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The Ecology of Sabellaria spinulosa Reefs

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THE ECOLOGY OF *SABELLARIA SPINULOSA* REEFS

by

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Copyright Statement

Abstract

Bryony Pearce - The Ecology of *Sabellaria spinulosa* Reefs

Reef habitats built by the tubiculous polychaete *Sabellaria spinulosa* have been identified as a habitat with significant conservation importance, based on their historic decline across Europe and the assumption that, like many other biogenic reef systems, *S. spinulosa* reefs enhance biodiversity. Despite the high conservation status of this habitat very little work has been undertaken to explore the role that *S. spinulosa* reefs play in marine ecosystems, or their sensitivity to anthropogenic disturbance. Observations of the reproductive ecology and population dynamics of the reef building organism indicate that *S. spinulosa* exhibit life-history traits typically associated with *r*-strategists, indicating that this species is likely to have the ability to recover quickly following most anthropogenic disturbance events. A series of surveys on *S. spinulosa* reefs identified at the Thanet Offshore Wind Farm site, where the extent of the reef habitat was found to have increased between the pre-construction and post construction survey despite extensive cable laying and turbine installation, corroborates these findings. Detailed investigations into the macrofauna associated with *S. spinulosa* reefs in the eastern English Channel revealed that *S. spinulosa* reefs support macrofaunal communities that are comparable to those associated with adjacent muddy sandy gravel and gravelly muddy sand in terms of species composition, taxonomic breadth and beta-diversity. A consistent enhancement in species richness, abundance and biomass was identified in samples collected from *S. spinulosa* reefs when compared with adjacent sedimentary deposits, as well as a corresponding reduction in the equitability of species, indicating that some macrofauna are able to exist in higher densities within this habitat. The increase in macrofaunal biomass associated with *S. spinulosa* reefs was found to influence the diet of demersal fish species, with some species feeding on the reef organism itself while others feed on species found in high densities on the reefs. The high abundance of juvenile flatfish associated with this habitat also suggests that *S. spinulosa* reefs may provide an important nursery habitat.

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List of Abbreviations

AA	Appropriate Assessment
AMBI	AZTIs Marine Biotic Index
BAP	Biodiversity Action Plan
BCD	Below Chart Datum
BRUV	Baited Remote Underwater Camera
CBD	Convention on Biological Diversity (Rio)
CFP	Common Fisheries Policy
DAPSTOM	Database and Portal for Fish Stomach Records
Defra	Department of Environment Food and Rural Affairs
DEM	Digital Elevation Model
DOENI	Department of the Environment Northern Ireland
EC	European Commission
EEA	European Environment Agency
EFH	Essential Fish Habitat
EIA	Environmental Impact Assessment
EMS	European Marine Site
ES	Environmental Statement
EUBS	EU Biodiversity Strategy
EUNIS	European Nature Information System
FOCI	Feature of Conservation Importance
GES	Good Environmental Status
HAP	Habitat Action Plan
IMS	Industrial Methylated Spirit
JNCC	Joint Nature Conservation Committee
IEEM	Institute of Ecology and Environmental Management
IROPI	Imperative Reasons of Over-riding Public Interest
MALSF	Marine Aggregate Levy Sustainability Fund
MBES	Multibeam Echo Sounder
MCZ	Marine Conservation Zone
MEPF	Marine Environmental Protection Fund
MESL	Marine Ecological Surveys Limited

MMO	Marine Management Organisation
MPA	Marine Protected Area
MSFD	Marine Strategy Framework Directive
NRA	National Rivers Authority
ODPM	Office of the Deputy Prime Minister
PMF	Priority Marine Feature
PSA	Particle Size Analysis
RA	Reference Area
REC	Regional Environmental Characterisation
SAC	Special Area of Conservation
SACFOR	Superabundant, Abundant, Common, Frequent, Occasional, Rare
SE	Standard Error
SEA	Strategic Environmental Assessment
SEM	Scanning Electron Microscope
SNCB	Statutory Nature Conservation Body
SNH	Scottish Natural Heritage
SPA	Special Protection Area
SPM	Suspended Particulate Matter
TCE	The Crown Estate
TRO	Total Residual Oxidant

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I am most grateful for the advice and suggestions of Dr Paul Somerfield of the Plymouth Marine Laboratory and Professor Jason Hall-Spencer of the University of Plymouth, both of whom have taken an active interest in my research. Sincerest thanks also go to Professor Mike Cowling of The Crown Estate and Ian Reach of MarineSpace Ltd (formerly of Natural England) who have also taken an active interest in my research and provided valuable research funds. I am particularly grateful to Dr Andrew Bellamy of Tarmac Ltd, Graham Singleton of Cemex Marine Ltd and Dr Ian Selby of The Crown Estate (formerly of Hanson Aggregates Marine Ltd) who have supported my research financially through the Resource Management Association (RMA) as well as providing me with valuable industry data and allowing me access to their development sites during the course of my research. Likewise, I am grateful to Kirsty Goodwin of Vattenfall and Gregory Shaw of Haskoning DHV UK Ltd for giving me permission to use data collected at the Thanet Offshore Wind Farm site for licensing surveys in my PhD studies and subsequent publications, as well as providing me with supplementary data and reports. Special thanks are due to Sarah Culloty and Sharon Lynch of the University of Cork for their assistance and the use of their laboratory facilities for my histological analyses, to Greg Harper of Plymouth University for his assistance with my Scanning Electron Microscopy work, Christian Wilson of OceanDTM Ltd for his assistance with acoustic data processing, Jose Fariñas-Franco of Heriot Watt University for his work to obtain automated tube counts from seabed images and Stanislas Dubois who very kindly provided me with larval specimens from his personal reference collection. Last but by no means least, my sincerest thanks to all of the staff of Marine Ecological Surveys Ltd, too numerous to list, who have assisted with field and laboratory work, especially those that were involved in the tireless task of taking measurements from individual worms.

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3. MEPF 08/P39 Impacts of Aggregate Extraction on Adjacent *Sabellaria spinulosa* Aggregations and Other Benthic Fauna: MALSF 2008/11
4. MAL0027 (Extension) The significance of benthic communities for higher levels in the marine food-web at aggregate dredge sites using the ecosystem approach: MALSF 2007/08
5. MAL0027 Recoverability of *Sabellaria spinulosa* aggregations following aggregate extraction: MALSF 2006/07

Contributions made by colleagues to research tasks reported within this thesis are summarised overleaf in **Table A.1.**

Table A.1 Summary of the contributions made by the author of this PhD thesis and her colleagues to the completion of the research activities reported herein.

Survey / Study	Tasks undertaken by the author	Tasks undertaken by the author with assistance from colleagues	Tasks undertaken by colleagues under the supervision of the author
Aggregate Extraction Licence Area 360-377 (Hastings Shingle Bank)	• Author of research proposal • Survey design & project management • Management of survey, including supervision of other staff • Data analysis • Author of research report	• Sample acquisition and on-board processing • Benthic sample processing and species identification • Biometric measurements of individual *Sabellaria spinulosa*	• Drop-camera survey • Particle size analysis of sediment samples
Aggregate Extraction Licence Area 447 (Cutline)	• Author of research proposal • Survey design & project management • Management of survey, including supervision of other staff • Author of research report	• Sample acquisition and on-board processing • *Sabellaria spinulosa* histology • Analysis of plankton haul samples to remove *S. spinulosa* • Scanning Electron Microscope (SEM) work	• Benthic sample processing and species identification (not reported here)
Thanet Offshore Wind Farm 2005 Baseline Study	• Survey design • Acoustic and seabed image acquisition and on-board processing • Statistical analysis of benthic data • Author of survey report	• Benthic sample processing and species identification • Interpretation of side-scan sonar data	• Benthic sample acquisition • Particle size analysis of sediment samples
Thanet Offshore Wind Farm 2007 Pre-Construction Study	• Biological analysis of seabed images (taxonomic identification and % cover calculations) • Statistical analysis of benthic data • Author of survey report	• Interpretation of side-scan sonar data	• Acoustic and biological sample acquisition and on-board processing • Particle size analysis of sediment samples • Benthic sample processing and species identification • Automated tube counts from seabed images using ImageJ
Thanet Offshore Wind Farm 2014 Post-Construction Monitoring Study	• Biological analysis of seabed images (taxonomic identification and % cover calculations)		• Acoustic and biological sample acquisition and on-board processing • Particle size analysis of sediment samples • Benthic sample processing and species identification

			• Automated tube counts from seabed images using ImageJ • Statistical analysis of benthic data • Survey report
East Coast Regional Environmental Characterisation (REC) Study	• Ad hoc collection of fish gut contents from trawls containing *S. spinulosa* • Statistical analysis of benthic data • Author of benthic and epibenthic research report chapters	• Survey design • Biological sample acquisition and on-board processing (including additional targeted acoustic data collection)	• Particle size analysis of sediment samples • Benthic sample processing and species identification
East Coast REC Extension	• Author of research proposal • Author of research report (funded by The Crown Estate)	• Interpretation of side-scan sonar and multi-beam swathe bathymetry data • Supplementary fish stomach content extraction and analysis • Scanning Electron Microscope (SEM) work	

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award. No work submitted for this degree forms part of any other degree at the University of Plymouth or at any other establishment.

A programme of advanced study was undertaken which included a two week advanced statistical workshop entitled "Detecting Biological and Environmental Changes: Design and Analysis of Monitoring Experiments" by Lisandro Benedetti-Cecchi (University of Pisa), Bob Clarke (PRIMER-E) and Marti Anderson (University of Auckland) at the University of Bologna, Italy in 2008 and a week-long course in PERMANOVA by Marti Anderson (University of Auckland) and Bob Clarke (PRIMER-E) at the Marine Biological Association of the United Kingdom, Plymouth in 2010.

Relevant scientific seminars and conferences at which work from this study was presented include:

- Joint Nature Conservation Committee (JNCC) Inter-agency workshop on *Sabellaria spinulosa* reefs (Peterborough, 2007)
- Marine Aggregate Levy Sustainability Fund (MALSF) Annual Scientific Conferences (Southampton 2006, London 2007, London 2008)
- Porcupine Marine Natural History Society Annual Conference (Plymouth 2008)
- World Conference on Marine Biodiversity (Aberdeen, 2011)
- Geohab (Marine Geological and Biological Habitat Mapping) (Orcas Islands, 2012; Rome 2013)
- European Congress of Conservation Biology (Glasgow, 2012)
- European Marine Biology Symposium (Cork, 2013)

Four papers have been identified for publication. One has been published;

> Pearce, B., Fariñas-Franco, J.M., Wilson, C., Pitts, J., deBurgh, A., Somerfield, P.J. 2014. Repeated mapping of reefs constructed by *Sabellaria spinulosa* Leuckart 1849 at an offshore wind farm site. Continental Shelf Research. **83:** 3-13.

And three others are in preparation.

Word count of main body of thesis: 72,820

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Date……01.04.2014……………………………..

Chapter 1. Introduction

1.1 Background

Reef habitats can be separated into two broad classes, biogenic reefs, the structure of which is created by a living organism and geogenic reefs where biological complexes grow on rock or coarse substratum such as cobbles (EC 2013). Biogenic reefs are formed by a wide variety of marine animals though the term reef has become more or less synonymous with coral structures. With significant focus being attached to coral reefs, biogenic structures created by other organisms are often overlooked. Biogenic reefs found in UK waters include deep-water corals, mussel beds, oyster beds and polychaete reefs (Wilson 1971; Hall-Spencer et al. 2002; Chapman et al. 2007; Lindenbaum et al. 2008; Soeffker et al. 2011; Green and Crowe 2013). The following represents a review of the ecology of the latter, polychaete reefs, with an emphasis on reefs built by the Sabellariid polychaete *Sabellaria spinulosa*. Relatively few studies have been carried out on the ecology of *S. spinulosa* reefs (George and Warwick 1985; Foster-Smith 2001; Foster-Smith and White 2001; Foster-Smith and Hendrick 2003; Hendrick 2007; Condie 2009; Last et al. 2011a) and hence this chapter draws heavily upon work carried out on other species in this family. Attempts have been made here, to identify trends and variations in the ecology of Sabellariid reefs as a means to better understand the ecology of *S. spinulosa*. However, examination of the available literature has highlighted the imperative requirement for further research into the life-history and ecology of this species and the biogenic structures it creates.

Tube building is a common trait amongst polychaetes and a great variety of tube morphologies exist (**Figure 1.1**). Some tubiculous polychaetes have a highly selective preference for building materials, the character of the tube depending on the species as much as the materials available (Philips Dales 1967). For example, oweniid polychaetes are selective in their tube building materials using only very flat shell or sand particles which they arrange on an organic, secreted base, like tiles on a roof (Noffke et al. 2009). The tube building behaviour of some species also changes with age, for example adult ‘sand-mason’, *Lanice conchilega* use larger particles to build their tubes than the juveniles (Callaway 2003). Perhaps the most impressive tube building abilities though, are those of the pectinariids which construct very precise, conical tubes from sand and shell fragments as illustrated in **Figure 1.1B.** Sabellid polychaetes also use sediment in their tube construction although they tend to favour finer sediments giving rise to a more flexible tube (Hayward and Ryland 1998) similar in appearance to the leathery tubes built by the much larger chaetopterid polychaetes

(Rees et al. 2005). Serpulid worms are also tubiculous, converting carbonate material into a protective cover (Vinn et al. 2008).

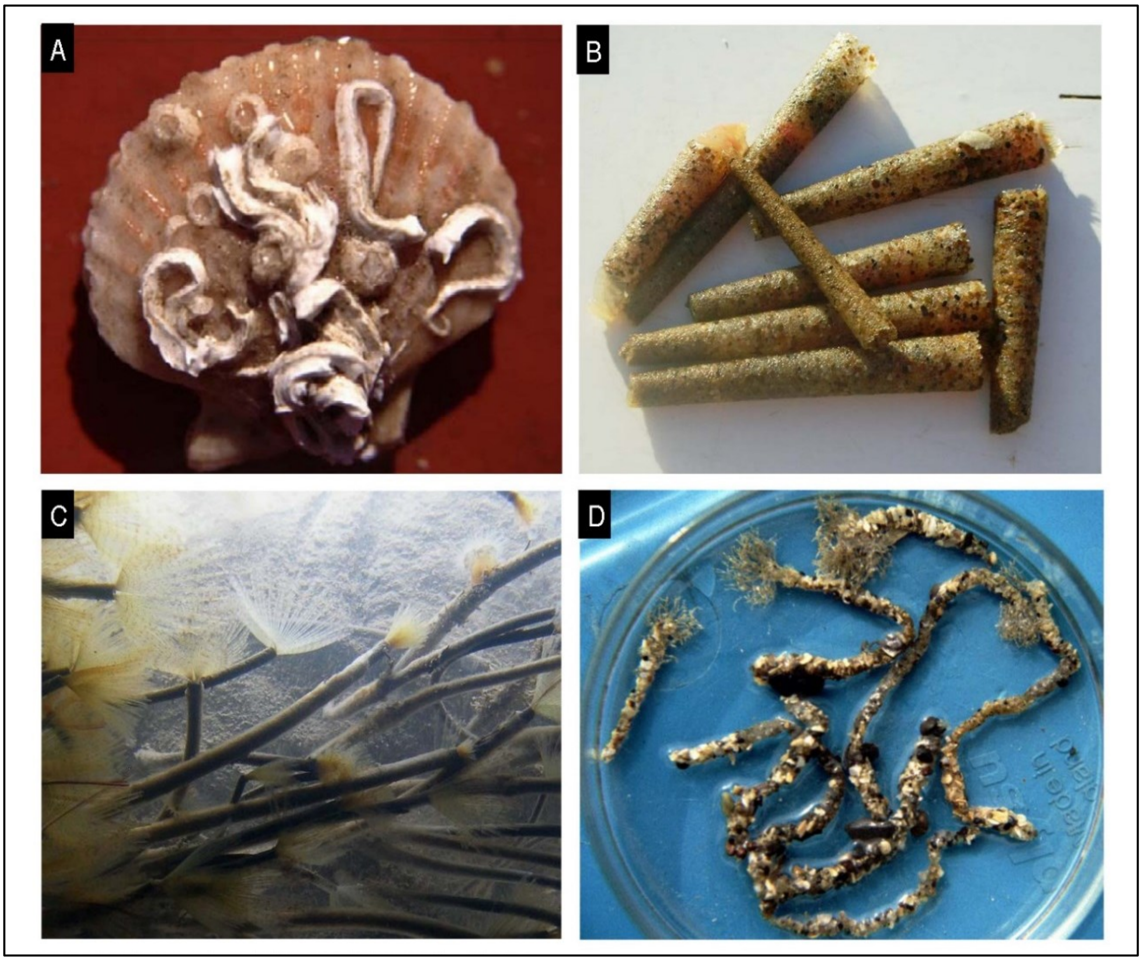


Figure 1.1 Photographs illustrating the morphological variety that exists amongst polychaete tubes. The calcareous tubes of the serpulid *Pomatoceros* sp. (A), the smooth conical tube of the pectinariid, *Lagis koreni*, (B) the flexible silty tubes of the sabellid *Pseudopotamilla reniformis* (C) and the coarse sand tube of the cirratulid *Lanice conchilega* (D).

Although tube building is a common trait amongst polychaetes, not all are gregarious and reef-building behaviour has only been identified in a small number of families: Serpulidae (Fornos et al. 1997; Moore et al. 2009), Sabellariidae (Kirtley and Tanner 1968; Wilson 1971) and Cirratulidae (Rabaut et al. 2009). Hendrick and Foster-Smith (2006) suggest that in order to be classified as a reef an aggregation of worms needs to significantly alter a number of habitat characteristics: elevation, sediment consolidation, associated biodiversity, community structure and stability. They also state that a reef should be long lived, spatially extensive (although possibly patchy) and that it must contain high densities of the reef builder itself. However, since aggregations of most tubiculous polychaetes occur only on a relatively small scale (Noji and Noji 1991; Bolam and Fernandes 2003) there are often insufficient observations to determine the influence they have on associated communities or the sediments in which they occur. The sand mason *Lanice conchilega* is known to form dense beds but there remains some debate about whether or not they constitute reef habitats (Godet et al. 2008; Rabaut et al. 2009). Rabaut et al (2007), Godet et al (2008) and Van Hoey et al (2008) have illustrated that the presence of dense *L. conchilega* aggregations increases biodiversity and provides important foraging grounds for birds and fish. Rabaut, et al (2009) also found that *L. conchilega* beds were significantly elevated when compared with the surrounding substrata, and exhibited some consolidating influence. On the basis of their observations, Rabaut, et al (2009) went on to suggest that *L. conchilega* possesses all of the necessary characteristics to be classified as a reef builder. Similarly detailed studies on other tubiculous polychaetes such as the oweniids and sabellids would be beneficial in elucidating the reef-building qualities that exist within these phyla.

Although most polychaete aggregations are small and inconspicuous (Bolam and Fernandes 2002; Dodd et al. 2009), some have been found to cover tens if not thousands of square kilometres causing considerable alterations to both the physical and biological environment (Kirtley and Tanner 1968; Caline et al. 1992; Fornos et al. 1997). The serpulid *Ficopomatus enigmaticus*, for example forms a continuous layer up to 3 m thick in the coastal lagoons of the western Mediterranean (Fornos et al. 1997). Here the reefs double the annual sediment input into the lagoons through the construction and subsequent decay of their calcareous tubes. Serpulid worms also influence the oxygen and nutrient levels of subtropical lagoons (Keene 1980). Aggregations of spionid polychaetes can also cause significant changes in the physical environment despite their limited longevity (Noji and Noji 1991; Bolam and Fernandes 2003). Spionids are early colonisers and as such perform a key role in conditioning largely afaunal sediments for colonisation by other species (Noji and Noji 1991). Their tube beds can increase the organic content of the environment by acting as a trap for silt, clay and faecal material. This ultimately changes the fauna able to coexist with the spionids. For example, the increase in organic matter may be advantageous to mud-dwelling species such as *Macoma balthica* (Bolam and Fernandes 2003) but may conversely suffocate other organisms (Noji and Noji 1991). The final fate of the spionids in their tube beds will either be a reduced abundance, coexisting with other species or total replacement by other fauna. The ephemeral nature of these beds would almost certainly exclude them from being considered as reefs according to the scoring system identified by Hendrick and Foster-Smith (2006).

The evolutionary foundations of gregarious behaviour in polychaetes is as yet unknown although some gregarious species have been found to respond to chemical or protein cues given off either by the living adults of conspecifics (Toonen and Pawlik 1996; Callaway 2003) or by their living and dead tubes (Wilson 1968; Wilson 1970a; Pawlik 1986). There are obvious ecological advantages to gregarious behaviour in polychaetes, most notably, increased reproductive success (Thomas 1994b). Most tubiculous polychaetes are broadcast spawners, that is, they release their gametes into the water column, either in discrete, coordinated events or semi-continuously throughout their breeding season (Wilson 1970a; Eckelbarger 1976; Toonen and Pawlik 2001). Living in dense aggregations therefore increases the chance of gametes being fertilised. By relying on the cues of their conspecifics the larvae also have a greater chance of locating suitable conditions for successful settlement. Whatever the evolutionary foundation of worm reefs there is no doubt that these structures play an important role in marine ecosystems. They have been found to stabilise and trap sediments, alter water quality and the composition of benthic communities. They are true ecological engineers, perhaps none more so than the sabellariids. Subsequent sections of this chapter will look in detail at the reefs built by sabellariid polychaetes, the most prolific reef building worms in our oceans (Kirtley and Tanner 1968; Caline et al. 1992; Kirtley 1994).

