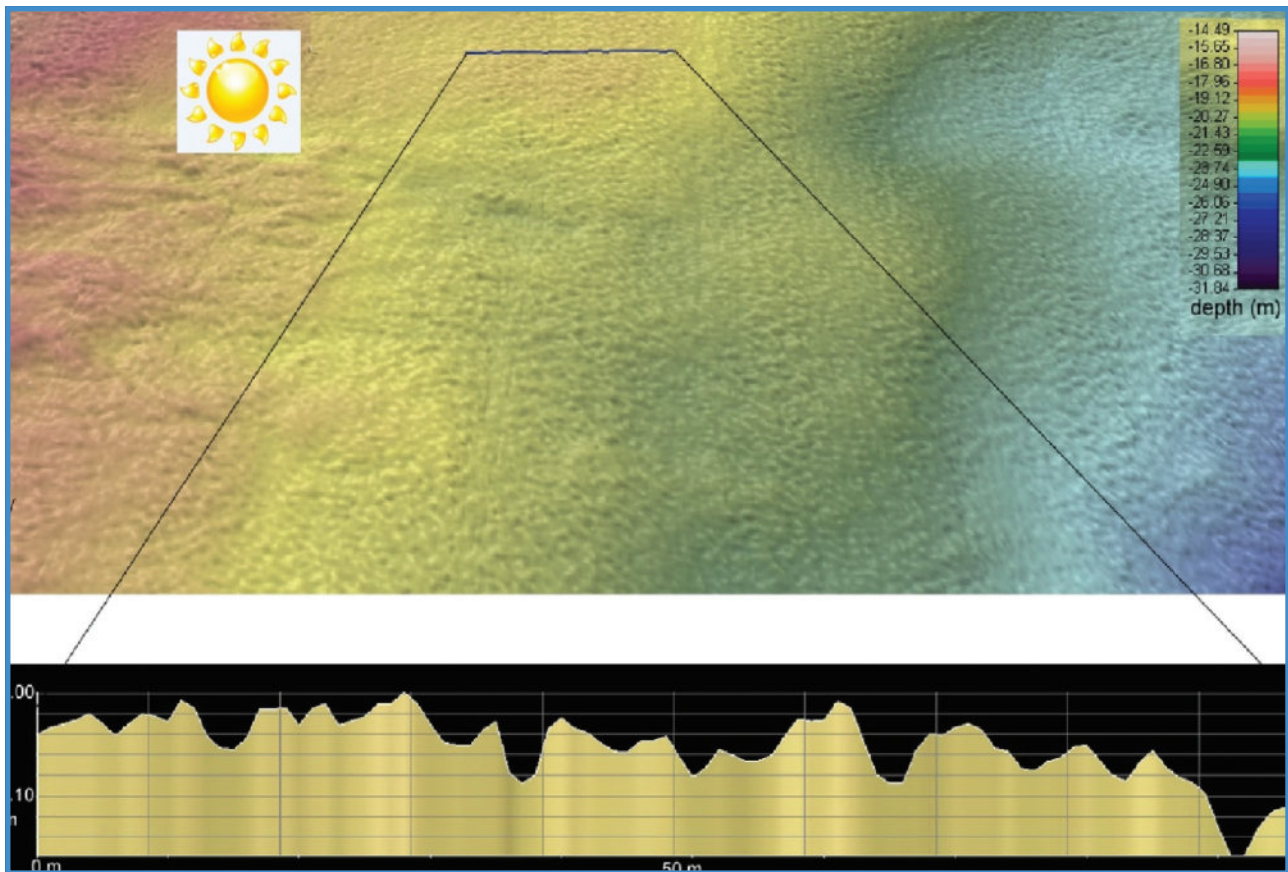


Figure 9. High-resolution multibeam bathymetric data from licensed extraction site Area 107: The top panel shows the DEM as viewed from a 45° angle with false illumination from the top left. The colour scale has been chosen to accentuate the small changes in depth across the image. The lower panel is a profile taken from the DEM showing small-scale topography in the order of a few centimetres (Limpenny *et al.*, 2010).

still provide additional information on sediment characteristics by overlaying the values on swath images at very little extra effort.