1.2 The Biology and Reef Building Capacity of *Sabellaria spinulosa*

1.2.1 Morphology

Sabellaria spinulosa has heteronomous segments, that is, segments that perform different functions. It has a distinct head, thorax and two abdominal sections, the abdomen and cauda (**Figure 1.2**). Each of the thoracic segments have parapodia containing oar chaetae which protrude sideways holding the worm upright in its tube (**Figure 1.3**). These chaetae also maintain a space between the animal and tube walls, allowing the movement of water in and out of the tube (Schafer 1972). Water enters the tube on the dorsal side of the worm where gills waft it down toward the posterior end of the tube. Gametes are liberated from the body cavity and directed out of the tube by the second section of the abdomen, the cauda.

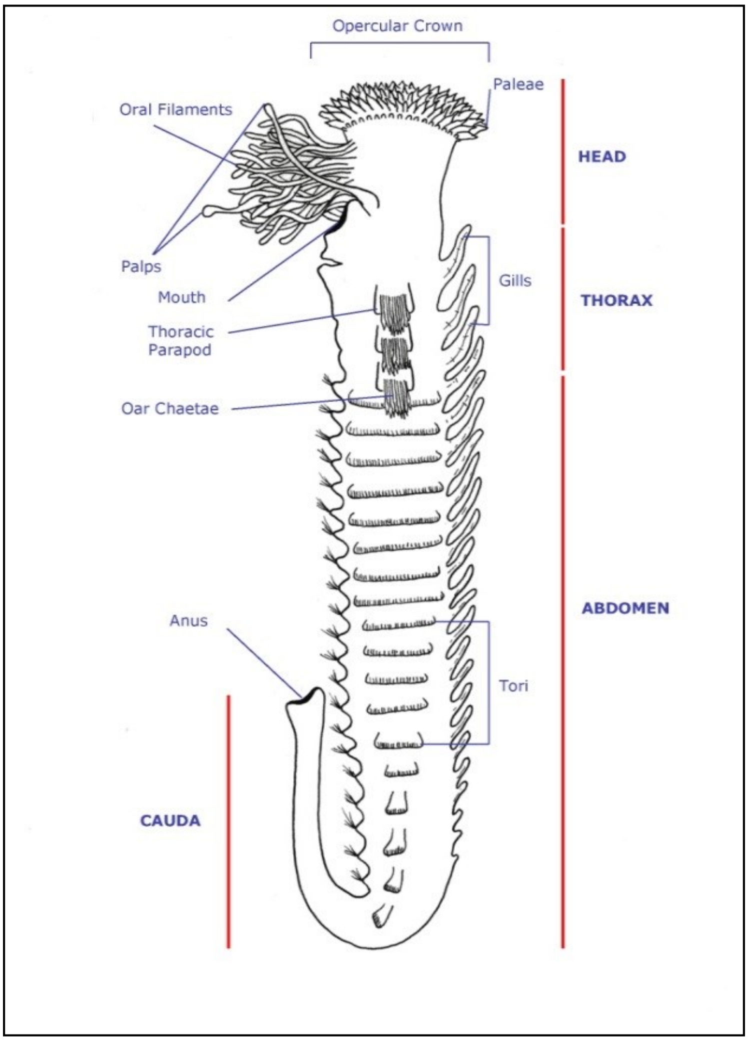


Figure 1.2 Systematic illustration of *Sabellaria spinulosa* showing the different body sections and key anatomical features (not to scale).

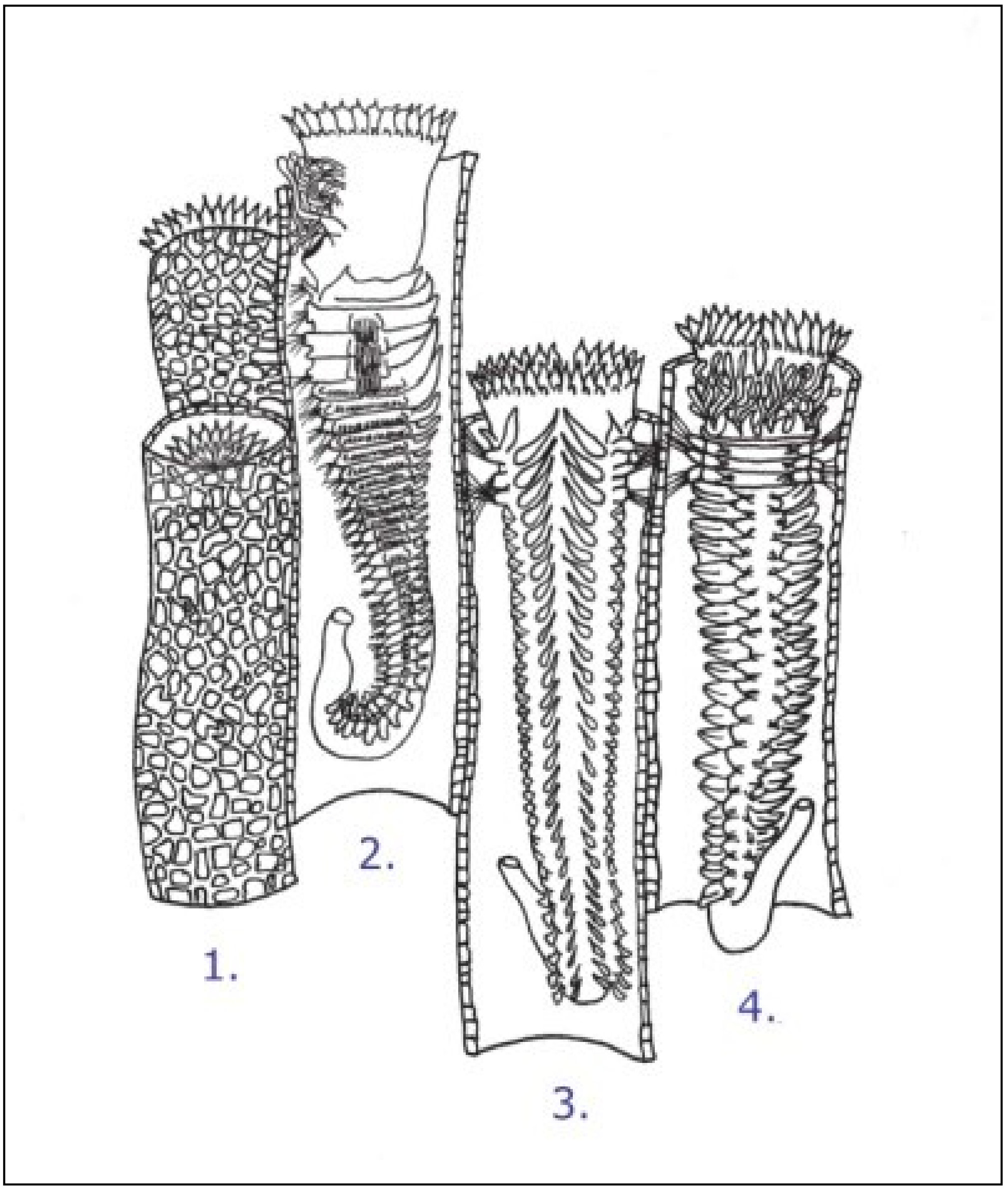


Figure 1.3 Illustration of *Sabellaria spinulosa* worms in their tubes, showing how the oar chaetae hold them in place. **1** Shows an external view of the worms in their tubes with the operculum open (above) and closed (below). **2 - 4** Show internal views of *S. spinulosa* in their tubes with a side-on view (**2**), a dorsal view (**3**) and a ventral view (**4**). Illustration adapted from Schafer (1972).

1.2.2 Reproduction

Sabellariids, or at least those species that have been well studied, are known to have separate sexes and like many other sedentary marine organisms release their gametes into the water column during spawning events (Kirtley 1994). The frequency and timing of *Sabellaria spinulosa* spawning events is largely unknown, although there have been several reports of settlement occurring between March and April (Wilson 1970b; Eckelbarger 1978a; George and Warwick 1985). Wilson (1970b) also reports observations made of spawning behaviour in *S. spinulosa* between January and March. Other sources report observations of *S. spinulosa* larvae in the plankton between August and November (Garwood 1982) and from January to September (MBA 1957). Most of these reports however, relate to incidental recordings and where targeted sampling appears to have been carried out, there is insufficient detail of the sampling employed to know how comprehensive this has been (Wilson 1970b). It is therefore impossible to determine how representative these records are of the general life cycle.

1.2.3 Tube Building

Sabellariid worms catch sand grains using their contractile palps, before moving them to the mouth where they are coated with a protein cement and laid down as the building blocks of their protective tubes (Schafer 1972; Caline et al. 1992; Kirtley 1994). The cement hardens in seawater, and the inside of the tube is constantly lined with new cement to maintain the structural integrity (Schafer 1972). The mouth organ plays a central role in tube building and its size is hence the main limiting factor in the size of sand grains which can be utilised by the worms (Gruet 1982). Many intertidal sabellariid species use elongate shell fragments to construct a characteristic ‘hood’ or ‘porch’ at the orifice of each tube, giving a ‘honeycomb appearance’ to the colonies (Wells 1970a; Wilson 1971; Achari 1974; Posey et al. 1984; Zale and Merrifield 1989; Kirtley 1994; Pandolfi et al. 1998; Pohler 2004; Bailey-Brock et al. 2007). This structure is absent in reefs formed by *Sabellaria spinulosa* (**Figure 1.4**) and other subtidal sabellariids indicating that these hood structures are in some way linked to high energy environments, perhaps affording the worms some protection from the force of the waves. A study by Thomas (1994a) into the roles of different extensions or ‘hoods’ built by *Phragmatopoma californica* indicate that these structures serve to reduce the rate of fluid exchange between the aggregation surface and the main water flow and also decrease the deflection and hence damage caused to the feeding tentacles by the water flow. The hood structure has also been shown to slow the dissipation of sperm during spawning (Thomas 1994b) which may increase the chances of reproductive success in high energy environments.

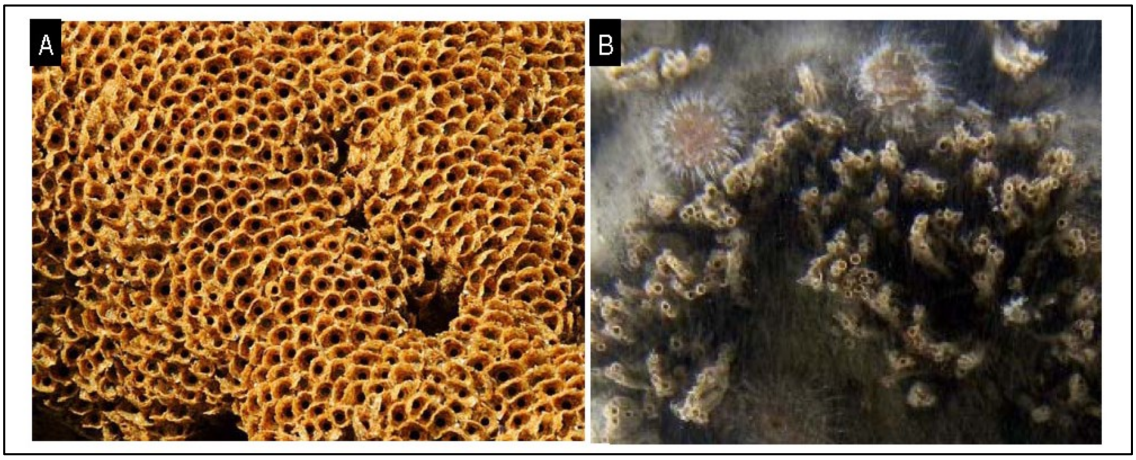


Figure 1.4 Photographs of A) an intertidal sabellariid colony (*Sabellaria alveolata*) © Laura Bush and B) a subtidal sabellariid colony (*Sabellaria spinulosa*), illustrating the difference in reef and tube structure which is evident across the family.

The composition of the tubes built by Sabellariid polychaetes are highly variable, sand grains are often supplemented or even replaced with other mineral grains, shell fragments and detrital material, including foraminifera tests, ostracods, faecal pellets and sponge spicules. In most cases this would appear to merely be a reflection of the composition of the surrounding sediments although Reuter et al (2009) demonstrate strong selectivity in the tubes built by both *Neosabellaria clandestina* and *Sabellaria chandraae* at Meenkuunu Beach, south west India. The tubes of both species were found to contain very high quantities of the tests of the rotallid foraminifera *Ammonia beccarii*, which were only found sporadically in the surrounding sediments. A preference for foraminifera as a building material in *Neosabellaria clandestina* was also reported by Kirtley (1994) some years earlier indicating that the preference for foraminifera is consistent in this species. Pohler (2004) also reports selectivity in the building material choices made by *Neosabellaria vitiensis* tubes in Fiji. In a detailed study of the sediment composition of *N. vitiensis* tubes, Pohler (2004) demonstrated that the worms had a greater proportion of coarser grained sediment particles than were present in the surrounding sediments. Pohler (2004) concluded that the disparity between the composition of the tubes and the surrounding sediments was an indication that the very fine sediment particles which dominated the surrounding sediments were unsuitable for tube building. It is not yet known whether any of these species actively select their building materials or whether the process is more passive. It is possible for example that the local hydrodynamic regimes cause some density fractionation of the suspended material making certain particle sizes a more readily available source of building material.

Many descriptions of the building strategy employed by Sabellariid polychaetes suggest that large numbers of the larvae settle and start building their tubes simultaneously (Wilson 1971; Schafer 1972; Caline et al. 1992; Kirtley 1994). Subsequent settlements select peripheral sites and avoid settling on top of other tubes (Wilson 1971; Posey et al. 1984; Zale and Merrifield 1989; Caline et al. 1992). Where this behaviour is employed the worms are able to utilise a wall of the neighbouring individuals' tube as part of their own, giving rise to a very regular and organised structure which resembles that of a honeycomb (Wilson, 1971). This building behaviour is common amongst intertidal Sabellariid species with a "honeycomb" structure being reported for numerous species around the world (Kirtley and Tanner 1968; Achari 1974; Caline et al. 1992; Kirtley 1994; Pohler 2004). A more irregular and self-contained structure is observed in subtidal and abyssal species however (see **Figure 1.4**) suggesting that there is considerable variation in building behaviour, which may have evolved in response to the prevailing environmental conditions.

1.2.4 Reef Development

To date there have been no studies on the natural life-cycle or temporal stability of the reefs built by *Sabellaria spinulosa* although several long-term studies have been carried out on reefs built by its congener *S. alveolata* (Wilson 1968; Wilson 1971; Wilson 1974; Wilson 1976; Gruet 1982; Gruet 1986b; Caline et al. 1992; Gruet and Bodeur 1997). *Sabellaria alveolata* matures in the first year, spawning in the second summer following settlement (Wilson 1971) and has a typical life span of 9 years (Gruet 1982). In his comprehensive studies of *S. alveolata* reefs in the Bay of Mont Saint–Michel, Yves Gruet (Gruet 1970; Gruet 1971; Gruet 1977; Robert et al. 1979; Gruet 1982; Gruet and Lassus 1983; Gruet 1984; Gruet 1986a; Gruet 1986b; Gruet et al. 1987; Gruet 1991; Caline et al. 1992; Gruet and Bodeur 1994; Gruet and Bodeur 1995; Gruet and Baudet 1997; Gruet and Bodeur 1997) found that Sabellarian reef morphology was the result of a constantly disturbed and precarious balance between biological and physical factors. Gruet and Bodeur (1995) describe the formation, growth and degradation of Sabellariid reefs in five phases as summarised in **Figure 1.5.**

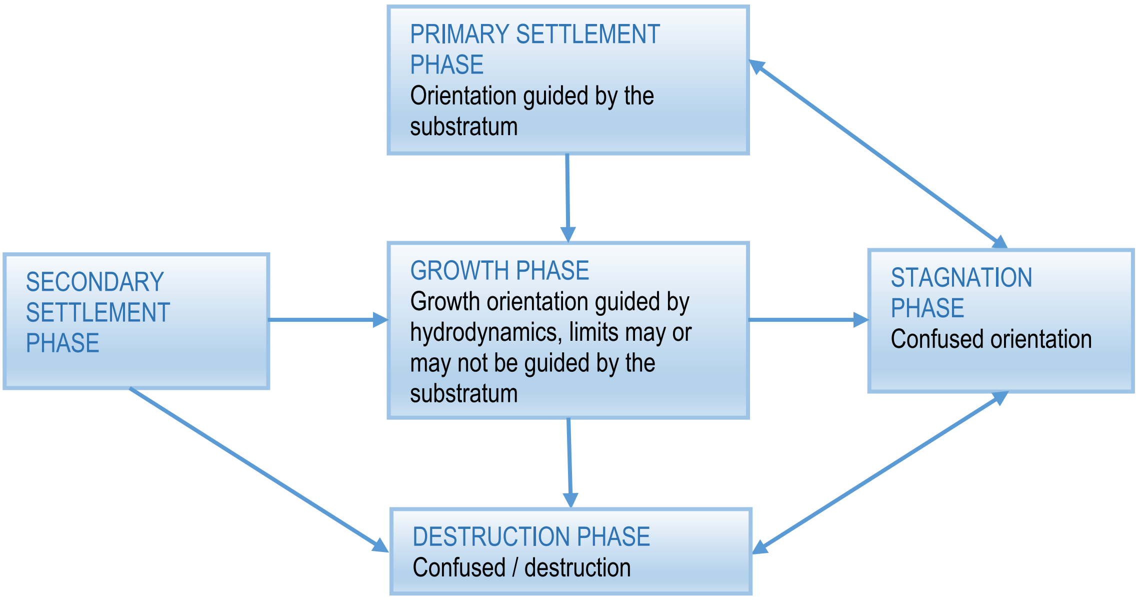


Figure 1.5 Main phases of sabellariid reef development and orientations of the structures adapted from (Gruet and Bodeur 1995).

Once *S. alveolata* have settled they undergo a rapid growth phase. Growth rates (tube length) of 10-15 cm/year have been reported in the first year of settlement slowing to 6 cm/year in the second year (Wilson 1971; Gruet 1982). Since tube lengths do not typically exceed 30 cm in this species (Wilson 1971), this level of growth is presumably not sustained for the life of the individual. Similarly rapid growth rates have been reported for other Sabellariid species, for example average growth rates of 4-10 cm/year in the Pacific sabellariid *Idanthyrsus cretus* (Chen and Dai 2009). These growth rates were calculated on the basis that this species had formed extensive reefs over wave breakers which had been installed between 4 and 12 years previously and hence no attempt was made to investigate the relationship between growth rate and age. No direct records of the growth of *S. spinulosa* were found although studies of the size-frequency distribution of a reef undertaken by Hendrick (2007) between May 2003 and August 2005 did indicate that a small cohort observed in July 2004 (mean cephalic diameter 0.26 mm) underwent rapid growth, doubling in size by November. This shows good agreement with similar work undertaken by George and Warwick (1985) in the Bristol Channel. George and Warwick (1985) identified a new settlement in March which had merged with the main adult cohort by November of the same year. Whilst these two studies show differences in the specific growth rates, both indicate rapid growth in the early stages of development, in-line with what is known of other sabellariid species.

Gruet and Bodeur (1995) report that the tubes of *S. alveolata* first grow horizontally, then vertically resulting in ball-shaped constructions, with secondary settlements increasing the vertical growth in a more or less symmetrical fan shape. Where dominant waves occur in the same direction as the flood tide, the construction lengthens in a direction perpendicular to the main current. These reef structures can form barriers in some cases altering the flow through channels. Barriers can also join to form platforms as is the case in the extensive reefs in the Bay of Mont-Saint-Michelle, also known as the 'Banc des Hermelles' (Gruet 1982). At this stage growth is slower, with the majority of building occurring over the winter months when storms and strong currents put more sand into suspension stimulating new growth (Gruet 1971). New growth on these platform reefs tends to be strongly directional and in some cases destruction and simultaneous new settlement can stimulate horizontal movement (Gruet and Bodeur 1995). It has also been reported that reefs can become inundated with sand and then develop again as superimposed structures (Caline et al. 1992; Gruet and Bodeur 1995). A similar cycle of development and degradation has been reported for the sabellariids off the coast of Florida where Kirtley and Tanner (1968) noted that fragments of sabellariid reef material, both living and dead, were broken off during storms but were incorporated into subsequent growth.

The ephemeral nature of *S. spinulosa* reefs in the UK has been alluded to by numerous authors (Holt et al. 1998; Hendrick 2007; UKBAP 2007b) although this is mostly thought to apply to "crusts" a loose term given to less stable and less developed reef complexes "crusts are not considered to constitute true *S. spinulosa* reef habitats because of their ephemeral nature which does not provide a stable habitat enabling associated species to become established where they are otherwise absent" (UKBAP 2007b). The basis of this differentiation however, is questionable especially in light of studies on other sabellariid reefs which have shown that degraded reefs support a greater biodiversity than living reef (Dubois et al. 2002). The recent disappearance of Saturn Reef, a seemingly stable and extensive reef in the southern North Sea, casts further doubt on the accuracy of this statement. Saturn Reef disappeared only a year after its first discovery with no conclusive evidence for the cause of its decline (Hendrick 2007; Limpenny et al. 2010). The stability of fully developed *S. spinulosa* reefs cannot therefore be assumed.

1.3 The Ecology of Sabellariid Reefs

Sabellariid species are well known for their gregarious nature, forming mound and tabular formations and in some cases distinct reefs, throughout the temperate and tropical oceans (Achari 1974; Posey et al. 1984; Lana and Gruet 1989; Zale and Merrifield 1989; Caline et al. 1992; Nishi and Nunez 1999; Bailey-Brock et al. 2007; Chen and Dai 2009; Nishi et al. 2010). The family Sabellariidae contains two sub families and 12 genera which are further subdivided into over 100 species (Kirtley 1994). Aggregations formed by sabellariid polychaetes are reported to occur mostly in the intertidal or surf zone where there is an abundant supply of unconsolidated sand-sized sediment and strong currents (Wilson 1971; Achari 1974; Gruet 1982; Zale and Merrifield 1989; Bailey-Brock et al. 2007; Dubois et al. 2007; Barrios et al. 2009). There are also numerous records of sabellariid aggregations from intermediate depths on continental shelves and slopes (Kirtley and Tanner 1968; Achari 1974; Lechapt and Gruet 1993; Gherardi and Cassidy 1994; Hendrick 2007; Chen and Dai 2009) as well as a limited number of records from abyssal plains (Lechapt and Kirtley 1998). Given that sampling effort decreases rapidly with depth, it is unclear whether sabellariid aggregations are any more or less common in intertidal areas. Although there are a limited number of sabellariid records from abyssal depths, these are restricted to systematic species descriptions. There are no published studies on the ecology or distribution of sabellariid reefs beyond the continental shelf, indicating that this is an area of deep sea ecology that been neglected to date. Zale and Merrifield (1989) hypothesised that at depths greater than 2 m wave action is insufficient to provide enough turbulence to keep feeding and building materials in suspension for the intertidal species, *Phragmatopoma lapidosa*. Sabellariid aggregations however, are frequently found at greater depths (Kirtley 1994) and it is likely therefore that submarine currents also play a key role in maintaining the required levels of turbidity.

1.3.1 Distribution

Sabellariid reefs are common worldwide in intertidal and nearshore areas where vigorous wave and current action maintain high levels of suspended sediments (Posey et al. 1984; Kirtley 1994; Pohler 2004; Chen and Dai 2009). Reefs can extend for hundreds if not thousands of square kilometres in some areas such as the massive *Sabellaria vulgaris* reefs described in Delaware Bay (Curtis 1978); the extensive

Phragmatopoma lapidosa reefs in Florida (Kirtley and Tanner 1968); *Phragmatopoma californica* reefs in California (Simmons et al. 2005) and *Sabellaria alveolata* reefs in Mont Saint-Michel in France (Gruet 1970; Marchand and Cazoulat 2003). There are no records of sabellariid reefs of this scale in the UK, but there is evidence to suggest that the extent of *S. alveolata* reefs has become more restricted in some areas (Cunningham et al. 1994) and hence larger reefs may once have existed on our shores. Similar reef building polychaetes have been recognised in the fossil record from as far back as the Cambrian (approx. 480-550 my ago). Indeed, interest in the reef-building behaviour of sabellariids first came from geologists and palaeontologists, rather than biologists, who made comparisons between their structures and those of the Cambrian “pipe rock” quartzites, or *Skolithus*, found in Scotland and Sweden and similar Lower Devonian (approx. 400 my ago) trace fossils of the Eifel Mountains at Neroth in Germany (Schafer 1972). These early marine tube relics were widely assumed to have been formed by burrowing animals although more recent studies (Eckdale and Lewis 1993) indicate that these fossils strongly resemble the tube structures of modern sabellariids casting doubt on earlier assertions about their origin. Recognisable sabellariid tube fossils have been reported from the Quaternary (approx. 2-3 my ago) in Chile, Baja California and the deep floor of the eastern Mediterranean (approx. 2000-3000m) and from the Cretaceous (approx. 300 my ago) from Oklahoma. It is clear then that sabellariids have strong historic roots, perhaps another indicator of their adaptive and resilient nature.

Like the geological history of sabellariids, the modern history is also somewhat uncertain. The literature indicates that sabellariids are currently found between latitudes of 67° North and 57° South, but with new species and new distribution records for this family being reported relatively frequently (Lana and Gruet 1989; Lechapt and Gruet 1993; Lechapt and Kirtley 1996; Lechapt and Kirtley 1998; Nishi and Nunez 1999; Bhaud and Fernandez-Alamo 2001; Bremec and Giberto 2004; La Porta and Nicoletti 2009; Nishi et al. 2010; Souza Dos Santos et al. 2011; De Assis et al. 2012; Hutchings et al. 2012; Bremec et al. 2013; Linero-Arana 2013) it is possible that their range extends beyond this.

Sabellaria spinulosa has the widest geographical range of all the sabellariids, according to current records, encompassing Iceland, the Skagerrak and the Kattegat, the North Sea, the English Channel, the northeast Atlantic, the Mediterranean, the Wadden Sea and the Indian Ocean (Achari 1974; Riesen and Reise 1982; Reise and Schubert 1987; Hayward and Ryland 1998; Foster-Smith 2001; Collins 2005). In addition there are at least four varieties of *S. spinulosa* which increase the species range further; *S. spinulosa var. fuciola* which has been identified on the coast of South Africa (Day 1967), *S. spinulosa var alcocki* which is found alongside *S. spinulosa* in the Indian Ocean as well as in southern Africa (Day 1967; Achari 1974), *S. spinulosa var eupomatoides* found in South Africa (Day 1967) and *S. spinulosa var ranjhi* found on the west coast of India (Achari 1974). It should be noted however, that the recorded distribution of *S. spinulosa* is currently based on morphological descriptions alone, and to date no genetic work has been carried to confirm the very broad geographical range of this species.

Significant losses of *Sabellaria spinulosa* have been reported in the Wadden Sea (Riesen and Reise 1982; Reise and Schubert 1987; De Jong et al. 1999; Wolff 2000), where extensive colonies were once common in the subtidal shallows. Commercial shrimp fisheries have been implicated in the demise (Reise and Schubert 1987), although coastal eutrophication may also have played a role (Vorberg 2000). Saturn Reef, which was the first subtidal *S. spinulosa* reef to be awarded candidate Special Area of Conservation (cSAC) status in the UK, has also disappeared although this extinction is on a much smaller scale (Hendrick 2007). Records of *S. spinulosa* distribution are somewhat uncertain and much of the seafloor, both in the UK and overseas, remains un-surveyed it is impossible to make a judgement on how the distribution has changed in recent years. New observations could indicate an expansion in range or could simply be an artefact of increased sampling efforts. Nevertheless, there have been some significant losses highlighting the need to better understand the requirements of this species in order to conserve important reef habitats into the future.

Sabellaria spinulosa is widely distributed around the UK whereas *Sabellaria alveolata* has a more restricted distribution occurring mostly on the western coast of the UK in intertidal or very shallow subtidal environments (**Figure 1.6**). *S. spinulosa* occurs mostly in subtidal environments with notable intertidal exceptions in Harwich, the Wash and parts of Scotland (McIntosh 1922; Unicomarine 1998; Hendrick 2007). Whilst the depth range of *S. spinulosa* is known to be greater than that of *S. alvelolata* its distribution in the UK appears to be limited to the continental shelf (**Figure 1.6**). There are very few records of *S. spinulosa* in Scotland held in the National Biodiversity Network database (**Figure 1.6**) but this may be an artefact of reduced sampling effort. *S. spinulosa* reefs have historically been recorded off the shores of St Andrews and Hilbre Island so more comprehensive sampling would almost certainly reveal the presence of *S. spinulosa* in these areas. (McIntosh 1922).

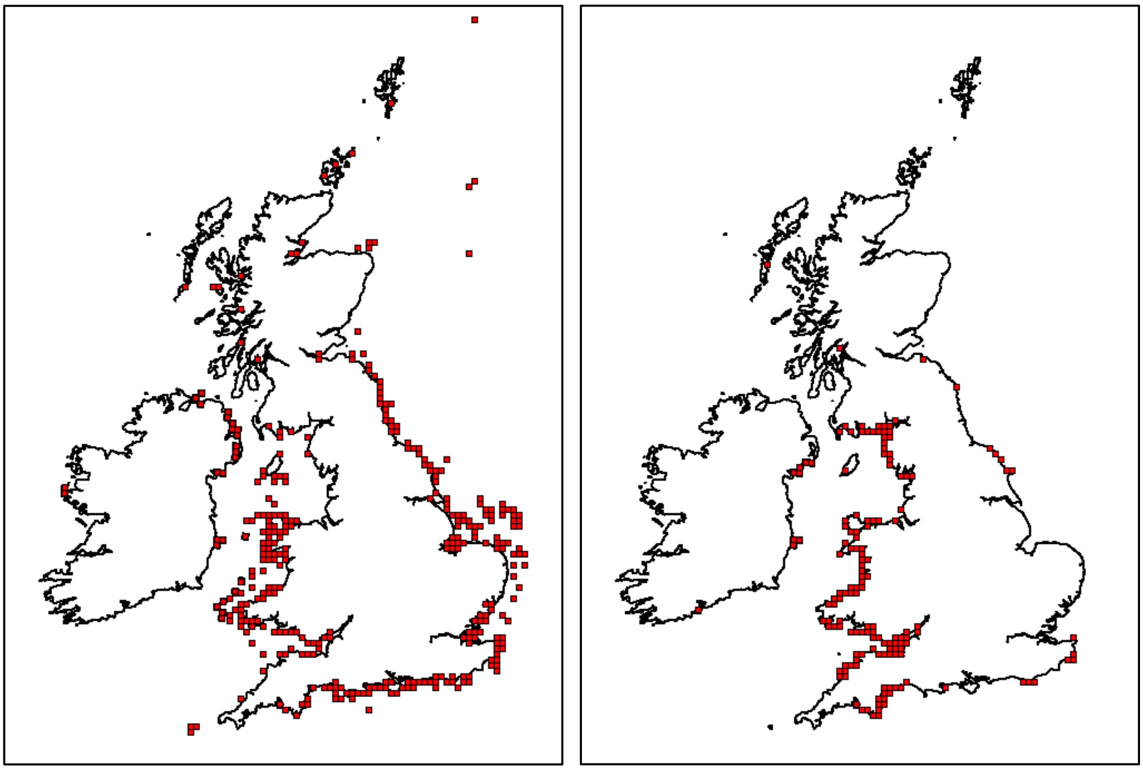


Figure 1.6. Distribution of A) *Sabellaria spinulosa* and B) *Sabellaria alveolata* in the UK, based on publically available data records. Data courtesy of the NBN Gateway and provided by Natural Resources Wales (NRW), Joint Nature Conservation Committee (JNCC), the Marine Biological Association (MBA), Natural England, Marine Conservation Society, South East Wales Biodiversity Records Centre, Cumbria Biodiversity Data Centre, Centre for Environmental Data and Recording, Scottish Natural Heritage, Yorkshire Naturalists' Union Marine and Coastal Section, Merseyside BioBank, Bristol Regional Environmental Records Centre and Porcupine Marine Natural History Society.

It has been inferred by many authors that *Sabellaria spinulosa* is most frequently encountered as solitary individuals or small clumps (George and Warwick, 1985; Holt et al., 1998; Jackson and Hiscock, 2008). The majority of studies on sabellariids are concerned with the formation and function of the reefs which they build. This therefore biases sampling towards the densest aggregations making it difficult to assess the occurrence of different growth forms across the family. There are however, records of other sabellariid species occurring as solitary individuals (Wells 1970a; Smith and Chia 1985; Thomas 1994b) and indeed some sabellariids have been reported as having an entirely solitary life-history (Eckelbarger 1977; Wilson 1977; Pawlik and Faulkner 1988). Laboratory studies on the settlement behaviour of *Phragmatopoma lapidosa* indicate that hydrodynamic flows may play an important role in the distribution of individuals (Pawlik and Chia 1991; Pawlik and Butman 1993). Here the fastest flows were found to dilute the concentration of larvae on the seafloor through enhanced turbulent mixing. It seems likely then that the majority of sabellariids will occur in both solitary and gregarious forms in varying proportions depending on the prevailing hydrodynamic regime.

1.3.2 Environmental Niche

Depth

Sabellariid polychaetes have a eurybathic distribution occurring from the intertidal zone down to abyssal depths (Wilson 1971; Achari 1974; Caline et al. 1992; Lechapt and Kirtley 1998; Bhaud and Fernandez-Alamo 2001; Simmons et al. 2005; McCarthy et al. 2008), though they are most commonly encountered in the intertidal and very shallow subtidal. *Sabellaria spinulosa* itself has a predominantly subtidal distribution (Riesen and Reise 1982; Reise and Schubert 1987; Sotheran et al. 1997; Foster-Smith 2001; Collins 2005) although its range is known to extend from very shallow intertidal environments (McIntosh 1922; Unicomarine 1998; Hendrick 2007) to bathyal depths (Hartmann-Schroder 1971; Achari 1974). Whilst depth does not appear to be a limiting factor in the range of the species, *S. spinulosa* has rarely been recorded at depths exceeding 45-50m in UK waters. This perceived restriction may however be due to other environmental conditions which correlate with depth, such as temperature, or may simply be an artefact of sampling effort, with far more effort having been afforded to coastal areas than the deeper shelf areas.

Turbidity / Suspended Sediments

The sabellariids' requirements of material for building and of turbulence are widely quoted (Kirtley and Tanner 1968; Posey et al. 1984; Caline et al. 1992) . Being sedentary in nature they depend upon current action for a supply of both food and building materials and also to wash away metabolic waste (Schafer 1972; Holt et al. 1998). The diet of sabellariids has been afforded little attention in the published literature although Kirtley (1994) describes Sabellariids as filter feeders, feeding on microalgae and other organisms encrusting sand and shell fragments as well as planktonic meiofauna such as diatoms and foraminifera. Wells (1970b) describes briefly the feeding mechanisms of *Sabellaria kaiparaensis*, whereby particles too large to be ingested are incorporated into the walls of the tubes. Wells also mentions that feeding could not occur without aeration since suspended matter would foul the ciliary feeding mechanism under stagnant conditions. Since no reference to the feeding preferences or habits of *Sabellaria spinulosa* could be found it can only be assumed that they exhibit similar preferences as those described for other Sabellariids. This is an area that would benefit from further research.

Water movement is doubtlessly important in the provision of feeding material but it has been postulated that the most limiting environmental requirement of sabellariids may be in the supply of material for tube building (Holt et al. 1998; Jones 1998). Water movement of a sufficient intensity to suspend sand and shell particles is required, making them available for use as tube building material (Cunningham et al. 1994). Numerous examples of this have been described in the literature with turbidity being caused both by waves and currents. Given that S*. spinulosa* mostly occurs subtidally it is likely that water movements through currents are of as much significance in determining distribution as wave action.

Simmons et al. (2005) hypothesised that within-rock aggregations are enhanced by local boulder induced flow, since the recirculation zone that forms in the lee of the boulders would preferentially retain larvae, enhancing settlement in these areas. Turbulence may also then be acting to improve larval retention in other areas, at least partially explaining the commonly reported ability of sabellariid aggregations to quickly colonise wave-breakers and other artificial structures placed on the seafloor (Pohler 2004; Chen and Dai 2009)

Substratum Preferences

Sabellariids, like other sedentary organisms, have been reported to require a hard substratum upon which to settle and establish their tubes (Caline et al. 1992; Kirtley 1994; Holt et al. 1998; Jones et al. 2000; Jackson and Hiscock 2008), though unfortunately this assertion has never been tested. *S. spinulosa* reefs have been recorded in association with large mobile sandbanks in the Bristol Channel for example (George and Warwick 1985) casting some doubt on this assertion.

Sabellariids are able to settle on a wide variety of substrata and are often reported as growing on dead or even living shells, as was the case with the first discovery of *Sabellaria tottoriensis* found on living *Turbo torquatus*, or Turban shells in the Sea of Japan (Nishi et al. 2004). *Neosabellaria vitensis* has been reported as settling on Suva Marl, a crumbly mixture of clay, sand and shell fragments, rocks including seawalls and even mangrove roots in Fiji (Pohler 2004; Bailey-Brock et al. 2007) whilst *Sabellaria cementarium* and *Idanthyrsus ornamentatus* have been observed attached to sandstone bedrock in Oregon (Posey et al. 1984). In 2008 *Idanthyrsus cretus* reefs were discovered for the first time in the western Pacific (Chen and Dai 2009), having colonised wave-breakers which had been installed near Hialien Port in eastern Taiwan between 1996 and 2003 (Chen and Dai 2009).

Sabellaria spinulosa has also been recorded on a wide range of substrata including dead oyster and mussel shells (Rees and Dare 1993: Figure 1.7.), sandy gravel and rock substrata (Seiderer and Newell 1999; Newell et al. 2001), crab carapaces (Hartmann-Schroder 1971), large gastropod shells (Warren and Sheldon 1967; Schafer 1972), and man-made surfaces including subsea pipelines (Braithwaite et al. 2006). Once a colony has been established it is possible for the extent to increase without a requirement for hard substrata (Gruet and Bodeur 1995) which may explain the occurrence of extensive *S. spinulosa* reefs on what appear to be relatively mobile areas of sand (Warren and Sheldon 1967; Schafer 1972; George and Warwick 1985).

Figure 1.7. *Sabellaria spinulosa* growing attached to the surface of an empty horse mussel, *Modiolus modiolus,* shell

No experimental studies of the substratum preferences of *S. spinulosa* were found in the literature, although given the wide ranging substrata upon which this species has been recorded; substratum composition seems unlikely to be a limiting factor in the distribution of this species, except perhaps for the complete absence of suitable building materials. High levels of mud and silt may also be prohibitive since they are thought to clog the feeding apparatus of *S. spinulosa* (Wells 1970b).

Salinity

Sabellaria spinulosa is predominantly found in subtidal areas where salinity would be expected to be fully marine, although the presence of aggregations in estuaries such as the Humber (Holt et al. 1998; Foster-Smith 2001), the Thames (Attrill et al. 1996) the Crouch and the Mersey (Killeen and Light 2000) indicates that this species must exhibit at least some tolerance to changes in salinity. Other sabellariids have been reported to tolerate salinities outside the range of fully marine or euhaline waters (30-35 ‰). *Neosabellaria vitiensis* for example is found in salinities ranging from 26-31 ‰ in Fiji (Pohler 2004; Bailey-Brock et al. 2007). *S. vulgaris* has been found in salinities ranging from 15-31 ‰ in Delaware Bay in the USA (Wells 1970a) whilst sabellariid polychaetes in the Florida area are reported to survive salinities as low as 10 ‰ for several days, although this is considered an adaptation unique to this region (Zale and Merrifield 1989). It seems likely then that *S. spinulosa* would be capable of surviving in variable salinity environments although laboratory experiments would be required to determine the full tolerance range of this species.

Temperature

The extensive biogeographical range of *S. spinulosa* from Iceland to India and from intertidal to bathyal depths, demonstrates that this species is tolerant of a very broad range of temperatures. Like the majority of other sabellariids, *S. spinulosa* is able to withstand several hours of exposure during low tide (Unicomarine 1998; Hendrick 2007), presumably retaining sufficient seawater within its tube to maintain body temperature and oxygen levels. However, under these conditions episodes of extreme temperature variations are likely to be detrimental. High levels of mortality were observed in intertidal *S. alveolata* reefs during the cold winter of 1963 (Crisp 1964) and similarly sabellariid reefs suffered considerable deaths on the Delaware coast following a period of extreme heat (Miller 2001). The ideal temperature for growth in *P. lapidosa* is reported by Zale and Merrifield (1989) as being between 18-27°C. In contrast, *Neosabellaria vitiensis* is found at temperatures ranging from 27-30°C (Pohler 2004; Bailey-Brock et al. 2007), and as these records were made on an overcast day, they indicate that this species is able to survive temperatures in excess of 30°C. Bamber and Irving (1997) reported that *S. alveolata* maintained higher metabolic rates and tube-building activity in the vicinity of the cooling water outflow of Hinkley point, which is usually 8 to 12°C above ambient water temperatures indicating that higher water temperatures could be beneficial to sabellariids in the UK.

1.3.3 Interactions with the Physical Environment

Stabilisation of sediments

It has been hypothesised that sabellariids can impound up to 96% of the sediment that washes over them (Pandolfi et al. 1998), although it is unclear how this figure was derived. Nevertheless, the ability of these polychaetes to impound sediments makes them an important agent of coastline development in some areas. Indeed it has been suggested that seeding and protecting sabellariid reefs might form an important facet in future beach-erosion control programmes in Florida (Kirtley and Tanner 1968). In Fiji where beach erosion is also a major issue aggregations built by *Neosabellaria vitiensis* along a seawall were noted as having a positive effect which was twofold (1) the structures dampened the force of incoming waves on the base of the seawall by exerting some drag on the incoming currents (2) the worm colonies also reduced the wave energy that was reflected back off the seawall. Wave reflection is a major cause of coastal erosion which is why sea walls are problematic structures, often aggravating erosion as much, or more than they alleviate it (Kraus and McDougal 1996). Others have also noted the stabilising influence that sabellariid reefs have on sediments (Cunningham et al. 1994; Chen and Dai 2009). Sabellariids extract and agglutinate material suspended in the water column. By impounding sand on their landward side they also drive propagation of beaches. Cracks and crevices in the reefs structure are likely to aid the retention of sediment further by acting as sediment traps.

Kirtley and Tanner (1968) infer that a process of cementation converts dead tubes of Sabellariid polychaetes to beach rock. Large platforms of this tube-derived rock are thought to form the foundations of the “perched” barrier islands which characterise the southeast coast of Florida (Tanner 1960; Multer and Milliman 1967). The processes by which lithification occurs are not fully understood, but it would seem that the protein cement is somehow replaced by calcium carbonate, which is presumably derived largely from the fine shell fragments favoured for tube construction by sabellariid species in this area (Kirtley and Tanner 1968). The warm waters of Florida are also likely to contribute to this process, since lithification is known to occur more readily at higher temperatures (De Boer et al. 1977).

Miller (2001) suggests that strategies to attract Sabellariid polychaetes could be employed to utilise the stabilising effect of the reefs in beach management. He suggests that this could be achieved by relocating boulders already colonised by sabellariids, placement of suitable settlement materials (boulders & large rocks) on sandy beaches and in the intertidal zone to slow water currents and potentially provide more stable reefs which could themselves improve the sabellariid larval supply leading to the development of further inshore reef systems.

Impact on Water Quality

The serpulid worm *Ficpomatus enigmaticus* forms reefs of calcareous tubes. Davies et al. (1989) calculated that a substantial population of *F. enigmaticus* that had colonised a large marina could completely filter the marine water in 26 hours. Serpulid worms have also been noted as influencing the oxygen and nutrient levels in subtropical lagoons (Keene 1980). It is likely that sabellariid reefs may have a similar influence on water quality where dense aggregations exist in closed or semi-closed water bodies. All of the recorded occurrences of sabellariid reefs in the UK are in open water systems though, so any changes in water quality are likely to be heavily diluted, although this might be an interesting topic for future research.