5.2 Sampling

Sampling biogenic reefs can be problematic because: firstly, the sensitivity of the habitat often precludes destructive sampling (especially dredges and trawls); secondly, the inherent patchiness of reef habitats may mean that replicate sampling is required to be confident that reef is absent; and thirdly, high turbidity often found at reef habitats limits the use of video/camera.

For most purposes, a light weight towed video system provides the ideal ground truthing tool since it can sample continuously along a transect of a few hundred metres (ensuring heterogeneity is properly quantified), and it does minimal damage to the reef. High definition video can provide good quality frame grabs and the inclusion of a stills camera on

the sledge (whilst providing higher quality images) may not be justifiable. Also, moving images give a better idea of the three dimensional structure of reef features than stills. Forward looking video is favoured because, given reasonable visibility, it shows a wider field of view than vertical systems. Systems for analysis of video to extract quantitative or semi quantitative information are well established (Holt & Sanderson, 2001; Envision, 2010).

Water lens (or water curtain) cameras have been used in areas of very poor visibility that have a freshwater filled chamber between camera and the sea floor. The results can be disappointing since the chamber can accelerate the near-seafloor water current and disturb the sediment. Nevertheless, they may be the only option if there is no flexibility in the survey to use periods of calm weather/neap tides for ground truthing.

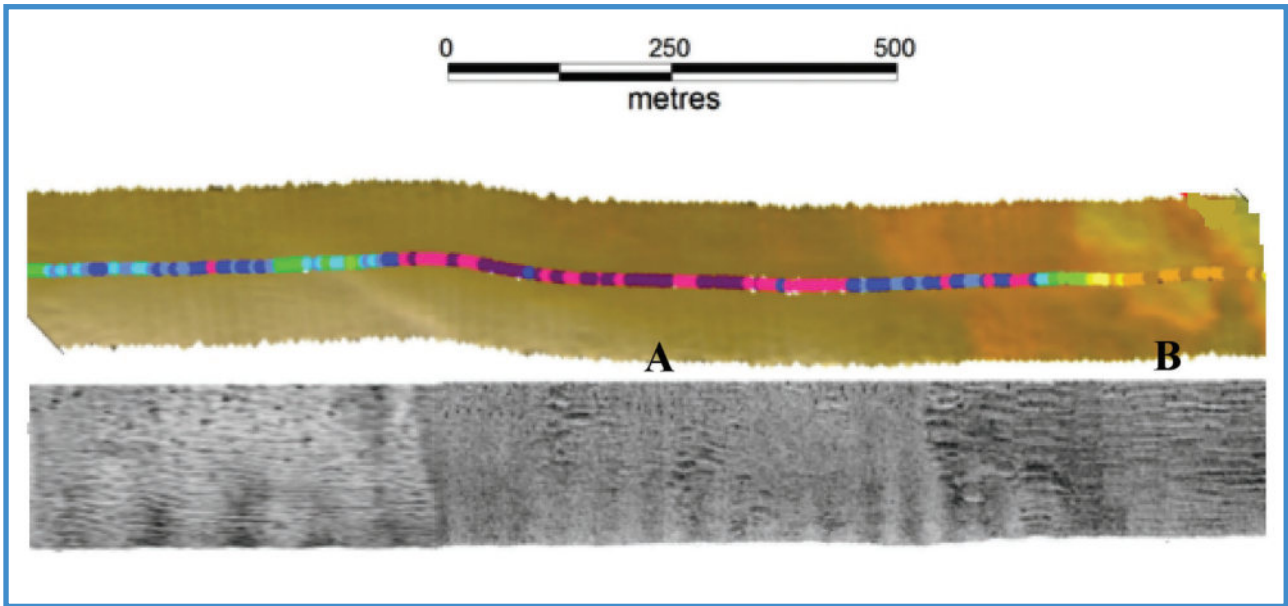


Figure 10. An area of fairly uniform topography from the Norfolk coast: Multibeam bathymetry (top) and backscatter (bottom) with an ADGS system – RoxAnn™ hardness values superimposed on the multibeam. Ground truthing indicated position 'A' was gravelly sand and small clumps of ross worm were found at position 'B' where the sediment gave a much softer echo (Envision 2008).

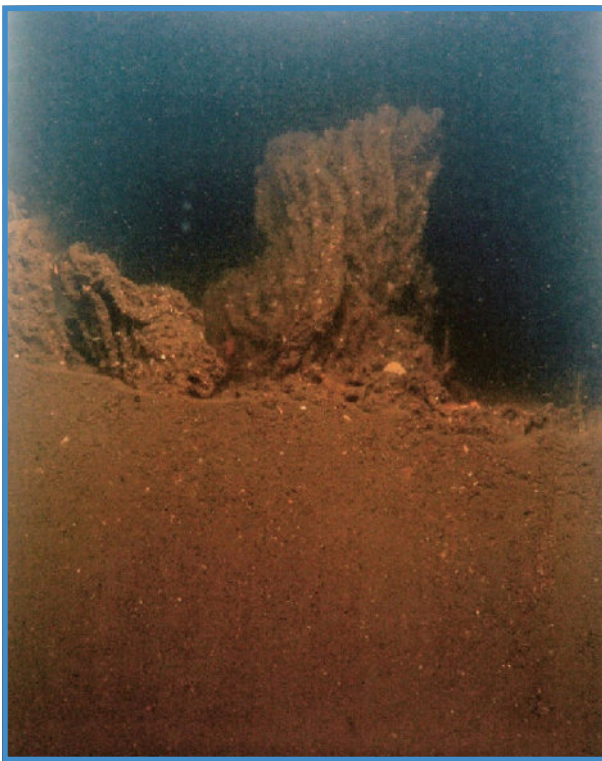


Figure 11. Ross worm tubes approximately 5 cm in height, on a sandy sediment taken with the SPI camera. The image shows clearly that the tubes are superficial and not deeply rooted into the sand (Image © CEFAS).

Sediment profile imagery (SPI) is a rapid method for characterising the benthic habitat at and below the surface of the seabed (Solan *et al.*, 2003). The system consists of a camera mounted above a wedge shaped prism with a plexiglass faceplate. The prism has a mirror mounted at a 45 degree angle which reflects the profile of the sediment water interface to the camera mounted above it. The prism is pushed into the sediment under gravity and a photograph taken of the vertical profile through the sediment and any structures above the sediment surface (Figure 11). It can obtain images in poor visibility and also gives an insight into the subsurface structure of biogenic reefs.

Remotely operated vehicles (ROVs) have also been used and can produce high quality data if the visibility is good. However, their expense and the time involved with each deployment make small towed systems an attractive option for obtaining large numbers of samples in a short time. Other specialist observation systems include cameras combined with sidescan (Foster-Smith *et al.*, 2010) and landers with scanning sonar and cameras (Limpenny *et al.*, 2010).

Taking samples using a grab may be the most certain way of establishing the presence of reef-building animals, especially when low lying reef-like structures are important. Additionally, information