1.3.4 Trophic Interactions of Sabellariid Reefs

Biodiversity

Kirtley and Tanner (1968) state that sabellariid reefs on the east coast of Florida support an elevated biodiversity "the reefs…..are the basis for an elaborate marine community of encrusting, boring, shelter-seeking, parasitic and predatory marine animals, in addition to an abundant marine flora". Wells (1970a) makes similar inferences about *Sabellaria vulgaris* reef masses in Delaware Bay, stating that "each *Sabellaria* mass provides crevices and attachment sites for a variety of living associates…creating a distinct community of organisms dependent on the masses for protection, shelter and food". Chen and Dai (2009) state that *Idanthyrsus cretus* reefs in Taiwan have a comparable ecological role to tropical coral reefs, providing substrata for a diverse epifauna and infauna. However, these statements, like so many others in the literature which infer enhanced biodiversity associated with sabellariid reefs (Lechapt and Gruet 1993; Dubois et al. 2002), were not backed up with quantitative comparisons with other habitats. In fact, very few studies have investigated the fauna associated with sabellariid reefs quantitatively indicating that the inferences about enhanced biodiversity which are so prevalent in the literature should be treated with some caution until such a time as this hypothesis is tested more comprehensively.

A study of *Sabellaria spinulosa* reefs in the Wash reported that the reefs supported twice as many species and three times as many individuals as the surrounding sediments (excluding the worms themselves), suggesting that in this area sabellariid reefs are exerting a significant structuring influence on benthic communities (NRA 1994). However, these figures were derived from comparisons made between samples that contained high abundances of *S. spinulosa* (>100 individuals in 3 Day grab samples) and samples that contained low abundances of *S. spinulosa* (<100 individuals in 3 Day grab samples) with the latter category containing many more sites (n=58) than the former (n=8). These comparisons may not therefore accurately describe the influence of reef presence, particularly as the non-reef / low *S. spinulosa* abundance category included a number of sites thought to be negatively influenced by both natural and anthropogenic disturbances (NRA 1994). George and Warwick (1985) studied the production of *S. spinulosa* aggregations in the Bristol Channel and noted an increase in the number of species associated with the reefs when compared to the surrounding deposits, although no direct comparisons were made. The sub-tidal communities of the Bristol Channel are frequently exposed to periods of anoxia and high levels of scouring meaning that the macrofauna are generally impoverished (Mettam et al. 1994; Warwick and Somerfield 2010). Reefs formed by *S. spinulosa* are more commonly found in association with more stable sedimentary deposits in the eastern English Channel and North Sea which are known to support a more diverse suite of fauna (Heip and Craeymeersch 1995; Rees et al. 1999). Hence the increase in diversity observed in the Bristol Channel is unlikely to be repeated where the reefs have formed in areas with more stable environmental conditions.

Dubois et al. (2002) investigated the biodiversity of fauna associated with different stages of reef development although no comparisons were made with fauna inhabiting the surrounding sediments. This study found that the highest levels of biodiversity were associated with degraded reefs, a phenomenon also reported in earlier studies by Dias and Paula (2001) and Gruet (1982). As the reefs get older and parts die off or break up, crevices are created which can be utilised by small fish, crabs and molluscs (Gruet 1982). This raises questions about the relationship between the health or developmental stage of these reefs and the associated biodiversity and ecological functioning. It is generally accepted that ecosystem function is positively correlated with biodiversity although a review of this topic found that few studies demonstrate improved function at higher levels of species richness (Schwartz et al. 2000). It is also generally accepted that a climax reef community will support the highest levels of biodiversity and provide the broadest range of ecosystem functions (Hooper et al. 2005; Ieno et al. 2006). Since enhanced biodiversity associated with sabellariid reefs has been used as a justification for their conservation status (UKBAP 2007b), further research is urgently required to establish the relationship between reefs created by *S. spinulosa*, biodiversity and the ecological functions they provide.

Despite the gaps that exist in our understanding of the fauna associated with sabellariid reefs, some associations are well documented. Crustaceans, for example have been widely reported as showing a preference for sabellariid reefs. Lechapt and Gruet (1993) noted that pagurids and cirripedes were associated with the deep water species *Bathysabellaria neocaledoniensis* although these associations were based on a small number of observations. In southeast Florida crustaceans are reported to make up the largest component of fauna living in the sabelariid reef with at least two species being restricted to it (Gore et al. 1978). Crustaceans were also observed in association with *Neosabellaria vitiensis* in Fiji although no analysis of the associated fauna was undertaken (Pohler 2004). In the UK the Ostracod *Hemicythere villosa* (Sars) (Horne 1982) as well as the pink shrimp *Pandalus monatgui* (Warren and Sheldon 1967) have been reported in association with sabellariid reefs. The widely documented association between crustacea and sabellariid reefs is perhaps another indication of their stabilising influence since this component of the benthos is usually considered as an indicator of a low level of environmental stress (Pearson and Rosenberg 1978).

The hermit crab *Disorsopagurus schmitti* is the only crustacean reported to be both ecologically dependent upon, and geographically restricted to, sabellariid reefs (Gherardi and Cassidy 1994). This species lives exclusively inside empty *Sabellaria cementarium* tubes and adults of this species have been shown to actively select them in laboratory experiments, even when presented with gastropod shells (Gherardi 1996).

The fact that juveniles and megalopae preferentially select gastropod shells, seems to indicate that the switch in housing preference has perhaps evolved in response to competition for more conventional gastropod homes (Gherardi 1996). *D. schmitti* is very small in size compared to most other hermit crabs, allowing it to occupy the narrow microhabitat created by the worm tubes but perhaps making it less able to compete for possession of gastropod shells. The maintenance of sabellariid reefs will prove essential for the survival of this species.

Competition and Succession

Some early studies of sabellariid reefs suggest that these dense worm colonies, particularly those less than two years old, are able to out-compete all other littoral species (Wilson 1971; Cunningham et al. 1994). As reefs age, and are damaged, crevices and gaps are often utilised by other filter feeding animals including crustaceans (see previous section) and molluscs (Cunningham et al. 1994). Sabellariid reef / mussel successions have been frequently reported in the literature (Achari 1974; Riesen and Reise 1982; Reise and Schubert 1987; Cunningham et al. 1994; Holt et al. 1998; Pohler 2004) and it would seem that, because there is an overlap between their environmental niche occupied by these two animals, even a slight change in the environment, for example sediment composition, is likely to alter the community, favouring one or the other group. Such a pattern has been observed in the Wadden Sea where *S. spinulosa* reefs were once prevalent alongside oyster beds. These have disappeared and been replaced by beds of the mussel *Mytilus edulis*. This has been attributed to a combination of fishing and dredging pressures as well as coastal eutrophication (Riesen and Reise 1982; Reise and Schubert 1987). Holt et al. (1998) document further evidence of this in Morecombe Bay. Here *S. alveolata* reefs developed on a boulder scar which had previously been populated by the mussels *M. edulis*. It was postulated that changes in the sediment regime, including an increased availability of coarse sand as a result of new sea defences, had allowed the *S. alveolata* to outcompete the mussels. Barnacles and oysters have also been reported as competing with sabellariids for space (Zale and Merrifield 1989).

Most sabellariid reefs are monospecific but *Sabellaria cementarium* and *Idanthyrsus ornamentus* have been recorded in association with one another as well as with dense aggregations of the ampheretid *Schistocomus hiltoni* (Posey et al. 1984). Sabellariids have also been reported as components of other mixed polychaete reefs, particularly in association with serpulids belonging to the genus *Hydroides*. For example Nishi et al. (2004) observed *Sabellaria tottoriensis* in association with *Hydroides ezoensis*, both densely encrusting living *Turbo torquatus*. *Lanice conchilega* is known to colonise the periphery, and on occasion the interior, of the "banc des Hermelles" although the nature of this interaction is unknown. Where they reach high densities, they are thought to aid settlement by *S. alveolata* by consolidating sediments and providing more stable surface for attachment (Caline et al. 1992). Although there is some overlap between the environmental niche of our two native sabellariid species, *S. alveolata* and *S. spinulosa* have only rarely been reported as occurring in the same location (Last et al. 2011a).

Some crustacean species such as *Pachycheles monlifera* in south east Florida (Gore et al. 1978) are also reported to compete with sabellariids for food, since they too feed on plankton and other suspended organic material, although in some cases they have also been reported as predating on the worms themselves (Zale and Merrifield 1989). *Idanthyrsus* sp. has been found growing amongst colonies of scleractinian corals in Okinawa, Japan (Nishi and Nishihira 1999), which may also compete for food. The impact of these filter feeding competitors may not only be in their reduction of food but also in their active removal of larvae from the water column, making them a very real threat to the longevity of the reef systems. George and Warwick (1985) suggested from their observations of *S. spinulosa* in the Bristol Channel that growth and recruitment might be inhibited, or even prevented, by the dense populations of the brittle star *Ophiothrix fragilis*. Detailed investigations into the interactions between sabellariid reefs and other filter feeders may therefore be crucial in understanding the best methods for their conservation.

Parasites

Killeen and Light (2000) report a recurring association between *Sabellaria* spp and two marine snails; the pyramidellid gastropod *Noemiamea dolioformis* and the aclid, *Graphis albida*. Based on their co-occurrence in samples taken from 24 locations around the British Isles and France, it was inferred that these and other pyramidellid species were feeding on *Sabellaria*. Pyramidellidae are small white gastropods, all of which are ectoparasites of other marine organisms particularly polychaetes and molluscs. It is likely therefore that the author's inferences are correct although, without direct observations, predation on the fauna associated with the sabellariids cannot be ruled out. Further work would be required to investigate the nature of the relationship between *Sabellaria* and these small mollusc species. Unfortunately most work in this area focuses in macrofauna (>0.5mm in estuarine environments and >1mm in marine environments) meaning that these very small animals are likely to be overlooked.

Predation

Kirtley (1994) concluded that sabellariids themselves must make an important contribution to the food web because of the high attrition rates he observed. Zale and Merrifield (1989) also concluded that the presence of sabellariid reefs substantially enhances diversity of small fish, indicating that these features play an important role in supporting marine food webs. In the UK *Sabellaria spinulosa* is reported to be a major component of the diet of pink shrimp *Pandalus montagui*, although this seems mostly to be based on the co-occurrence of the two species (Warren and Sheldon 1967). More detailed studies have found sabellariids to be an important component in the diet of other *Pandalus* species though, indicating that there may be some truth behind this assertion (Chuhukalo and Shebanova 2008). In Cumbria the shore crab (*Carcinus* sp.) and the shanny (*Lypophrys pholis*) were found to have sabellariid remains in their stomachs (Taylor et al. 1962), and *Carcinus maenus* preyed upon transplanted reefs in Somerset (Bamber and Irving 1997). The scale worm *Lepidonotus* is also thought to be a predator of *Sabellaria spinulosa*, attacking the worm by inserting its everted pharynx into the tube and pulling the worm's head off with its four jaws (Schafer 1972).

It has been mentioned in the literature (Holt et al. 1998) that flatfish including sole and plaice could easily obtain sabellariids by crunching up the brittle tubes although no direct evidence of this has been presented. Since the worms are known to be able to retract considerable distances down their tubes (Wilson 1971; Cunningham et al. 1994) it seems unlikely that they would represent a readily available prey source for fish. However, Posey et al. (1984) reported direct observations of the black rockfish *Sebastes lanops* and the stripe surfperch *Embiotica lateralis* feeding on the extended crowns of sabellariids alongside hermit crabs *Pagurus* spp. It has also been accepted practice in a number of commercial fisheries to search for *Sabellaria* reefs with hand held dredges before setting down demersal trawling gear (personal communications with fishermen), indicating a strong association between these reefs habitats and some commercial flatfish species. Given the reported association between sabellariid reefs and crustacean species it is perhaps more likely that the associated fauna are attracting fish rather than the worms themselves, it is also possible that the flatfish are utilising gaps in the reef to take refuge from predators. Wilson (1971) also regarded predation to be of little overall importance to *S. alveolata* in North Cornwall, though this is obviously an area that would benefit from more rigorous research.

1.4 Sensitivity to Disturbance

The sessile nature of biogenic reefs formed by polychaete worms makes them vulnerable to changes in the environment as they have a limited capacity to move away from unfavourable conditions. There is little direct exploitation of sabellariids, although they are used as fishing bait on a small scale (Holt et al. 1998). However, the occurrence of sabellariid reefs in areas utilised by man means that there is significant potential for adverse anthropogenic impacts. Significant losses of *Sabellaria spinulosa* reefs have been reported in the Wadden Sea (Riesen and Reise 1982; Reise and Schubert 1987) and more recently with the disappearance of Saturn Reef (Hendrick 2007) making it all the more pertinent to understand the sensitivity of these habitats. Despite this, very few studies have been carried out, either experimentally or in the field, to ascertain the sensitivity and vulnerability of sabellariid reefs to anthropogenic activities.

1.4.1 Changes in Suspended Solids (Water Clarity)

A major physical impact associated with marine developments is the release of fine sediment into the water column, increasing turbidity. For example aggregate extracted by dredging is often screened, a process which adjusts the composition of the sediment load to meet consumer requirements usually by releasing finer (less valuable) sediments back into the sea (Newell et al. 2004). Sediment is also released as a result of substratum disturbance and overspill. As *S. spinulosa* is often found in turbid waters and is known to rely on suspended sediments for feeding and building materials, it is likely that this species will be resilient to increased sediment loads. It is possible that an increased sediment load could even have a positive impact on the development of *S. spinulosa* aggregations. However, the tolerance of this species to turbidity is likely to vary depending on the composition of the suspended sediment.

Dubois et al. (2009) found that concentrations of suspended particulate matter (SPM) up to 55.5 mg L^{-1} had no adverse impacts on feeding activity of *S. alveolata* and noted an increase in the number of individuals feeding at concentrations between 6.5 and 12.3 mg L^{-1}. Similarly, Davies et al. (2009) and Last et al. (2011b) have demonstrated that the growth rates of *S. spinulosa* are significantly reduced in zero sediment conditions when compared to growth rates in intermediate and high sediment regimes. This further supports the assumption that *S. spinulosa* requires at least some suspended sediment and is tolerant of turbid conditions. However, Last et al. (2011b) noted that an increased number of *S. spinulosa* exhibited no tube growth under the highest SPM regime, indicating that in some instances high turbidity could impact the tube building abilities of this species. Turbidity levels experienced by sabellariids in the field have not been well documented to date, however predicted and recorded turbidity levels from estuaries in which sabellariid reefs are known to occur indicate that SPM concentrations could far exceed the levels used in the afore mentioned laboratory experiments (Uncles et al. 2006; Devlin et al. 2008; Uncles and Mitchell 2011; Mitchell et al. 2012). The persistence of sabellariid reefs in these estuaries indicates that the tolerance of these species exceeds expectations based on laboratory tests alone.

The apparent tolerance of *Sabellaria spinulosa* to fluctuations in turbidity may not extend to situations where sediment loadings are reduced, indeed Davies et al. (2009) found that net erosion of tube structures occurs in sediment starved conditions. Reduced turbidity might occur where water movements are altered, perhaps as a result of marine constructions. This, however, is likely to be a rare occurrence in subtidal environments, with the exception perhaps of tidal barrages. *S. spinulosa* are therefore likely to be more susceptible to these impacts when they occur intertidally. Shore defences or harbour extensions are likely to interrupt sediment transport, reducing the supply of sand. Hence due attention should be afforded to this during any associated impact assessments. The offshore wind farm industry is in its infancy and the degree to which these structures alter the flow of water and sediments remains largely unknown. Large arrays may alter water movement, but the discontinuous nature of these developments makes increased turbulence more likely than a complete interruption to flow. More research would certainly be beneficial in this regard particularly given the scale of Round 3 wind farm developments (TCE 2013)

Although it is unlikely that the reef building organism itself will be adversely impacted by the levels of turbidity and turbulence associated with offshore developments, and may even thrive under these conditions, the impacts on the fauna associated with the reefs has not yet been determined.

1.4.2 Siltation Rate Changes Including Smothering

Pohler (2004) observed that episodes of sedimentation can smother *Neosabellaria vitiensis* reefs. Resettlement of the polychaetes occurred within a few weeks of smothering suggesting a rapid turn-over of reefs and plentiful larvae supply. Miller (2001) noted seasonal smothering of sabellariid reefs, with intertidal reefs suffering mass mortality every winter. Recruitment occurred each spring, indicating that these intertidal reefs were essentially being maintained by the more stable subtidal reefs. In contrast, Pohler (2004) concluded that new recruitments of *N. vitiensis* originated from more stable intertidal colonies along the coast, indicating that the larvae can also be distributed through longshore drift. Pohler (2004) also noted that large amounts of seaweed and litter washed up after tropical storms were having a detrimental effect on sabellariids, smothering and killing large areas of the reef.

Smothering is likely to represent a very real threat to *S. alveolata* which occurs in intertidal and shallow sublittoral environments where new constructions and beach nourishment programmes occur. *S. spinulosa* is less likely to experience smothering through anthropogenic activities as it occurs primarily in subtidal habitats, although marine construction and spoil dumping could present a potential threat of smothering. *S. spinulosa* reefs have been reported to occur on the boundaries between mixed gravel deposits and mobile sands (Hendrick 2007). Therefore smothering may also occur through natural storm events.

A recent study by Last et al. (2011b) found that *S. spinulosa* is tolerant of short-term (≤ 32 days) burial in fine sand with no effect of burial depth. Last et al. (2011b) describe the "emergence tube" built by *S. spinulosa,* seemingly as a mechanism for escape when buried. *S. spinulosa* constructs its fragile emergence tube at rates up to 1mm per day, which is likely to be a successful mechanism to avoid gradual burial. More rapid burial, which is perhaps more likely to impact *S. spinulosa*, has yet to be investigated. A comparable study on *P. lapidosa* (Sloan and Irlandi 2008) found that the effect of burial depth increased with increasing burial duration. Sloan and Irlandi (2008) also found latent effects of burial stress, a factor that was not considered by Last et al. (2011b). Latent mortality, recorded one week after the sediments were removed, reached 40 - 50% under the lowest level of burial stress (1cm for 72hrs), indicating that whilst the burial event did not cause instant mortality it did damage the worms significantly (Sloan and Irlandi 2008).

1.4.3 Pollution and Other Chemical Changes

Studies relating to water quality, in particular contamination of water caused by effluent discharges (Hoare and Hiscock 1974; Walker and Rees 1980; Last et al. 2011a), have found that *S. spinulosa* is more tolerant to these conditions than many other marine organisms. Hoare and Hiscock (1974) found that species richness and diversity showed a significant reduction within 150 m of the outfall of a bromide extraction plant in North Wales. The effluent had a pH of 4 and contained contaminants including free halogens. *S. spinulosa* was found closer to the outfall than any other marine species, and furthermore was found at higher densities at an intermediate distance. This indicates that whilst *S. spinulosa* may show some sensitivity to very marked reductions in water quality, it may favour intermediate levels of contamination or be more tolerant than other species, giving it a competitive advantage in these conditions. This is further supported by work carried out by Walker and Rees (1980), who found that sludge dumping in Dublin Bay appeared to encourage the growth of *S. spinulosa*. Laboratory experiments conducted by Last et al. (2011a) showed significantly higher rates of tube growth in *S. spinulosa* specimens held in the highest concentrations of aqueous chlorine (0.1 mg L^{-1} Total Residual Oxidant (TRO)) when compared to those held in lower concentration or control conditions. The authors offered no explanation for this observation, but as there were no differences in mortality rates between treatments it seems likely that *S. spinulosa* is tolerant of aqueous chlorine at these levels. However, it should be noted that although *S. spinulosa* itself may be tolerant to low water quality conditions the same may not be true of the reef inhabitants.

1.4.4 Physical Damage: Selective Extraction and Abrasion

The removal of substratum and physical destruction associated with marine activities is arguably the greatest anthropogenic threat that exists for *S. spinulosa* aggregations. However, the significance of this threat has yet to be assessed in terms of sustainable thresholds or the longevity of such impacts. It has been suggested that regeneration of *S. spinulosa* reefs could take between 15 and 150 years (UKBAP 2007b) although others have determined recovery of this habitat to be more rapid (Jackson and Hiscock 2008). There have been several instances in the UK where *S. spinulosa* aggregations have been reported to appear where aggregate extraction activities have ceased. Foster-Smith (2001) reported the presence of reefs in an area of the Wash were associated with ground clearly scarred by dredging activities. It was suggested that this was most likely due to a reduction in the overburden of sand resulting in a substratum more suitable for *S. spinulosa*. The recent discovery of significant *S. spinulosa* aggregations within and adjacent to active aggregate licence areas in the North Sea (EMU 2008) provides further evidence that the physical impacts of dredging activities on this species are short lived and restricted in extent. The influence of sediment released during dredging activities on *S. spinulosa* reefs is discussed in previous sections of this chapter and is the subject of on-going research being carried out by the Scottish Association of Marine Science (Davies et al. 2009).

Trawling, dredging, potting and net fishing are all thought to cause damage to *S. spinulosa* reefs (Holt et al. 1998; Hendrick 2007). It has been postulated that where parts of the reef are broken off or damaged the resulting hole may be enlarged further by wave action (Cunningham et al. 1994), potentially exacerbating damage caused by fishing . Towed fishing gear is thought to represent the largest global anthropogenic disturbance to the seabed (Jennings and Kaiser 1998; Kaiser et al. 2003; Queiros et al. 2006; Olsgard et al. 2008). In most cases these gears are used in direct contact with the seabed to capture target species that live on or within the seabed (Jennings and Kaiser 1998). It has long been accepted practice amongst commercial shrimp fishermen to search for *S. spinulosa* reefs using small hand held dredges (Warren and Sheldon 1967). The strong association between these habitats and demersal fish has also made them a target for beam trawlers (personal communications with fishermen in Ramsgate). Fishing is therefore thought to represent a significant threat to *S. spinulosa* reefs. However, the fact that *S. spinulosa* reefs continue to persist in the southern North Sea, despite many years of commercial fishing indicates that this habitat is somewhat resilient to this disturbance.