	Suitable Survey Area	Strengths	Weaknesses	Comments
ADGS based on a single beam echosounder	Any size.	Discrimination of sediment good. Ease of use, inexpensive.	Resolution very low. Incomplete coverage.	Use in conjunction with swath systems to assist discrimination.
Sidescan SONAR	Any size, but complete coverage at slow towing speeds time consuming. Targeted survey of 1 sq.km at slow towing speed, low altitude and restricted range best suited for reef survey.	Very high resolution and can reveal features 10cm tall. Good coverage. Images easy to interpret.	Image depends on deployment, especially towing height and speed. Does not record depth across the swath. Can miss features as detection depends on orientation. Towing can foul static fishing gear.	The system of choice if suitably deployed and this might be best suited for targeted survey.
Multibeam	Any size, but complete coverage time consuming. Can use fast vessel speeds (10+ knots).	Good resolution. Records depth and resulting images can show fine scale topography. Hull-mounted and less risk to fishing gear.	Backscatter images inferior to sidescan. Probably at limits of resolution for well developed biogenic reef.	Full bathymetric coverage probably outweighs resolution issues
Sledge-towed sidescan	Small areas.	Small, high resolution CHIRP sounders deployed close to the sea floor give excellent resolution. Can be combined with cameras.	Survey needs careful planning: Towing requires care and areas must be free of obstructions. May not be suitable for large survey vessels. Coverage of swath limited (20m).	Targeted survey for confirmation of reef development. Mapping small areas in detail.
Scanning sonar	Point locations.	Very high definition sidescan producing near photographic images. Combined with cameras.	Needs a 'lander' and is difficult to deploy in strong currents. Very limited coverage.	More of a ground truthing tool that can be deployed from any vessel.

Table 3. A summary of the strengths and weaknesses of acoustic remote sensing techniques that have been used for mapping reefs (based on the summary of findings in ALSF reports Foster-Smith *et al.*, 2010 and Limpenny *et al.*, 2010).

on the density of the reef builders and a quantitative assessment of associated biodiversity may be required for a full assessment of the development of the reef and for condition monitoring. The slight damage caused to the reefs must be offset against the gain in knowledge. It is customary to take three replicate samples for offshore biological surveys, but statistically robust sampling will undoubtedly require more sampling with the number of samples required determined by the effect size and levels of confidence required. A further refinement of grab sampling is to mount a small downward facing CCTV bullet camera on the grab so that the sample can be taken from the targeted habitat when the sea floor is heterogeneous.

The acoustic remote sensing techniques that have been used for mapping reefs and their strengths and weaknesses are summarised in Table 3 (based on the summary of findings in ALSF reports Foster-Smith *et al.*, 2010 and Limpenny *et al.*, 2010).

Section 6

Challenges to Management

There are many challenges for those tasked with the management of biogenic reefs, not least the difficulties posed by their detection, mapping and sampling as described previously. Distinguishing 'reef' from non-reef colonies, and protecting a naturally fluctuating habitat are also problematic.

6.1 Identification of 'Biogenic Reef'

The literature abounds with different definitions of 'biogenic reef'. This is unsurprising given the gradations that exist from solitary individuals of reef-building species to dense, continuous colonies leading to difficulties in deciding what does or does not constitute a 'reef'. The distinction is important since the conservation drivers relate solely to the reef habitat provided by dense colonies and not to the species themselves. The difficulty is compounded by slight differences in interpretation of the term by different regulations, and from the inconsistencies between them, particularly in regard to 'crustose' formations of the ross worm. This heightens the importance for a clear interpretation of the term in any given context since the ambiguity is unsatisfactory both to regulators and to industry, particularly in regard to predicting the potential effects of proposed offshore activities.

Holt *et al.* (1998) highlights the difficulty in categorising mussel reefs in their description of the semi-infaunal and infaunal forms of horse mussel colonies, whilst the difficulties of defining 'biogenic reef' are discussed in greater depth in Limpenny *et al.* (2010), in the context of the ross worm. The latter review illustrates that there is a degree of commonality between definitions. The characteristics which are important in the determination of the 'reefiness' of a structure incorporate some or all of the following:

- Physical characteristics: elevation, sediment consolidation, spatial extent and patchiness;

- Biological characteristics: density of reef-builder, biodiversity and community structure; and
- Temporal characteristics: longevity and stability.

To aid the assessment of a given ross worm colony, Hendrick & Foster-Smith (2006) devised a decision making support tool to improve clarity and consistency of the evaluation. The approach is, however, equally appropriate for colonies of the blue or horse mussel if adapted with appropriate scales and thresholds for these species. This multi-criteria scoring system to determine the 'reefiness' of a given colony reflects their multifaceted natures through scoring a series of physical, biological and temporal characteristic reef features. These features can be graded on a sliding scale of low-medium-high 'reefiness' adaptable to a variety of appropriate data types. Whilst an overall score summarising a series of complex features can be derived by this method and hence could be used as a threshold to distinguish between reef and non-reef, it is stressed that reliance on the single score is likely to be an oversimplification. The importance of the approach lies more in the structured consideration of all the reef characteristics and the scoring process itself.

It is further suggested that each individual reef characteristic score is augmented with a second score indicating the confidence in the former, and that both of these scores are weighted according to the perceived importance of the feature for the given application. It was thus hoped that the approach will provide a relatively robust, transparent and standardised procedure for classifying a ross worm colony, though recognising that numerous aspects of the scoring system will be subjective and that the practicalities of scoring each reef-feature may not be feasible in all instances. Nevertheless, it was expected that the breakdown of a particular assessment through focused consideration of multiple characteristics, each scored independently, will promote consistency of overall classification. Furthermore, whilst it is possible to allow for missing data in an algorithm to quantify overall reef quality,

many of these features are inter-linked. Hence as long as available information gives some indication of the physical, biological and temporal characteristics of the colony it was hoped that the approach would provide a reliable overall indication of the appropriateness of the categorisation 'reef' and of its quality, whilst highlighting areas where information was lacking.

Application of the approach to the UK definition of 'reef' in inshore and offshore waters as interpreted and clarified by the statutory nature conservation agencies (Johnston *et al.*, 2002), was discussed at an inter-agency workshop on defining and managing ross worm reefs (Gubbay, 2007). It has since been utilized in the assessment of several ross worm reefs (e.g. JNCC & NE, 2010b, c; Pearce *et al.*, 2007).

6.2 Challenges Posed by the Biology of Reef-Building Species

As discussed previously, the spatially patchy nature of reefs, which can be heterogeneous at very small scales – certainly from metre to metre (Foster-Smith, 2000; Foster-Smith & White, 2001), will complicate the ability to assess their status, particularly using point sample methodology. The temporal dynamics of the structures will complicate the ability still further. Although a reef as a whole may be a persistent feature, the formation of patches within it is a dynamic process (Svane & Ompi, 1993). Thus various different levels of scale need to be considered in any assessment of their dynamics or sensitivities. Differences in recruitment, growth and mortality are likely to occur at all scales and as will variations in the associated fauna and flora (Holt *et al.*, 1998).

In addition to the difficulty in assessing the status of a temporally dynamic structure, the apparently ephemeral nature of many of these biogenic reefs brings a further problem for their management. Protection of habitats through designation of a specific site is expectant of some degree of stability of the targeted habitat. The designation process itself is lengthy and the decline or disappearance of the target habitat before the process is completed can prove unpropitious. Unless conservation efforts can be targeted towards reefs of proven or predictable stability, supporting evidence for which

is not currently available, ring-fencing reef habitats for protection through long-term site designation could prove somewhat futile.

Instead, consideration of a much broader site within which are areas considered to be suitable/likely for reef development and/or with proven ability to support high density populations of reef builders may be more beneficial. Thus it may be expected that the target habitat is likely to be extant somewhere within the broader region at any one time although the probability of the habitat prevailing in any particular area within that wider region may vary. This approach is perhaps more comparable with that of conservation of mobile species rather than habitats, affording protection to the processes and environmental conditions which allow biogenic reefs to develop.

An alternative approach would be to designate smaller and more targeted biogenic reef sites, but with the expectation that they may only be enforced for a relatively short period whilst the reefs remained in existence. To be effective, designation must be achievable in a much shorter time scale (months rather than years), with the justification for continued protection of the site being assessed on a regular time scale (as frequently as possible though likely to be in keeping with current review periods and standards of reporting of 5-6 years). Such a strategy could prove particularly helpful if high density colonies prove to be an important larval source for the wider population since it could afford protection to the extant reef whilst being more lenient to offshore activities and developments with a relatively limited sphere of impact.