Shrimp fishing was implicated in the decline of *S. spinulosa* reefs in the Wadden Sea between 1924 and the 1980's (Riesen and Reise 1982; Reise and Schubert 1987). Local fishermen were reported to have deliberately ground the reefs with heavy gear because they ripped apart the nets when fishing for shrimp (Riesen and Reise 1982). There was no specific evidence of fishing having caused the Wadden Sea demise and others have speculated that coastal eutrophication, favouring *Mytilus*, contributed to the collapse (Reise and Schubert 1987). Since the biodiversity of fauna associated with sabellariid reefs has been reported as being highest in degraded structures (Dubois et al. 2002), it could be hypothesised that low levels of fishing have a positive influence on these habitats. This would certainly pose a difficult dilemma to those responsible for conservation of the marine environment, and is clearly an area that would benefit from further investigation.

1.5 Conservation and Management of *Sabellaria spinulosa*

1.5.1 Conservation Status

Sabellaria spinulosa reefs have been identified as a priority habitat for conservation in European and National legislation as summarised in **Table 1.1.** It should be noted that all such legislation applies to the habitat created by *S. spinulosa* and not to the species itself.

Table 1.1 Table summarising the legislative instruments used to protect *Sabellaria spinulosa* reefs in the UK.

Legislative Instrument	Mechanism for Protection
Environmental Impact Assessment Directive 1985, as amended in 2014	Avoidance of, or compensation for, significant impacts from marine developments
Strategic Environmental Assessment Directive 2001	Avoidance of significant impacts from marine developments
European Habitats Directive 1992	Special Areas of Conservation (SACs)
OSPAR Convention 1992	OSPAR Marine Protected Areas (MPAs)
Nature Conservation (Scotland) Act 2004	Scotland's Biodiversity Strategy
Natural Environment and Rural Communities Act 2006	England's Biodiversity Strategy Environment Strategy for Wales
Wildlife and Natural Environment Act (Northern Ireland) 2011	Northern Ireland's Biodiversity Strategy
Marine Strategy Framework Directive 2008	"Good Environmental Status" targets (particularly under D1 and D6)
Marine and Coastal Act 2009	Marine Conservation Zones (MCZ)
Marine (Scotland) Act 2010	Nature Conservation Marine Protected Areas (MPAs)

Environmental Impact Assessment Directive

The EIA Directive (85/337/EEC) has been in force since 1985, and covers a variety of public and private projects which have the potential to negatively impact the environment. Amendments made to the EIA directive in 1997, 2003 and 2009 were codified in 2011 (EIA Directive 2011/92/EU) and were amended further in 2014, expanding the scope of the directive and bringing it in line with the Espoo convention on transboundary issues and the Aarhus convention on public participation.

The aim of the EIA Directive is to ensure that due consideration is given to the environment during the planning process (IEEM 2006; IEEM 2010; SNH 2013). All natural resources that have the potential to be impacted by a new development are considered during the EIA process and the likelihood and significance of such impacts are reported in the environmental statement (ES). Where there is potential for the development to affect a European Marine Site (EMS) the developer must also provide a report with their planning application which details how the site might be affected together with sufficient information to enable an Appropriate Assessment (AA) if required (see following section on the European Habitats Directive). The application of the EIA Regulations has meant that even small areas of *S. spinulosa* reef, that do not form part of the UK's network of Marine Protected Areas (MPAs), have been afforded protection from potentially damaging activities such as marine aggregate extraction and offshore construction, through the administration of exclusion zones and alterations to construction plans (MESL 2006; EMU 2008; Pearce et al. 2014).

The Strategic Environmental Assessment Directive

The Strategic Environmental Assessment Directive (2001/42/EC) bares many similarities with the EIA Directive and the intention is for an assessment to be made of the environmental impacts of new plans, programmes and policies (ODPM 2005). In contrast to the EIA directive, the SEA directive is typically applied to new policies or the development of new sectors such as offshore wind energy and assessments are made at a strategic level.

European Habitats Directive

In 1992 the European Union adopted the Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora) through which it meets its obligations as a signatory of the Bern Convention on the Conservation of European Wildlife and Natural Habitats. The main aim of the Habitats Directive is to promote the maintenance of biodiversity by taking measures to maintain and restore natural habitats and wild species at a favourable conservation status, introducing robust protection for those habitats and species of European importance. The Habitats Directive was the first statutory driver to advocate the precautionary approach: permitting projects that have ascertained no adverse effect on the integrity of protected sites (although there are provisions for projects with overriding public interest). The Habitats Directive was initially applied out to UK territorial waters (12 nm) but following a legal challenge by Greenpeace this was extended to cover the whole of the UK Continental Shelf.

Sabellaria spinulosa reefs qualify under Annex I of the Habitats Directive where they are a type of "reef" to be protected by a network of Special Areas of Conservation (SACs). The Interpretation Manual of European Union Habitats (EC 2013) specifically lists *Sabellaria spinulosa* reefs of the sublittoral North Sea "*Sabellaria*-Riff des Sublittorals der Nordsee", though they may also be protected by virtue of their occurrence in broader physiographic habitats listed under the directive such as "Estuaries" and "Large Shallow Inlets and Bays".

In the UK the presence of well-developed and stable *S. spinulosa* reefs was one of the primary reasons considered for the designation of 'The Wash and North Norfolk Coast' SAC (UK0017075). Here the reefs are both an Annex I habitat in their own right and part of the broader 'Large Shallow Inlets and Bays' habitat. More recently, an additional three UK sites were put forward to the EU Commission for the protection of *S. spinulosa* reefs (Tranche 38, August 2010): Inner Dowsing, Race Bank and North Ridge (UK0030370); North Norfolk Sandbanks and Saturn Reef (UK0030358); and Haisborough, Hammond and Winterton (UK0030369). All have been approved by the Commission as Sites of Community Importance (http://jncc.defra.gov.uk/page-1488).

It is necessary to undertake a Habitats Regulations Assessment (HRA) where new plans or projects interact with designated *Sabellaria spinulosa* reefs, to determine the likelihood of the development interfering with the conservation objectives of the site. Where there is a potential for a plan or project to have a significant effect on a European site, either individually or in combination with other projects, then an Appropriate Assessment (AA) must be carried out. An AA explores the potential negative impacts of the plan or project and proposes avoidance or mitigation measures to reduce any effects to an insignificant level (IPC 2011). If it is not possible to reduce impacts to and insignificant level or there is any uncertainty as to whether or not this will be possible the development will only be granted consent if there are Imperative Reasons of Over-riding Public Interest (IROPI) (IPC 2011).

Until recently HRAs were only carried out on new projects and plans which meant that commercial fishing activities were excluded from the process. In 2012 however, Defra announced a revised approach to bring commercial fisheries in line with other activities (Defra 2013). UK and non-UK fishing vessels will now be subject to HRA for European Marine Sites within 12nm on a risk-prioritised basis. Furthermore, Defra intends to submit proposals for protection measures for EMSs outside 12nm to the European Commission in accordance with the Common Fisheries Policy (CFP). In combination these new approaches to the management of commercial fishing activities occurring within EMSs will ensure that protection levels are consistent with the Habitats Directive and as a consequence, designated S. spinulosa reefs will be afforded a much greater level of protection.

OSPAR Convention

The OSPAR Convention for the Protection of the Marine Environment of the North East Atlantic was adopted in 1992 combining and updating the 1972 Oslo Convention on dumping waste at sea and the 1974 Paris Convention on land-based sources of marine pollution. The OSPAR Convention aims to provide a comprehensive and simplified approach to addressing all sources of pollution which might affect the maritime area, as well as matters relating to the protection of the marine environment. It is through this commitment that international and regional OSPAR Marine Protected Areas (MPAs) are designated. The overarching aim of the OSPAR Convention is as follows;

"Our mission is to conserve marine ecosystems and safeguard human health in the North-East Atlantic by preventing and eliminating pollution; by protecting the marine environment from the adverse effects of human activities; and by contributing to the sustainable use of the seas"

The OSPAR Convention was adopted in 1992, and was sanctioned in the UK in 2000 as Annex V on the protection and conservation of ecosystems and biological diversity of the maritime area.

The OSPAR Biodiversity Strategy is made up of four elements:

1. Ecological quality objectives: in support of the ecosystem approach to the management of human activities a pilot on ecological quality objectives for the North Sea has been undertaken. Consideration is now being given to extending ecological quality objectives to other OSPAR sub-regions.

2. Species and habitats: assessments are made of species and habitats that are threatened or in decline and programmes and measures are developed for their protection.

3. Marine protected areas: an ecologically coherent network of well-managed marine protected areas is being created. This includes novel work on Marine Protected Areas in areas beyond national jurisdiction.

4. Human activities: the human activities in the OSPAR maritime area which may adversely affect it are being assessed and programmes and measures to safeguard against such harm are being developed.

Sabellaria spinulosa reefs were added to the “OSPAR list of threatened and / or declining habitats” based on the Texel-Faial criteria for identification of species and habitats in need of protection (OSPAR 2003; OSPAR 2008). Sensitivity, rarity, ecological significance and decline were cited as reasons for its inclusion with information also provided on threat (OSPAR 2013). The list is used as one of the criteria to designate MPAs in the UK (Cork et al. 2006). However, to date there has not been any assessment of the rarity or sensitivity of this habitat with only very minimal evidence is cited for the habitats ecological significance (OSPAR 2013).

Country Biodiversity Strategies

The Biodiversity Action Plan (BAP) (BRIG 2008) was the UK Governments response to the Rio Convention on Biological Diversity (CBD) signed in 1992. It describes the UK’s biological resources as well as detailed plans for the protection of these resources. *Sabellaria spinulosa* reefs are listed as a priority habitat for conservation and have a dedicated Habitat Action Plan (HAP) (UKBAP 2007b). The establishment of devolved governments in Scotland, Wales and Northern Ireland in 1998 led the four countries to develop their own country strategies for biodiversity and the environment, allowing conservation approaches to differ according to the different environments and priorities within the countries.

In 2007 a shared vision for UK biodiversity conservation was adopted by the devolved administrations and the UK government, described in ‘Conserving Biodiversity – the UK Approach’ (UKBAP 2007a). This document reflects the new key drivers for conservation action since the UK BAP was created, including the EU Gothenberg agreement in 2001 to halt the loss of biodiversity by 2010, and the findings of the Millennium Ecosystem Assessment (2005). Additionally, it outlines the need for the four countries to work together to meet shared challenges and achieve common goals, and describes the requirements for future work at a UK level.

The ‘UK Post-2010 Biodiversity Framework’ (JNCC and Defra 2012) now succeeds the UK BAP and ‘Conserving Biodiversity – the UK Approach’, and is the result of a change in strategic thinking following the publication of the CBD's 'Strategic Plan for Biodiversity 2011–2020' and its 20 'Aichi targets', at Nagoya, Japan in October 2010, and the launch of the new EU Biodiversity Strategy (EUBS) in May 2011. The framework demonstrates how the work of the four countries and the UK contributes to achieving the 'Aichi targets', and identifies the activities required to complement the country biodiversity strategies in achieving them.

In England and Wales *S. spinulosa* reefs are listed as Habitats of Principal Importance under Section 41 of the Natural Environment and Rural Communities (NERC) Act 2006. In Northern Ireland a *S. spinulosa* HAP is currently under implementation (DOENI 2005). The Scottish Biodiversity List was published to satisfy Section 2(4) of The Nature Conservation (Scotland) Act 2004. However, the list does not include *S. spinulosa* reefs.

Marine Strategy Framework Directive

The Marine Strategy Framework Directive (MSFD) was adopted in June 2008 and it is concerned primarily with preserving the general health of European marine habitats and the biodiversity associated with them.

Biogenic reefs formed by *Sabellaria spinulosa* have been identified as suitable Good Environmental Status (GES) targets for Descriptors 1 (Biological diversity) and 6 (Seafloor integrity) under the MSFD (Cochrane et al. 2010). As *S. spinulosa* reefs are identified under Community (EU Habitats Directive) and International (OSPAR) legislation they are considered a Special Habitat as defined in Table 1 of Annex III of the MSFD.

Marine and Coastal Access Act (2009)

The Marine and Coastal Access Act received royal assent on 12 November 2009 and introduced a new framework for managing the many demands placed on the sea, improving marine conservation and opening up access for the public to the English coast.

Provisions are made in Part 5 of the Act for designation and protection through a new type of marine protected area, called Marine Conservation Zones (MCZs). MCZs will exist alongside European Marine Sites (SACs and SPAs), to form a marine protected areas network. *Sabellaria spinulosa* reef is identified as a priority habitat for protection in the "Ecological Network Guidance" both as the Broad Scale Habitat, Subtidal biogenic reefs A5.6 and as the Habitat Feature of Conservation Importance (FOCI) Ross worm (*Sabellaria spinulosa*) reefs (NE and JNCC 2009).

Marine (Scotland) Act 2010

The Marine (Scotland) Act, which was introduced to Scottish Parliament on the 29th April 2009 and gained Royal Assent on 10th March 2010, provides the legal mechanism to help ensure clean, healthy, safe, productive and biologically diverse marine and coastal environments, managed to meet the long term needs of both nature and people, by putting in place a new system for improved management and protection of the marine and coastal environment.

The Marine (Scotland) Act introduces new powers relating to functions and activities in the Scottish marine area, including provisions enabling Scottish Ministers to designate three types of Marine Protected Area (MPA) across Scottish territorial waters: Nature Conservation MPAs – for the conservation of Scotland's most important marine biodiversity and geodiversity features; Historic MPAs – for the protection of historically important marine sites such as wrecks or national monuments; and Research/Demonstration MPAs – to demonstrate or research new methods of managing Scotland's marine environment. Scottish Ministers also have devolved responsibility under the UK Marine and Coastal Access Act 2009 for the designation of MPAs for the conservation of important marine biodiversity and geodiversity out to 200 nautical miles. *Sabellaria spinulosa* reefs are not specifically listed as an MPA Search Feature or a Priority Marine Feature (PMF) (Wilding et al. 2012), but may nevertheless be considered for inclusion in the Scottish MPS network based on their European conservation status.

1.5.2 Reef Definition

Despite the apparent conservation status of *Sabellaria spinulosa* reefs, no definitive definition of what constitutes a reef exists. Each piece of legislation outlined in the preceding sections has its own description, or refers to those of preceding legislation, though they are all relatively vague and seemingly without scientific premise:

European Habitats Directive

"Reefs can be either biogenic concretions or of geogenic origin. They are hard compact substrata on solid and soft bottoms, which arise from the sea floor in the sublittoral and littoral zone. Reefs may support a zonation of benthic communities of algae and animal species as well as concretions and corallogenic concretions."

The definition of biogenic reef was further refined by the UK Marine SAC Project:
"*Solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms.*" (Holt et al. 1998)

The following criteria were applied to further differentiate biogenic reef habitats:

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

BAP Description

“Sabellaria spinulosa reefs comprise of dense subtidal aggregations of this small, tube-building polychaete worm. Sabellaria spinulosa can act to stabilise cobble, pebble and gravel habitats, providing a consolidated habitat for epibenthic species. They are solid (albeit fragile), massive structures at least several centimetres thick, raised above the surrounding seabed, and persisting for many years. As such, they provide a biogenic habitat that allows many other associated species to become established. The S. spinulosa reef habitats of greatest nature conservation significance are those which occur on predominantly sediment or mixed sediment areas. These enable a range of epibenthic species with their associated fauna and a specialised ‘crevice’ infauna, which would not otherwise be found in the area, to become established. Studies have compared an area of S. spinulosa with other macrofaunal communities in the Bristol Channel and found that the former had a higher faunal diversity (more than 88 species) and higher annual production (dominated by suspension-feeders) than other benthic communities in the area.”

OSPAR Reef Definition:

"The tube-building polychaete Sabellaria spinulosa can from dense aggregation on mixed substrate and on rocky habitats. In mixed substrata habitats, comprised variously of sand, gravel, pebble and cobble, the Sabellaria covers 30% or more of the substrata and needs to be sufficiently thick and persistent to support an associated epibiota community which is distinct from surrounding habitats. On rocky habitats of bedrock, boulder and cobble, the Sabellaria covers 50% or more of the rock and may form a crust or be thicker in structure. In some areas, these two variations of reef type may grade into each other. Sabellaria reefs have been recorded from depths between 10 – 50 m BCD or more. The reef infauna typically comprises polychaetes species such as Protodorvillea kefersteini, Scoloplos armiger, Harmothoe spp, Mediomastus fragilis, Lanice conchilega, and cirratulids along with bivalves Abra alba and Nucula spp. and tube dwelling amplhipods such as Ampelisca spp. Epifauna comprise calcareous tubeworms, pycnogonids, hermit crabs, amphipods, hydroids, bryozoans, sponges and ascidians. S. spinulosa reefs are often found in areas with quite high levels of natural sediment disturbance: in some areas of reef, individual clumps of Sabellaria spinulosa may periodically break down and rebuild following storm events. S. spinulosa reefs have been recorded from all European coasts except the Baltic Sea, Skagerrak and Kettegat. Areas of dead Sabellaria reef indicate the site supported reef habitat in the past and should be reported as this habitat type".

In addition to the statutory reef definitions for *S. spinulosa* reef, there are four biotopes within the Marine Habitat Classification for Britain and Ireland Version 04.05 (Connor et al. 2004) and the European Nature Information System (EUNIS) classification scheme (EEA 2007) in which *S. spinulosa* is noted as being abundant or common, according to the SACFOR scale (Connor and Hiscock 1996) as summarised below in **Table 1.2**.

Table 1.2 Summary of the four main biotopes (Connor et al. 2004; EEA 2007) in which *Sabellaria spinulosa* are noted as being common or abundant (using the SACFOR scale (Connor and Hiscock 1996). Whether or not these biotopes are considered to be equivalent to the OSPAR threatened and declining habitat "*Sabellaria spinulosa* reef" is also noted.

Biotope Name	Biotope Code	*S. spinulosa* Reef	Biotope Description
Sabellaria spinulosa on stable circalittoral mixed sediment	SS.SBR.PoR.SspiMx EUNIS: A5.611	Yes	*Sabellaria spinulosa* at high abundances on mixed sediment. *Sabellaria* typically forms loose agglomerations of tubes forming a low lying matrix of sand, gravel, mud and tubes on the seabed. The infauna comprises typical sublittoral polychaete species such as *Protodorvillea kefersteini, Pholoe synophthalmica, Harmothoe* spp, *Scoloplos armiger, Mediomastus fragilis, Lanice conchilega* and cirratulids, together with the bivalve *Abra alba*, and tube building amphipods such as *Ampelisca* spp. The epifauna comprise a variety of bryozoans including *Flustra foliacea, Alcyonidium diaphanum* and *Cellepora pumicosa*, in addition to calcareous tubeworms, pycnogonids, hermit crabs and amphipods.
Sabellaria spinulosa encrusted circalittoral rock	CR.MCR.CSab.Sspi EUNIS: A4.221	Yes	Biotope with an almost entire crust of *Sabellaria spinulosa* tubes typically found encrusting the upper faces of wave-exposed and moderately wave exposed circalittoral bedrock, boulders and cobbles subject to strong and moderately strong tidal streams in areas with high turbidity. A diverse fauna may be found attached to the crust. There are two variants: The first (Sspi.ByB) contains turfs of bryozoans (including *F.foliacea, A. diaphanum* and *Bugula plumosa*); other scour tolerant species such as *Urticina felina, Tubularia indivisa* and *Nemertesia antennina* may also be present. The second variant (Sspi.As) has a dense turf of didemnid ascidians and scour-tolerant bryozoans including *F. foliacea* and *Cellaria* species. Sparse sponges and patchy occurrences of small ascidians such as *Polycarpa* spp. may also be observed. The fauna attached to the *Sabellaria* crust in many cases seem to reflect the biotopes on nearby rock.
Sabellaria spinulosa with kelp and red seaweeds on sand- influenced infralittoral rock	IR.MIR.KR.Lhyp.Sab EUNIS: A3.2145	No	*Laminaria hyperborea* kelp forest on shallow infralittoral bedrock and boulders characterised by encrustations of *S. spinulosa* tubes which cover much of the rock, together with sand-tolerant red seaweeds. Some of the richer examples of this biotope also have a rich fauna of ascidians, sponges, hydroids and bryozoans. A similar biotope is also found in the circalittoral zone, where it lacks the algal component (CR.MCR.CSab.Sspi).
Laminaria digitata and piddocks on sublittoral fringe soft rock	IR.MIR.KR.Ldig.Pid EUNIS: A3.2113	No	Soft rock, such as chalk, in the sublittoral fringe characterised by *Laminaria digitata* and rock-boring animals such as piddocks *Barnea candida* and *Pholas dactylus*, the bivalve *Hiatella arctica* and worms *Polydora* spp. *S. spinulosa* often colonises empty piddock burrows. Beneath the kelp forest, a wide variety of foliose and filamentous red seaweeds occurs together with bryozoans and hydroids. The undersides of small chalk boulders are colonised by encrusting bryozoans, colonial ascidians and the tube-building polychaete *Pomatoceros lamarcki.*

Two of these biotopes, "*Sabellaria spinulosa* on stable circalittoral mixed sediment" and "*Sabellaria spinulosa* encrusted circalittoral rock" are considered to be equivalent to the OSPAR threatened and declining habitat "*Sabellaria spinulosa* reef" whereas the other two are not. However, it should be noted that there is no measure of extent, elevation or any indication of longevity associated with these classifications. Both the reef and non-reef *S. spinulosa* biotopes are frequently applied to isolated point sample data where the community is dominated by *S. spinulosa*. However, this classification should be treated with some caution where there is a possibility that a reef classification has been applied to a localised habitat that would not otherwise be considered as a reef for conservation purposes, and similarly where non-reef biotopes have been applied to samples that have been taken from a more continuous feature which could qualify as a reef.

S. spinulosa exists in a wide spectrum of growth forms from solitary individuals and isolated clumps to extensive reefs. From a planning and conservation perspective the need for a quantitative definition is clear, and the lack of such a definition has led to the development of 'fuzzy' management tools based on reef attributes which currently have unknown ecological significance (Hendrick & Foster-Smith, 2006). In an expert workshop aimed at addressing the need for a more robust *S. spinulosa* reef definition thresholds were assigned to some of the attributes put forward by Hendrick and Foster-Smith (2006), as summarised in **Table 1.3.** This has now been accepted as the working *S. spinulosa* reef definition in the UK (EMU 2008). However, caution should be exercised as the definition is based solely on expert opinion and there remains an urgent need for research into the ecological significance (or otherwise) of these reef characteristics (Gubbay 2007). From an ecological perspective it seems likely that most reefs will contain a range of different developmental stages and that each of these stages will have some intrinsic ecological value (Dubois et al. 2002). From a management and conservation perspective, it would be advantageous to be able to determine the ecological value of different *S. spinulosa* aggregation types, such that the most valuable "reefs" are ultimately designated for protection and conversely, that costly protection measures are not wasted on the least valuable examples of the habitat (Lindeboom et al. 2005; Derous et al. 2007). Ecological valuations could usefully be converted to monetary valuations, such that the cost of protection can be directly compared with the value of the habitat being protected (Beaumont et al. 2007; Beaumont et al. 2008).

Table 1.3 Threshold ranges of *Sabellaria spinulosa* reef characteristics proposed by workshop participants (Gubbay 2007).

Characteristic	**Not a Reef**	**"Reefiness"**		
		Low	**Medium**	**High**
Elevation (cm) Average tube height	<2	2-5	5-10	>10
Extent (m^2)	<25	25-10,000	10,000-1,000,000	>1,000,000
Patchiness (% Cover)	<10	10-20	20-30	>30

1.5.3 Monitoring Reef Health

Where statutory duties and ministerial commitments exist towards the active management of *S. spinulosa* habitats, either explicitly or implicitly, some form of monitoring and / or assessment is undertaken. The status of *S. spinulosa* habitats is currently reported annually to OSPAR on the basis of trends (JNCC personal communications). For example, the total area identified as *S. spinulosa* reef this year compared to previous years. As these trends are based on a mixture of third party reports and limited sampling carried out by the SNCBs, the results are often a reflection of the relative sampling effort rather an accurate reflection of the status of this habitat. With the inception of the MSFD there is a move towards more sophisticated tools to monitor GES.

1.6 Aims and Objectives of the Study

This chapter has highlighted many gaps in our understanding of the ecological function and significance of *Sabellaria spinulosa* reefs. Their high conservation status and the need to designate a coherent network of areas to encompass the protection of *S. spinulosa* reefs make the need to gain this knowledge all the more pertinent. Whilst it would be impossible within the course of a single PhD, to address all of the research identified by this chapter, five key research objectives have been identified. By achieving these objectives this body of research will:

Establish the ecological function and sensitivity of *Sabellaria spinulosa* aggregations to anthropogenic disturbance in order to provide scientific grounding for their conservation and management.

1.6.1 Thesis Objectives & Hypotheses

1. Investigate the reproductive mode and life cycle of *Sabellaria spinulosa*

Elucidating the reproductive cycle of *Sabellaria spinulosa* is not one of the primary aims of this thesis. However, given the paucity of our knowledge in this area and the implications for the management of *S. spinulosa* reefs, additional sampling and analyses have been undertaken in a serendipitous manner, with the following broad aims:

A. Describe the ultrastructure of the gametes of *S. spinulosa*
B. Describe, histologically, the reproductive cycle of *S. spinulosa*
C. Examine the availability of *S. spinulosa* larvae in the water column
D. Refine our understanding of the timing and frequency of *S. spinulosa* spawning events

2. Establish the degree to which *Sabellaria spinulosa* reefs influence the composition and nature of the macrobenthos

Establishing the influence that *S. spinulosa* reefs have on the macrobenthos is one of the core aims of this thesis since the perception that the reefs enhance biodiversity underpins the high conservation status afforded to the habitat, despite there being little evidence to support this assertion. The degree to which *S. spinulosa* reefs influence the composition and nature of the macrofauna will be tested using the following hypothesis:

Hypothesis A

H_{OA}: *S. spinulosa* reef structures have no influence on macrofaunal biodiversity or community composition

H_{1A}: The macrobenthos found in association with *S. spinulosa* reefs is more diverse and abundant than the macrobenthos associated with comparable sedimentary deposits, and the reefs support fauna that would not otherwise occur in the area.

3. Determine whether or not demersal fish feed on *S. spinulosa* reefs and to investigate the commonalities between the diets and feeding behaviours of fish species associated with the reefs.

Due to the high conservation status of *S. spinulosa* reefs the opportunities for quantitative (destructive) sampling are very limited. The question of whether or not demersal fish feed on the reefs was therefore addressed using fish sampled serendipitously from reefs in the southern North Sea and the following three hypotheses:

Hypothesis B

H_{0B}: *Sabellaria spinulosa* and abundant reef fauna (e.g. *Pisidia longicornis*) are not present in the guts of demersal fish sampled from *S. spinulosa* reefs.

H_{1B}. *S. spinulosa* and abundant reef fauna (e.g. *Pisidia longicornis*) are dominant in the guts of demersal fish sampled from *S. spinulosa* reefs.

Hypothesis C

H_{0C}: The diet of demersal fish sampled from *S. spinulosa* reefs is comparable to published records

H_{1C}. The diet of demersal fish sampled from *S. spinulosa* reefs is markedly different from published records

Hypothesis D

H_{0D}: There is no structure in the diets of demersal fish associated with *S. spinulosa* reefs

H_{1D}: There are distinct feeding groups or guilds amongst the demersal fish associated with *S. spinulosa* reefs

4. Evaluate the feasibility of using remote sensing technology to delineate *S. spinulosa* reefs and explore the interaction between the reefs and the construction of an offshore wind farm.

Repeat surveys of *S. spinulosa* reefs at a wind farm development site were used as a means of testing the theory that remote sensing could be used to detect and map *S. spinulosa* reefs whist also establishing whether or the construction and operation of the wind farm had impacted the reef, positively or negatively using the following hypotheses:

Hypothesis E

H_{0E}: Substrates identified as being possible *S. spinulosa* reef using high resolution sidescan sonar are no more likely to contain *S. spinulosa* than areas not identified as being possible reef.

H_{1E}. *Sabellaria spinulosa* are present in significantly higher densities and cover a greater proportion of the substrate in areas identified as possible reef using high resolution sidescan sonar.

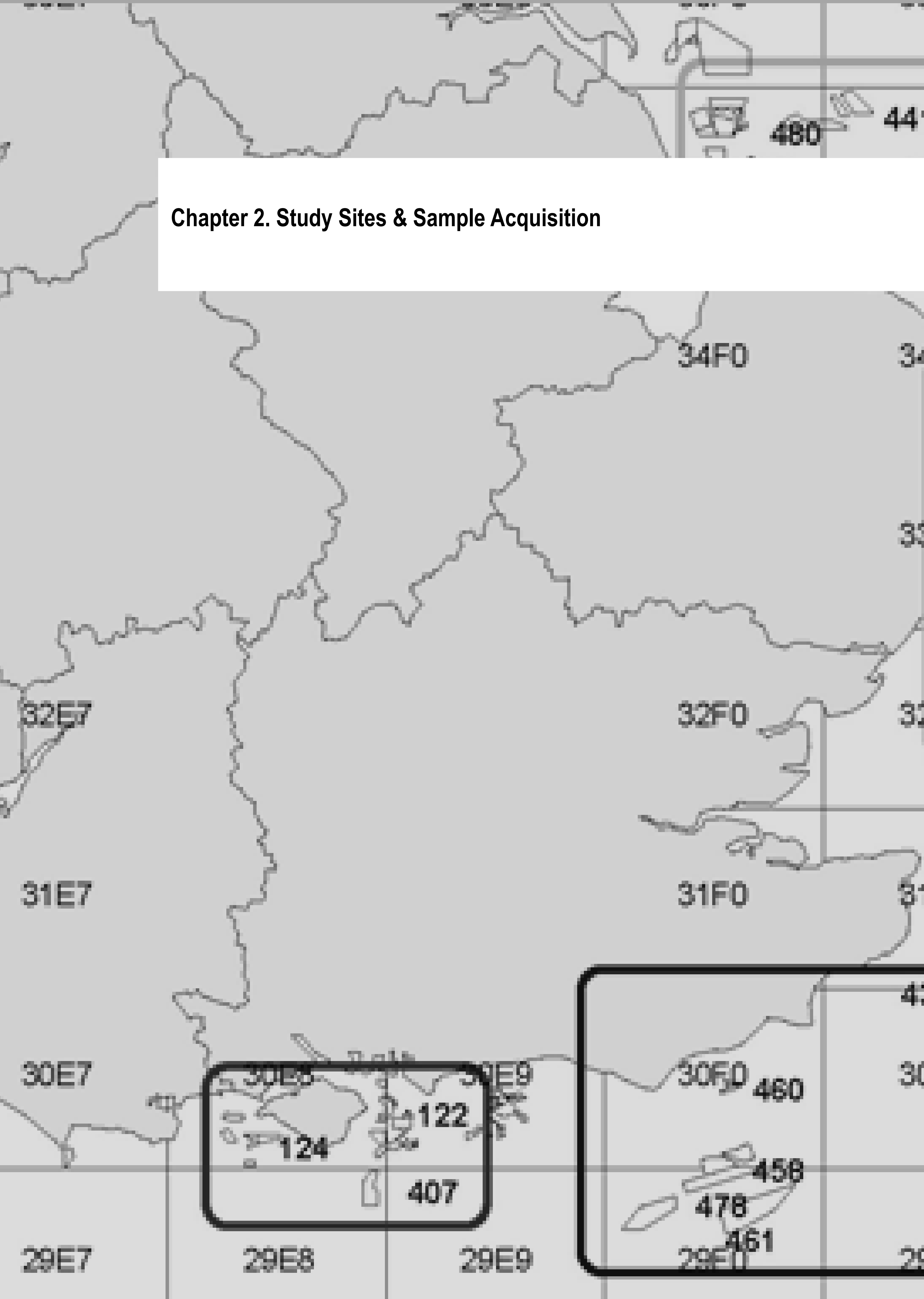
Hypothesis F

H_{0F}: *Sabellaria spinulosa* reefs are unchanged in terms of their extent and quality (worm density, % cover or the diversity of macrofauna) following the construction of an offshore windfarm.

H_{1F}. There is a reduction in *S. spinulosa* reefs in terms of either their extent or quality (worm density, % cover or the diversity of macrofauna) associated with the construction of an offshore windfarm.

H_{2F}. There is an enhancement in *S. spinulosa* reefs in terms of either their extent or quality (worm density, % cover or the diversity of macrofauna) associated with the construction of an offshore windfarm

Chapter 2. Study Sites & Sample Acquisition



2.1 Selected Study Sites

Four primary study sites were identified around the UK coast for inclusion in the present investigation:

1. Aggregate Extraction Licence Area 360-377 (Hastings Shingle Bank);
2. Aggregate Extraction Licence Area 447 (Cutline);
3. Thanet Offshore Wind Farm;
4. East Coast Regional Environmental Characterisation (REC) Survey Area.

Sabellaria spinulosa aggregations occurring within these sites are subject to a variety of different environmental conditions and anthropogenic pressures, facilitating a comprehensive assessment of the ecology and sensitivity of this habitat.

The sampling reported here was carried out by the author (see **Table A.1.** for details of contributions made by others) as part of three research projects and one commercial monitoring programme, undertaken in parallel to the current investigation. There was therefore an element of serendipity to the sampling programme and whilst additional targeted sampling was sometimes possible, the resulting sampling designs in many instances were not optimal. It was not possible to undertake any power-analyses to inform sample replication, and replication was not always allocated proportionately, or optimally across habitat types (Van der Meer 1997; Gray and Elliott 2009). Nevertheless, traditional stratified random sampling designs were possible in most instances and collecting data in this way has facilitated a much more robust and comprehensive assessment of the ecology of *S. spinulosa* reefs than would otherwise have been possible, due to the high costs associated with sampling these predominantly subtidal habitats.

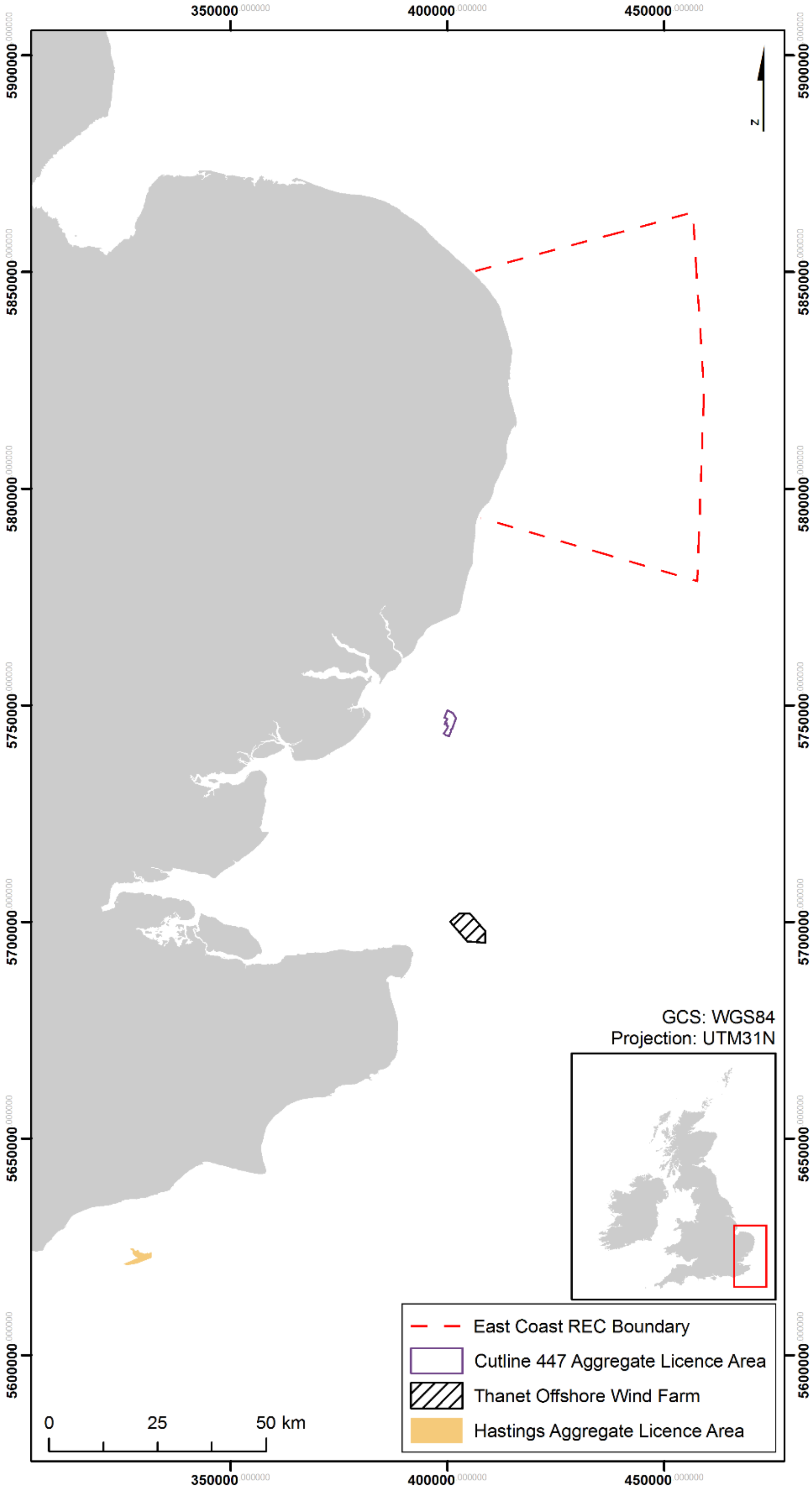


Figure 2.1 Overview of the four sites sampled as part of this study on the ecology of *Sabellaria spinulosa* reefs.

2.1.1 Aggregate Extraction Licence Area 360-377 (Hastings Shingle Bank)

Aggregate Extraction Licence Area 360-377 (hereafter referred to as Hastings Shingle Bank) is located in the eastern English Channel, approximately 20 km off the east Sussex coast. The Hastings Shingle Bank is a drowned gravel barrier complex which formed as a result of rapid post-glacial sea level rise during the Quaternary (Mellett et al. 2012). The surface sediments within the licenced aggregate extraction area range from sandy gravel to gravel, and are flanked by continuous sand deposits on all sides with occasional gravel patches to the west (MESL 2006). Sediment transport in the Hastings Shingle Bank area is tide-dominated and the hydrodynamic regime can be classified as meso-tidal with a tidal range of ca. 2-3 m (Anthony 2002). The sands adjacent to the Hastings Shingle Bank dredging area are mobile under the present-day regime (Dix et al. 2007). In contrast, the gravel deposits, that are the target of extractive activities, are relatively stable, supporting an epifaunal community that includes the soft coral *Alcyonium digitatum* and the bryozoan *Flustra foliacea* (Brown et al. 2004)

The Hastings Shingle Bank and the surrounding seabed have been well studied due to the interest in extracting aggregates from this site (Brown et al. 2004; Foster-Smith et al. 2004; Cooper et al. 2007; Cooper et al. 2008; Mellett et al. 2012). The Centre for Environment, Fisheries and Aquaculture Science (Cefas) also have a small number of regular monitoring sites within the Hastings Shingle Bank area which provide a valuable time-series record of the occurrence of *S. spinulosa* aggregations at this site (**Figure 2.2**). The known variability in the age of the different *S. spinulosa* aggregations at the Hastings Shingle Bank site derived from Cefas monitoring records and the history of dredging from Electronic Monitoring System (EMS) data (**Figure 2.3**) facilitated an investigation into some preliminary work on the population structure of these polychaetes.

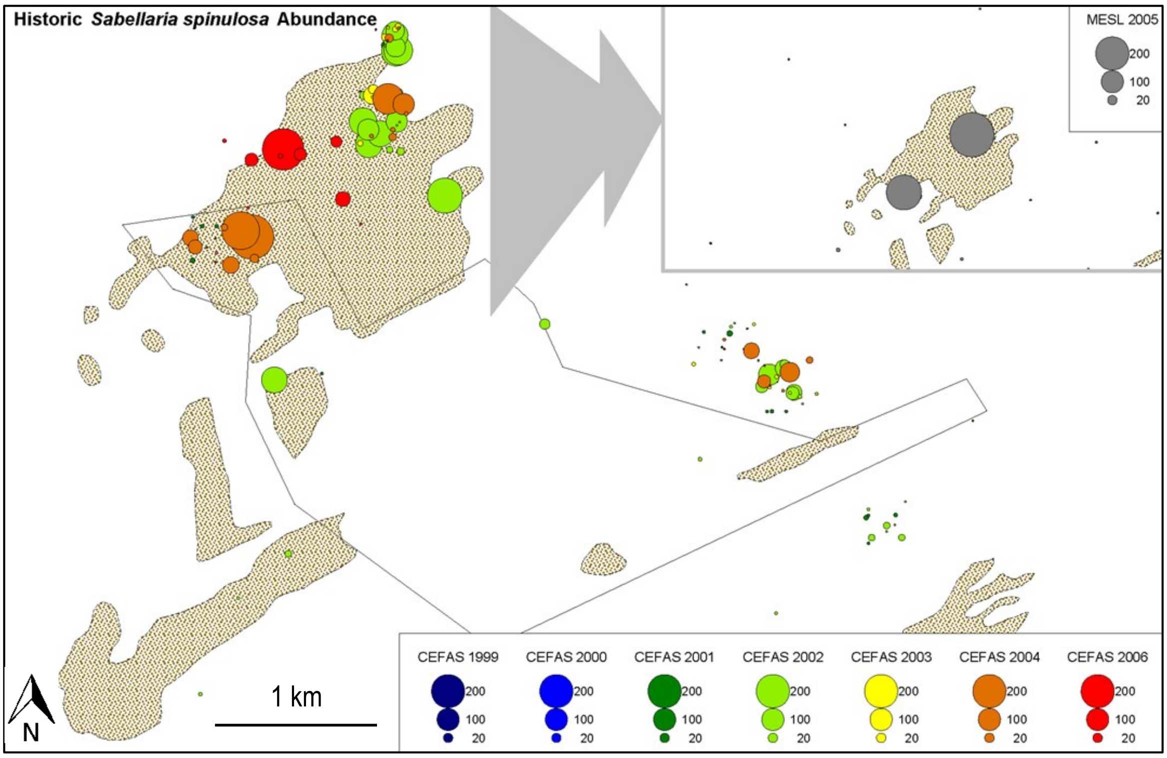


Figure 2.2 Abundance of *Sabellaria spinulosa* recorded from 0.1 m^2 Hamon grab samples collected by Cefas between 1999 and 2006 as well as those recorded by Marine Ecological Surveys Ltd (MESL) in 2005 (MESL 2006) within Licence Area 306-377 Hastings Shingle Bank in the eastern English Channel. *S. spinulosa* abundance records are overlaid on areas identified as being *S. spinulosa* aggregations (brown stippled polygons) using side-scan sonar data collected in 2005 (MESL 2006). The boundary of Aggregate Extraction Licence Area 360-377 is depicted by a grey line.