A synergy of the two approaches may prove even more constructive whereby extant reefs are regularly mapped within a larger supporting site boundary. Exclusion zones could then be established around the mapped reefs, ostensibly as a fishery management tool, with boundaries dependent on water depth and consequently trawl warp length, acting as a suitable buffer. Specific activities could then be managed through the Environmental Impact Assessment (EIA) process and mitigated through avoidance of mapped reef areas within the wider site. Developments in areas that have not been known to support reef are then likely to be given preference.

Finally, whilst this review focuses on just three reef-building species, it nevertheless indicates that there is perhaps surprisingly little consistency in the biology and ecology within the grouping 'biogenic reefs', which is to some degree an artificial conglomerate of biotopes with differing characteristics (Holt *et al.*, 1998). These reefs, and the constructor species, differ markedly in their responses to disturbances and their ability to recover, and cannot therefore, be considered a uniform entity that can be covered by the same management response. Instead, management should be tailored to each species on a case by case basis. Indeed management effort is typically targeted towards the ross worm and the blue mussel over that of the horse mussel, a reflection of the increasing challenges of their spatial variability.

Section 7

Summary of Gaps in Knowledge

This monograph highlights the complex nature of biogenic reefs and outlines their ecological importance. However, it is clear from this review that there are still many gaps in our knowledge of these habitats and we are far from a full understanding of the environmental conditions under which they form, the process of their development and decay, and an appreciation of what constitutes natural variation in reef habitats. Determining the acceptable limit of change for monitoring and management purposes is further complicated by the inevitable fluctuations in abundance and diversity of associated fauna and flora which will be superimposed upon the variations in the underlying reef habitat. A greater knowledge of all these aspects would aid the development of appropriate management plans.

At a basic level, there is still a great deal of uncertainty regarding the distribution and prevalence of reef habitats. This is due in part to the difficulty in deciding what constitutes 'reef' as opposed to a 'non-reef' habitat, although greater clarity in this distinction has been achieved for ross worm colonies in recent years. Further work is still needed in this respect for both blue and horse mussel colonies. Whilst remote sensing techniques have improved our appreciation of the extent and patchiness of reef, there are still difficulties in detecting subtidal reef habitats with certainty. The temporal instability of some ross worm colonies complicate efforts to map reef distributions still further. Where information does exist, collating colony descriptions into an accessible, centralised dataset together with any associated metadata would be enormously helpful not least for clarifying the extent of these biogenic resources, but also for putting colonies into context and for the identification of any trends.

A key aspect of the population dynamics that remains in question is the typical extent of larval dispersal, and the key source(s) of larvae for reefs of all the species discussed. The larvae of all three spend several weeks in the plankton so their dispersal potential is considerable. It is possible therefore, that

some reefs may be generated and/or perpetuated by larvae from distant sources such as the widely distributed, but low density population. Localised disturbances would therefore be less likely to impact on future larval supply than if the reefs are primarily self-recruiting, thus improving the likelihood of future reef development and recovery. However, reefs contribute a high percentage of individuals in the overall population (Limpenny *et al.*, 2010), thus it is also possible that they contribute significantly to the total larval supply, perhaps to the extent that high densities of larvae produced by reefs might be necessary for a heavy settlement of spat in order to establish a new reef. Larvae derived from a reef may also comprise the main larval source of the more widely distributed adults. This being the case, the loss of a particular dense colony will have far reaching consequences beyond its immediate vicinity, bolstering the importance of conservation measures to protect such habitats. A connectivity through larval supply between the ross worm reefs within the Wash and those in its approaches has been suggested given the predominant water currents associated with this region (JNCC & NE, 2010c). The possibility that more distant ross worm colonies are recruited from similar sources, is consistent with the results of a preliminary investigation which found minimal variations in RNA gene sequences between colonies sourced from a wide geographic range (Hendrick, 2007). Conversely, this finding may also be indicative of a high degree of genetic mixing within the population or that genetic isolation, if it has occurred, was relatively recent.