A stratified sampling design was employed at the Hastings Shingle Bank site with four sampling blocks located within and adjacent to areas of *S. spinulosa* aggregation in each of four areas that had not been impacted by dredging for different periods of time (**Figure 2.3**). Four sampling blocks were also placed within the actively dredged area to allow the results to be put into context with the anthropogenic impacts occurring at this site. Data were originally collected from this site as part of a study investigating the recoverability of *S. spinulosa* reefs following the cessation of aggregate extraction (Pearce et al. 2007) however, the stratified sampling design is also well suited to an investigation of the macrobenthos associated with the reefs as well as a study of the populations size structure (Van der Meer 1997; Gray and Elliott 2009).

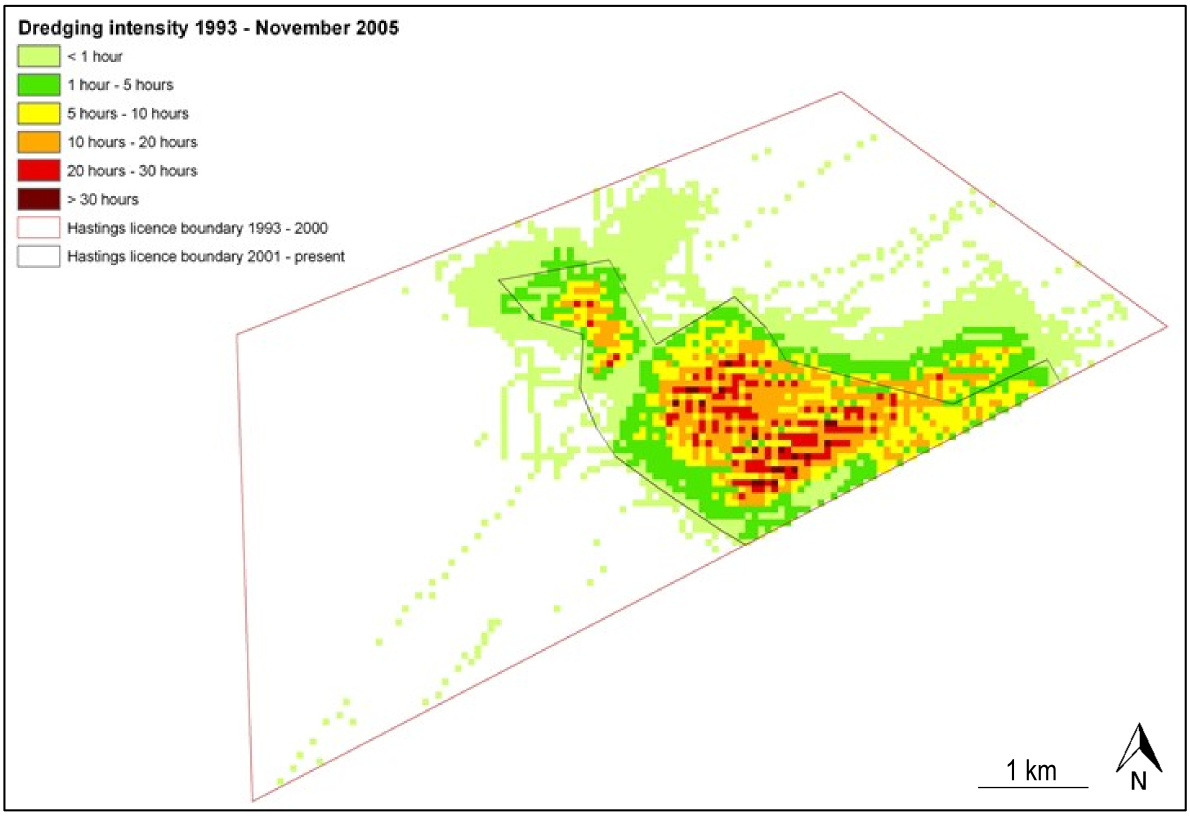


Figure 2.3 Intensity of aggregate extraction (hours), within Licence Area 306-377 Hastings Shingle Bank in the eastern English Channel, based on Electronic Monitoring System (EMS) data supplied by The Crown Estate for the period 1993-2005.

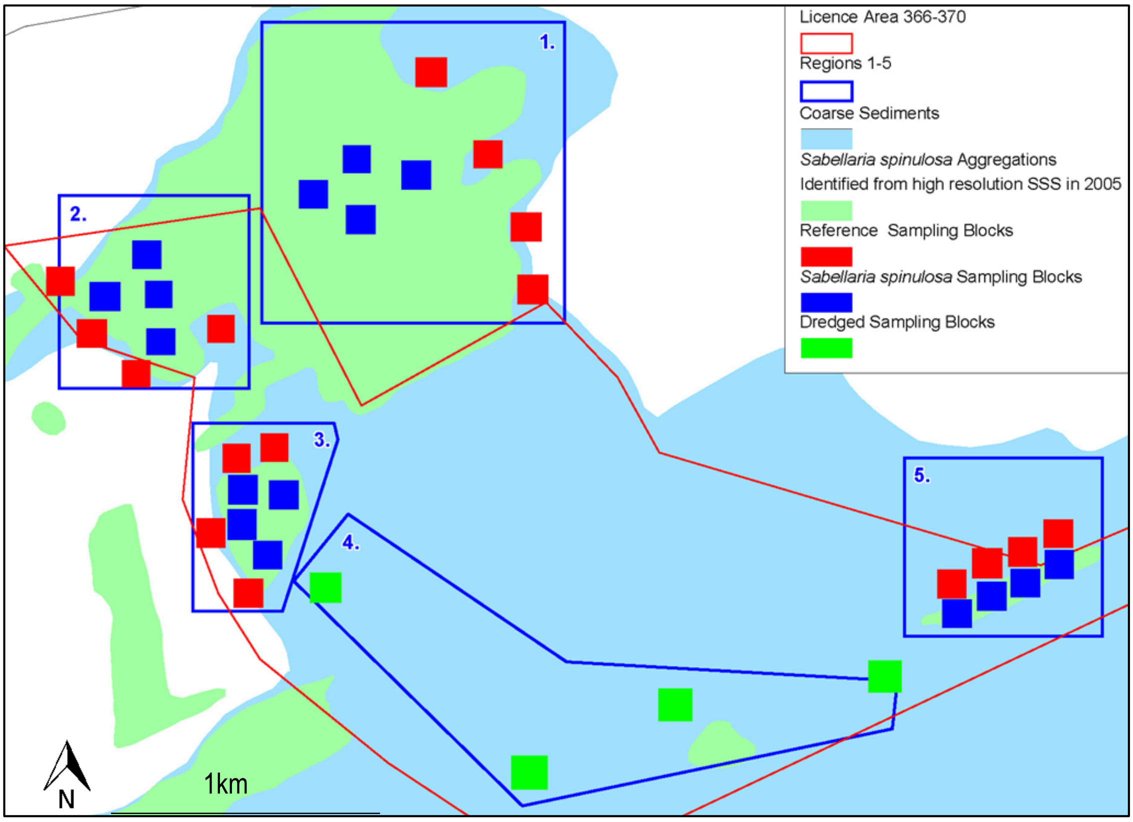


Figure 2.4 The stratified sampling design employed at Hastings Shingle Bank. Sampling blocks have been overlaid on areas identified as being *S. spinulosa* aggregations using side-scan sonar data collected in 2005 (MESL 2006). A description of the five sampling regions is provided in **Table 2.1.**

Table 2.1 Summary of the dredging history, previous reef observations and likely age of *Sabellaria spinulosa* reefs present in each of the five sampling regions (**Figure 2.4**).

Region	Dredging History	Reef First Recorded	Likely Age of Reef (as of Sept 2006)
1	Dredging ceased in 2000	2002	4-5 years
2	Dredging ceased in 2003	2004	3-4 years
3	Dredging ceased in 2003	2002	4-5 years
4	Actively dredged	n/a	n/a
5	Dredging reduced in Feb 2005 and ceased end of May 2005	August 2005 (visible on side-scan sonar)	16-18 months

Grab Sample Collection

Benthic grab samples were collected from four positions within each of the treatment blocks (**Figure 2.4**) using a 0.1m^2 Hamon grab. An earlier study of a *S. spinulosa* reef in the Bristol Channel (George and Warwick 1985) used a small (0.07m^2) Day grab but found that the grab penetrated to varying depths, often resulting in incomplete sections of reef. Wash-out can also be a problem with this type of grab as small pebbles, or reef sections, can easily get caught between the jaws (Eleftheriou and McIntyre 2005). The Hamon grab is recommended for sampling in coarse deposits as "wash-out" is minimised by the orientation of the bucket once it has tripped (Davies et al. 2001; Cefas 2002; Eleftheriou and McIntyre 2005; Ware et al. 2011). Upon retrieval, sediments were released from the grab into a plastic fish box and a photograph of the sample was then taken before a small sub-sample was removed for Particle Size Analysis (PSA). As far as possible an 'average' sample was obtained by pooling several successive small scoops of sediment taken randomly from the sample. Where samples contained *S. spinulosa* aggregations, sediment sub-samples were taken from the underlying sediments.

The residual sediment was then sieved over a 1mm mesh sieve in order to retain the macrofauna. The sample was then gently elutriated to remove excess fine sediment without damaging fragile fauna. The residual sample was then transferred to a plastic bucket, preserved in a 4% buffered formalin solution and sealed prior to further separation and analysis in the laboratory.

2.1.2 Aggregate Extraction Licence Area 447 (Cutline)

Aggregate Extraction Licence Area 447 (hereafter referred to as Cutline) is located offshore from Harwich in the southern North Sea. Side-scan sonar data collected across the area identified gravelly sand deposits extending down the western half of the area and rippled sand to the east and north (**Figure 2.5**). The tides in this area run approximately north-east to south-west (**Figure 2.5**) and typically range from 2 to 3.5 m, with the highest tidal range reported to be 4.47 m (Source: Admiralty Chart Datum for Harwich).

Surveys carried out as part of the licence application process revealed the presence of *Sabellaria spinulosa* aggregations both within and adjacent to the licence area. An exclusion zone was placed around the *S. spinulosa* aggregations that were identified within the site (**Figure 2.5**), and those identified to the south of licence area were surveyed as part of a research project designed to investigate the impacts of aggregate extraction on adjacent reefs and other benthic fauna (Pearce et al. 2011a). A total of

198 0.1 m^2 Hamon grab samples were collected from this site, during the course of eight surveys spanning a two year period (**Table 2.2**). In order to maximise the value of these time-series surveys four 5 minute surface and sub-surface plankton hauls were also collected to determine the availability of *S. spinulosa* larvae in the water column (**Table 2.2**). *S. spinulosa* were also retained from the grab samples to facilitate a histological examination of their reproductive state throughout the year. However, the grab samples were not collected or processed for the purpose of histological examination and hence only a small subset of the *S. spinulosa* present in the grab samples were complete enough for this purpose (**Table 2.2**).

Table 2.2 Summary of the surveys carried out at Licence Area 447, Cutline between April 2008 and April 2010, and the biological samples collected.

Survey	Month	Hamon Grab Samples	Total *S. spinulosa*	*S. spinulosa* Specimens for Histology	Plankton Hauls
1	April 2008	24	994	3	8
2	July 2008	24	623	45	4
3	September 2008	25	69	14	8
4	February 2009	25	22	7	8
5	March 2009	25	28	8	8
6	July 2009	25	79	12	7
7	November 2009	25	104	36	8
8	April 2010	25	17	0	8

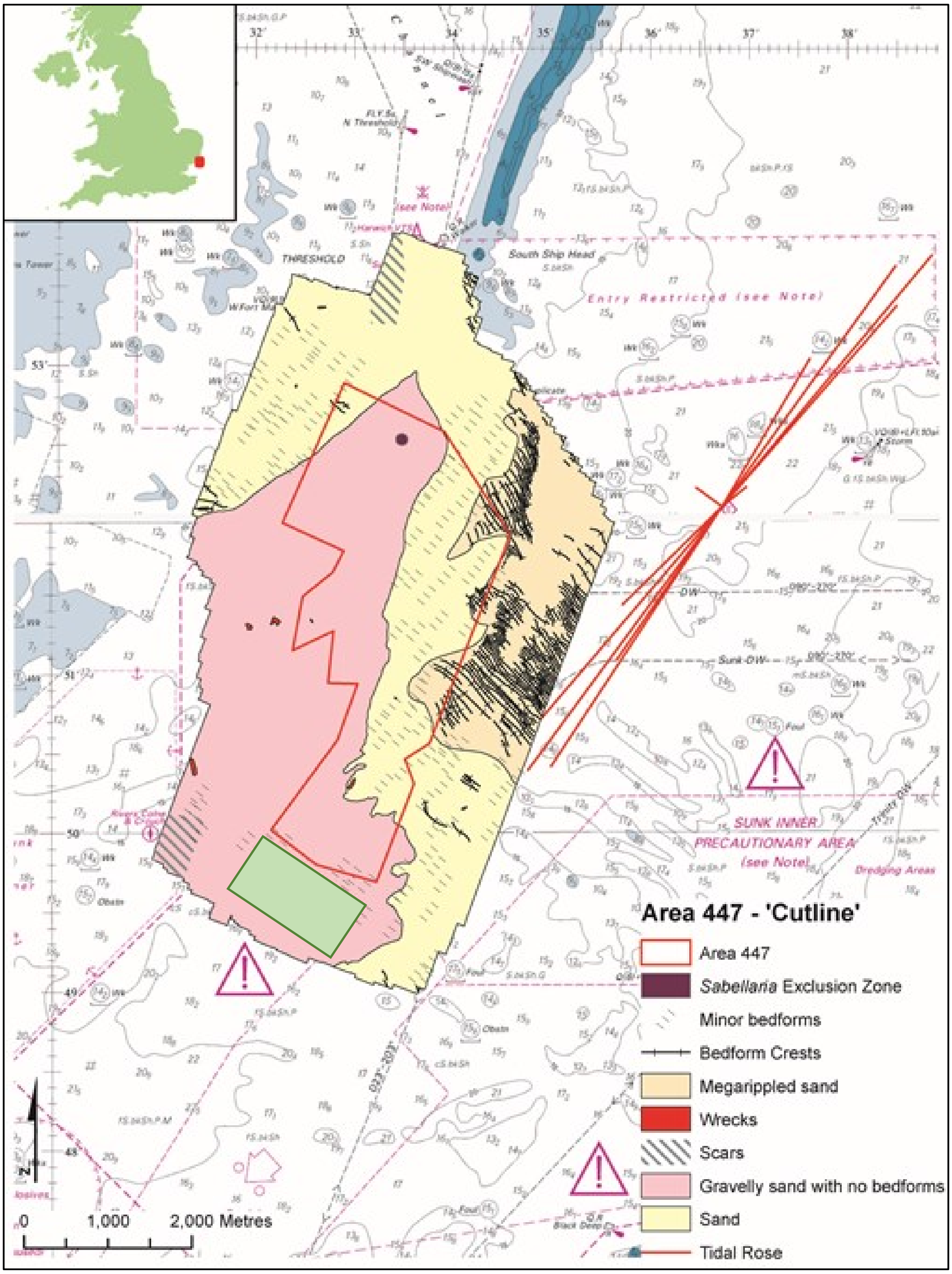


Figure 2.5 Side-scan sonar interpretation carried out by the Resource Management Association (RMA) in 2007 as part of their licence application for Area 447 Cutline. © CEMEX UK Marine Ltd, Hanson Aggregates Marine Ltd & United Marine Dredging Ltd. Plankton haul and 0.1 m^2 Hamon grab sampling was carried out to the south of the licence area within the green shaded box. ARCS charts 2052, 1975 & 1610 used under licence from the UK Hydrographic Office

Plankton Hauls

Plankton samples were collected by towing plankton trawls fitted with a 53 µm mesh filter for 5 minutes. Two trawls were towed simultaneously at the surface and at a depth of approximately 5m, attached to the grab wire. Samples were decanted into small plastic jars and preserved in Industrial Methylated Spirit (IMS) for subsequent microscopic identification back at the laboratory.

2.1.3 Thanet Offshore Wind Farm

The Thanet offshore wind farm site is located 12 km off Foreness Point in Kent, in the English southern North Sea (**Figure 2.6**), occupying an area of approximately 35 km^2 in water depths ranging from 15 to 27 m CD (Chart Datum). The site is meso-tidal during neap tides, with an estimated tidal range of 2.5 m, and macro-tidal during spring tides, with an estimated tidal range of 4.3 m (Haskoning 2005). The Thanet site is also exposed to northerly and easterly waves generated from the North Sea, as well as waves generated in the English Channel that can propagate from the south. Locally generated waves caused by winds blowing across the Thames Estuary from west to north-westerly directions are also significant (Haskoning 2005).

Surficial sediments at the site range from sand to sandy gravels with a small area of gravel in the far north-west. Much of the wind farm site is characterised by sand with megaripples trending in an east-west direction (Gardline 2007; Gardline 2012). The sand waves typically reach a maximum height of 3 m and are asymmetrical, with the lee to the south, indicating that the predominant current runs in a southerly direction (Gardline 2012). To date there have been no studies on the mobility of these sand waves although it is assumed that some degree of migration occurs, as has been observed at other sites across the North Sea (Haskoning 2005).

The sedimentary processes occurring at the Thanet offshore wind farm site are dominated by the tidally driven current regime which typifies the southern North Sea (Pietrzak et al. 2011). High turbidity levels (monthly average Suspended Particulate Matter (SPM) > 20 mg l^{-1}) are observed year round, peaking between January and April when the erosion of cliffs along the English coasts is also at its greatest (Pietrzak et al. 2011). Strong tidal currents (peak spring tides of 1.0 m/s) and sediment inputs from the Thames estuary and the East Anglian Plume (Holt and James 1999) are all thought to contribute to the high turbidity levels experienced at this site (Pietrzak et al. 2011).

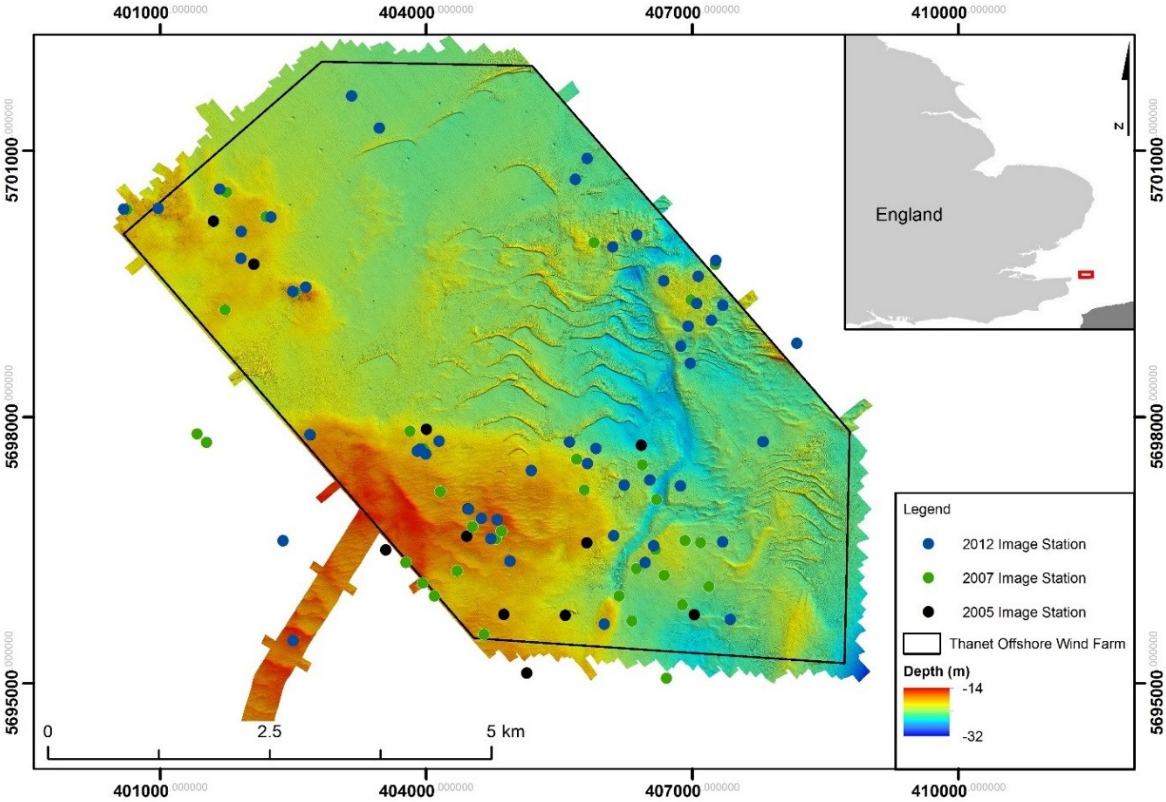


Figure 2.6 The Thanet offshore wind farm site and stations sampled with a fresh water lens camera in 2005, 2007 and 2012 (MESL 2005; MESL 2007b; MESL 2012). Sampling stations are overlaid on the 2012 digital elevation model (DEM) derived from high resolution multibeam echo sounder data (Gardline 2012).

Samples were collected and processed as part of the normal regulatory process for the wind farm, although additional sample and data analysis was carried out as part of this investigation to maximise the research potential of this site. A baseline characterisation survey was undertaken at this site in 2005, followed by a pre-construction survey in 2007 and, most recently, the first post-construction monitoring survey in 2012. *S. spinulosa* aggregations were identified at this site during the baseline characterisation surveys and these were subsequently re-surveyed and mapped using high resolution side-scan sonar and seabed imagery. Permission was granted for the development of this site on the proviso that turbines were micro-sited to avoid the best parts of the reef, and the pre-construction survey was used for this purpose. This habitat will now be monitored as part of the licence conditions attached to this development using seabed imagery. The use of extractive sampling using a sediment grab to monitor this habitat was limited by the Statutory Nature Conservation Bodies (SNCBs) and prohibited completely in the most recent survey. There is therefore only a limited amount of quantitative data from these aggregations, collected before the wind farm was constructed.