Identification of the larval source is only the first step of the whole life history of the reef structure that requires greater clarification. It is only with full understanding of the whole process of reef formation, growth and decay that the severity and temporal extent of a given disturbance can be fully identified against a background of natural variation, and for predictions of the timescale of recovery to be made with any confidence. Such understanding requires further investigation of the role of biotic

disturbances, particularly predation, on reef structure and function, and of their environmental requirements in regard to turbidity, sediment supply, water quality and movement for instance.

Finally, an improved understanding of the relationship between biogenic reefs, their associated communities and the surrounding physical environment at any given stage in the developmental cycle of the reef is necessary to determine how habitats are structured by reef evolution. Only little is known about how water flow interacts with biogenic structures. The intensity of this fundamental interaction is critical in driving other processes such as particle flux, entrainment and ultimately biodiversity. It is important that we further our understanding of these processes as it is likely to determine how individuals form reefs, how a reef is sustained over time and how the degradation of a reef will affect the wider biotic community. Currently a lack of evidence leads to uncertainty in the management of reef species, limiting the ability of scientists, conservationists and managers to effectively conserve structure-forming organisms and the habitats that they create. Addressing these gaps in knowledge will allow better predictions of the communities that are likely to result following the loss of a reef structure in any given location.

Section 8

Glossary of Terms

Aggregation

Organisms (usually of the same species) living closely together, but not physically connected (cf. 'colony').

Benthic zone

The ecological region at the lowest level of a body of water, including the sediment surface and some sub-surface layers. The organisms living within this zone are called **benthos**.

Biodiversity (biological diversity)

"The variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems." (UN Convention on Biological Diversity, 1992).

Bioherm

A circumscribed mass of rock exclusively or mainly constructed by marine sedimentary organisms such as corals, algae, and stromatoporoids. Also known as organic mound.

Biotope

A term referring to the combination of physical environment and its specific assemblage of conspicuous species.

Byssus threads

A silky filament by which certain molluscs attach themselves to hard surfaces.

Circalittoral

The area of the continental shelf sea-bed that lies below the zone of periodic tidal exposure.

Colony

1) A group of organisms of the same species living connected together in a common mass (cf. 'aggregation'). 2) A group of organisms connected by behavioural or sociological factors (e.g. seabird colony, seal colony).

Conspecific

Belonging to the same species.

Fauna

The animal life of a particular region. This includes the following subdivisions:

Epifauna

Animals living on the surface of the seabed.

Infauna

Benthic animals which live within the seabed.

Macrofauna

Benthic animals that are more than 1 mm in length.

Semi-infaunal

Organisms that live partially buried in the seabed.

Fecundity

The potential reproductive capacity of an organism or population.

Gregarious

Living in groups or communities, growing in clusters.

Heterogeneity

The quality or state of being heterogeneous or lacking in uniformity.

Hydrodynamics

The branch of science concerned with the mechanical properties of fluids.

Metamorphosis

A profound and relatively abrupt physical change in the life history of an organism through cell growth and differentiation.

Pseudofaeces

Filtered material which is rejected by bivalve molluscs without having passed through the digestive tract.

Sessile

Permanently attached to a substratum, at least in adult form.

Seston

The total suspended particulate matter in the water column, including plankton, nekton and both organic and inorganic suspended particulates.

Substratum (pl. substrata)

Surface available for colonisation by plants and animals.

8.1 Abbreviations Used in Text

AGDS

Acoustic Ground Discrimination System

BAP

Biodiversity Action Plan

DEM

Digital Elevation Model

EIA

Environmental Impact Assessment

HAP

Habitat Action Plan

JNCC

Joint Nature Conservation Committee

MarLIN

Marine Life Information Network

MCZ

Marine Conservation Zone

MPA

Marine Protected Area

OBIS

Ocean Biogeographic Information System

RNA

Ribonucleic Acid

ROV

Remotely Operated Vehicle

SAC

Special Area of Conservation

SCI

Site of Community Importance

SPA

Special Protection Area

SPI

Sediment Profile Imagery

Section 9

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