Acoustic surveys

Acoustic data were collected from the Thanet offshore wind farm site using side-scan sonar and multibeam bathymetry. The side-scan sonar data and the digital elevation model derived from the multibeam data, were examined in combination in order to delineate elevated areas of irregular texturing which are thought to be representative of *S. spinulosa* aggregations (**Figure 2.7**)

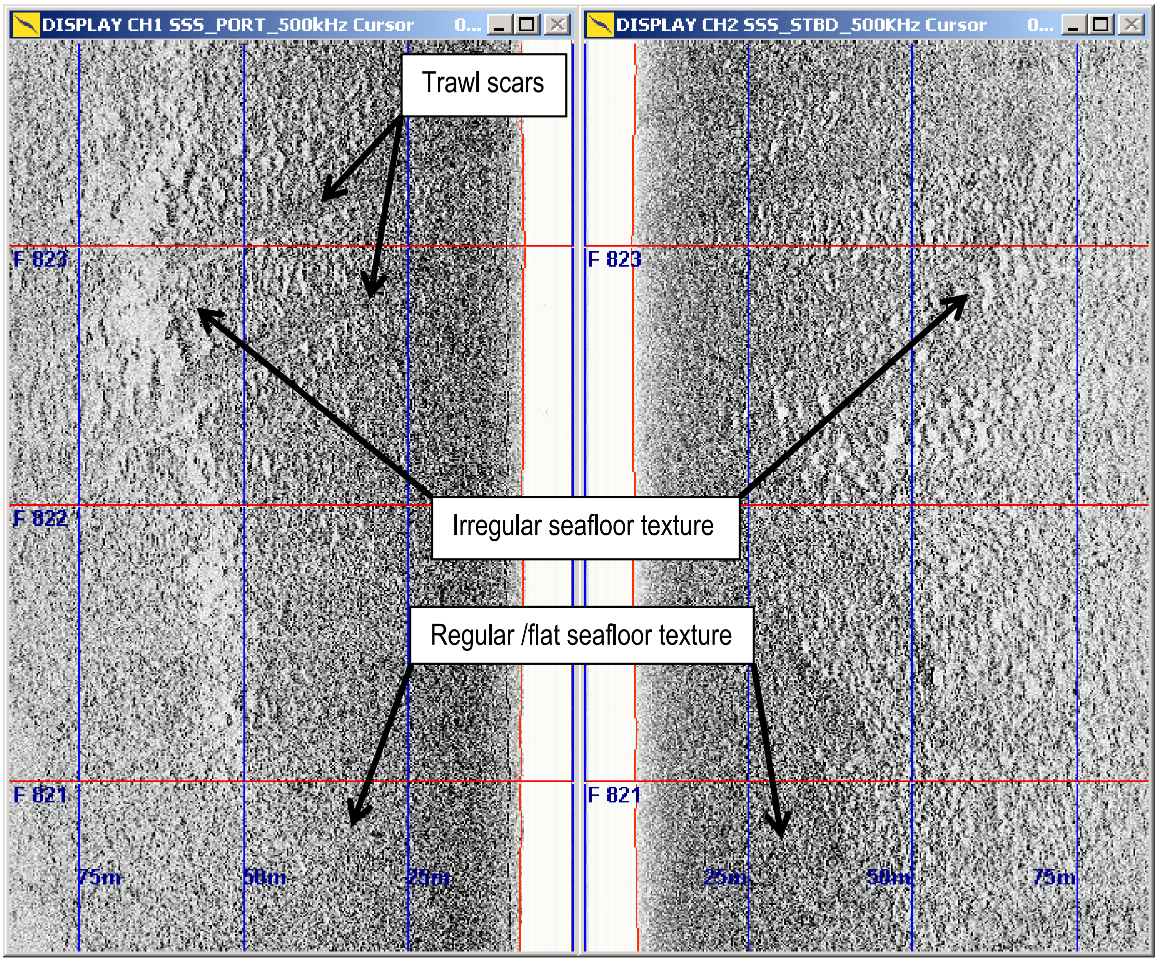


Figure 2.7 Raw, high resolution (500 kHz) side-scan sonar image showing the irregular seafloor texture used to delineate *Sabellaria spinulosa* aggregations. Also shown are the contrasting regular texture typical of flat seafloor sediments (in this case sandy gravel deposits) and trawl scars which reveal the elevation of the textured features.

The acoustic survey carried out in 2005 was concentrated in the south of the development site as *S. spinulosa* records from baseline macrofaunal sampling were limited to this area. In subsequent surveys the whole site was surveyed using acoustics to ensure the full extent of this habitat was captured.

2005 Baseline characterisation survey

In July/August 2005 sidescan sonar data were collected using a GeoAcoustics Dual Frequency sidescan sonar system, set at its highest frequency (410 kHz) in order to record fine scale seabed features. The sonar fish was towed at a depth of 10-12m below the surface, equivalent to between 7 and 15m above the seabed, and the transceiver was set to transmit 8 pings per second. A minimum of 100% coverage was achieved by running north-south survey lines at 150m intervals, with the data range set to between 75 and 85m. Infill lines were run at 75m intervals where time allowed, finally providing >200% coverage of over 60% of the area surveyed. In addition, two east-west cross-lines were run. Horizontal positioning accurate to approximately +/-1m was achieved for the recorded vessel track using a CSI dGPS MAX 12-channel parallel differential GPS receiver. The differential corrections used by the receiver were supplied by the IALA beacon system. The sonar tow fish position was calculated using recorded vessel position, vessel heading (from the ships compass) and measured cable 'out' between the vessel and the sonar tow fish. Accuracy of calculated tow fish position is estimated to be +/-3m. Navigation, data logging, real-time quality control, display and post-processing were carried out using C-View Navigation and C-View Seabed Data Management software packages (C-Products Ltd).

2007 Pre-construction baseline survey

The EdgeTech 4200FS side-scan sonar fish was flown at an approximate height 7.5 to 10m above the seabed. The sonar range was set at between 75m and 100m and data coverage of between 100% and 400% was achieved across the site. Sidescan sonar data was exported to Coda and digital recorder for post processing and interpretation. MBES data were simultaneously collected using a vessel mounted Simrad EM3002D system. Bathymetry data were processed using Caris HIPS and SIPS (version 7.1) software to produce a depth profile gridded at a horizontal resolution of $1m^2$ and a backscatter layer to aid in the determination of habitat boundaries. Velocity profiles were undertaken at 24 hour intervals throughout the survey using a Valeport SV&T probe. Positioning was managed using Gardline's Voyager5 navigation software integrated with the Seatex Seapath 200 positioning and orientating system for heave pitch, roll and yaw corrections. Differential corrections were provided by Fugro Starfix.

2012 Post-construction monitoring survey

The first in a series of planned post-construction monitoring surveys was undertaken at the site in April 2012, approximately 18 months after the construction of the turbines had been completed. Geophysical surveys were undertaken across the whole site using a combination of sidescan sonar and MBES with the same specifications as the 2007 pre-construction baseline survey.

Ground-truthing Sampling

Ground truth sampling surveys were undertaken shortly after each of the acoustic surveys allowing time for a preliminary interpretation of the acoustic data to be undertaken. As *S. spinulosa* reefs are considered to be sensitive to physical damage, direct samples were not collected to groundtruth the acoustics in all but the first baseline survey, although they were collected from adjacent sedimentary habitats as part of more general environmental assessment work (MESL 2005; MESL 2007b; MESL 2012). Ground-truthing was carried out using a drop-down camera system fitted with a fresh-water lens, especially designed to collect images in highly turbid environments as occur at this site (MESL 2005). Images collected in 2005 were excluded from all analyses as the quality and resolution was insufficient to estimate tube density, % cover or to facilitate the identification of associated fauna. The poor quality and resolution of seabed images taken in 2005 was a result of very high turbidity levels. The freshwater lens camera system was also in a very early stage of development which will also have contributed to the poor quality of the images acquired. The results reported here are therefore limited to those obtained from the seabed images collected in 2007 and 2012. Positioning accurate to approximately +/-1m was achieved for the ground-truth sampling using a differential GPS receiver. Between 3 and 5 images were collected at each sampling site.

2.1.4 East Coast Regional Environmental Characterisation (REC)

The Regional Environmental Characterisation (REC) surveys were funded through the Marine Aggregate Levy Sustainability Fund (MALSF) administered by Defra, as a means of providing some regional context to local Environmental Impact Assessments (EIAs) routinely carried out for the aggregate extraction industry in the UK. Four areas were chosen due to their strategic importance to the industry, the Humber, the East and South Coasts of England and the Thames (**Figure 2.8**). The four areas were surveyed with the aim of developing comprehensive, regional level geophysical and environmental maps to inform sustainable resource management.

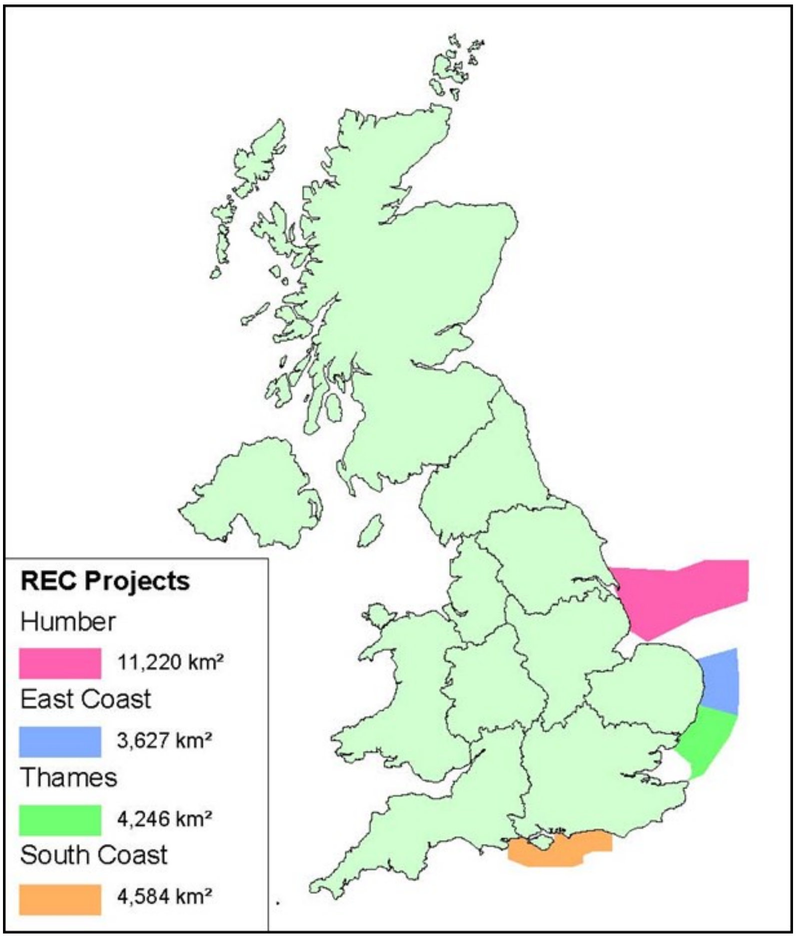


Figure 2.8 Chart showing the location and extent of the four Regional Environmental Characterisation (REC) studies funded through the Marine Aggregate Levy Sustainability Fund (MALSF) administered by Defra.

Previously un-recorded *Sabellaria spinulosa* aggregations were identified during the course of the East Coast REC surveys and additional high resolution acoustic data was collected across the *S. spinulosa* aggregations in order to map their extent (**Figure 2.9**). Demersal fish were also retained from trawl samples obtained, incidentally, from *S. spinulosa* aggregations across this site for subsequent stomach content analysis.

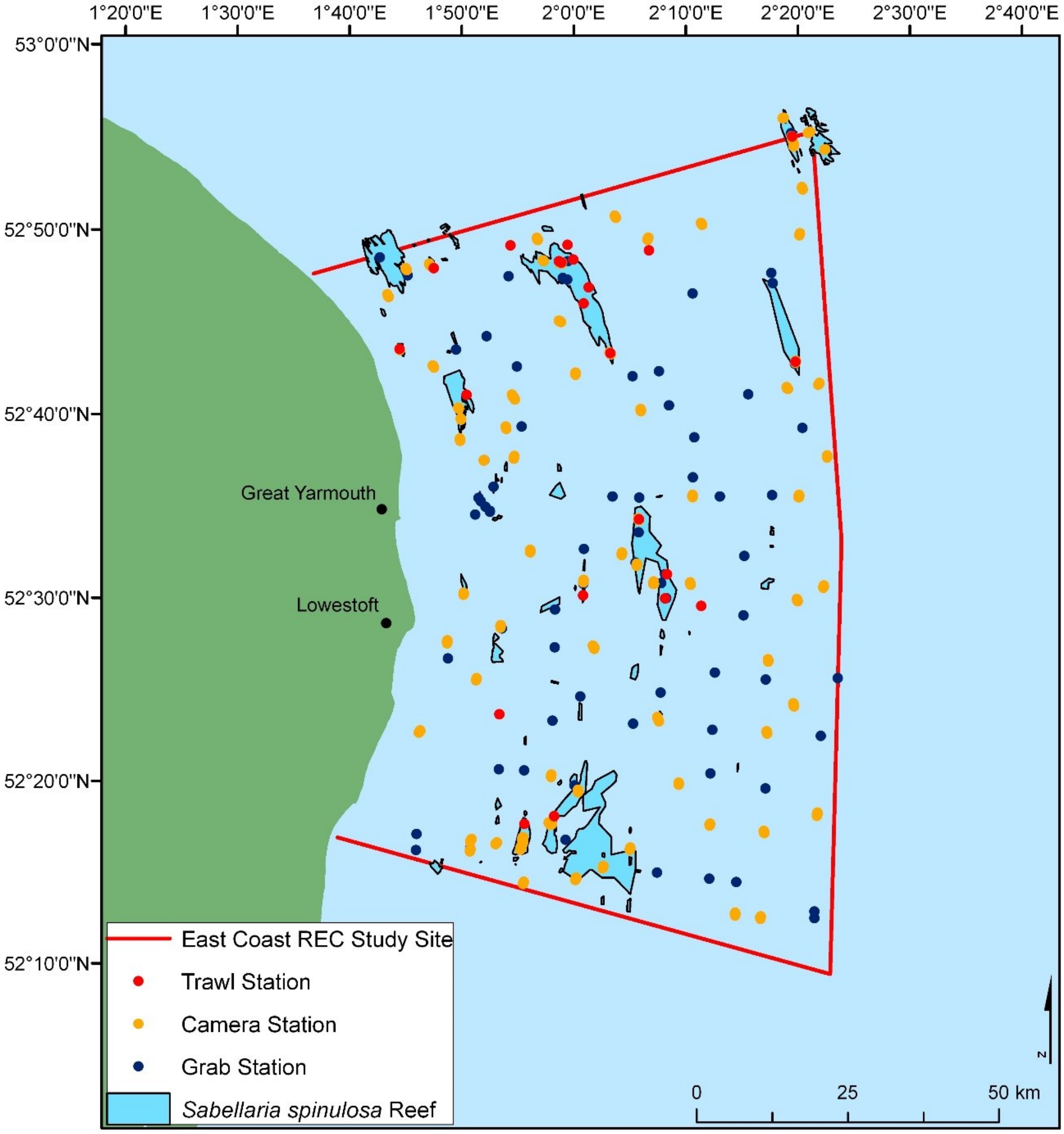
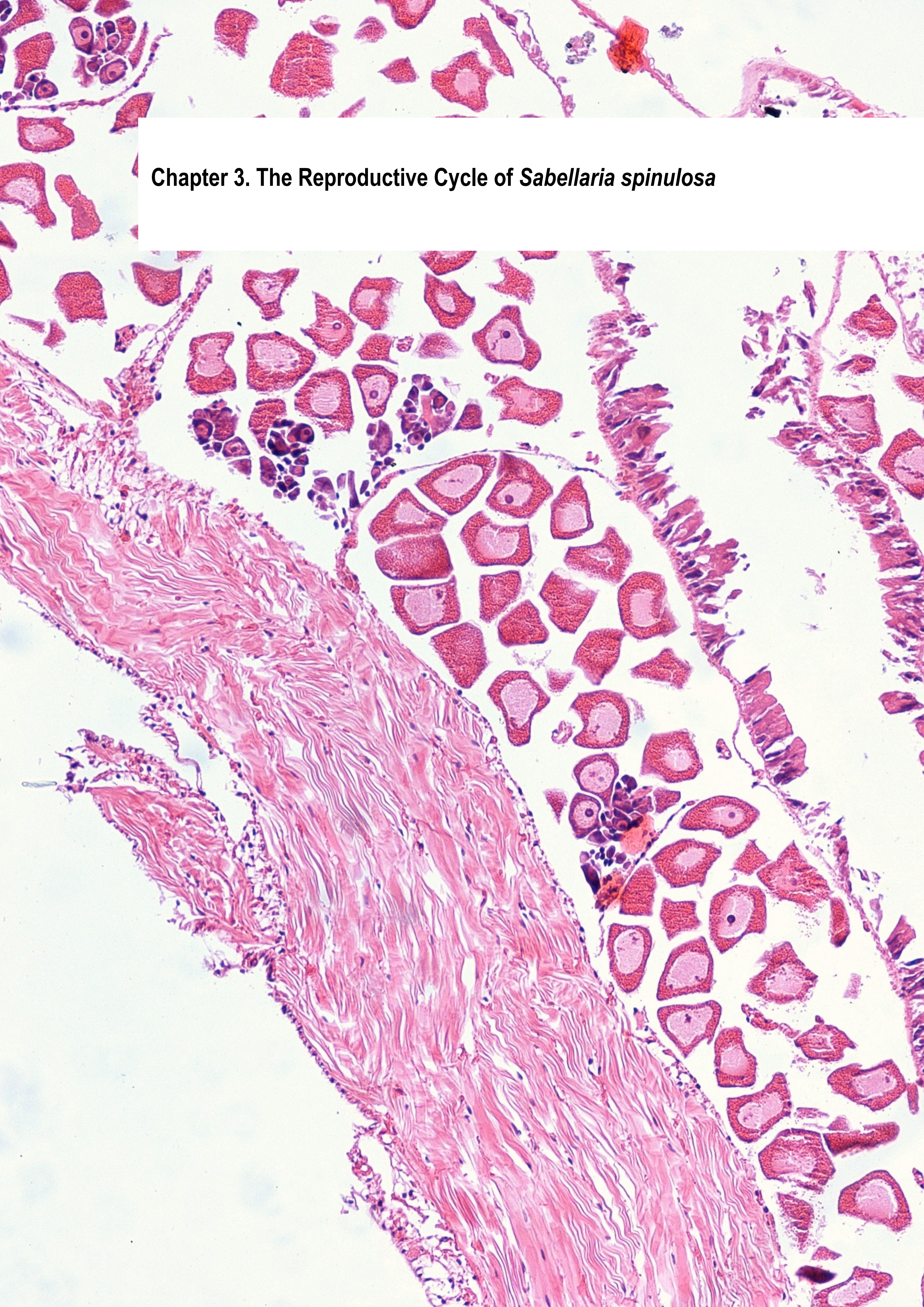


Figure 2.9 Chart showing the location of *Sabellaria spinulosa* aggregations (or reefs) identified using high resolution acoustic data, as well as the location of all biological sampling undertaken during the East Coast REC survey (Limpenny et al. 2011).

2.2. Raw Data and Sampling Positions

With the exception of data collected as part of the Thanet Offshore Windfarm site development process, which is commercially sensitive, the data used in this study are all publically available and can be accessed directly from the Marine Aggregate Levy Sustainability Fund (MALSF) website: http://www.marinealsf.org.uk/. The associated research reports, provided on the CD that accompanies this thesis, also contains all of the raw data and sampling positions.



Chapter 3. The Reproductive Cycle of *Sabellaria spinulosa*

3.1 Introduction

The life history of a species determines its success within a community (Sveshnikov 1985). Each of the main life functions: self-preservation, reproduction and dispersal, have evolved to collectively maximise a species' success (Grahame and Branch 1985). Understanding these life functions helps us to predict the ability of a species to survive and / or recover from changes in their environment (Newell et al. 1998; MESL 2007a). Understanding the life-cycle of a species can also assist the management and preservation of populations, for example, by limiting anthropogenic disturbance during important breeding seasons (Roeckmann et al. 2007).

Some aspects of sabellariid life-histories, such as larval dispersal, settlement and metamorphosis, have been well studied (Wilson 1968; Wilson 1970a; Wilson 1970b; Wilson 1977; Eckelbarger 1978a; Pawlik 1986; Pawlik and Faulkner 1986; Pawlik 1988b; Pawlik 1988a; Pawlik and Faulkner 1988; Pawlik et al. 1991; Pawlik and Chia 1991; Pawlik and Butman 1993; Naylor and Viles 2000; Ayata et al. 2009). Other aspects of sabellariid life-history, such as gametogenesis, spawning behaviour and population structure, have been afforded much less attention (Eckelbarger 1978b; Eckelbarger 1979; Eckelbarger 1984; George and Warwick 1985; Thomas 1994b; Hendrick 2007; Culloty et al. 2010).

Numerous authors have reared sabellariid polychaetes under laboratory conditions (Wilson 1929; Wilson 1968; Eckelbarger 1977; Curtis 1978; Eckelbarger 1978a; Pawlik 1986) and all have had good success, indicating that larvae belonging to this family of polychaetes are fairly resilient. Development from fertilization to metamorphosis in *S. spinulosa* is variable under laboratory conditions, taking anywhere from 5 to 36 weeks, although most individuals metamorphose by week 8 (Wilson 1970b). This long planktonic phase is thought to increase the dispersal potential of the species (Wilson 1970b). Dispersal can be advantageous as it acts to reduce competition for food and space, reduce the risks of inbreeding and it can also facilitate the colonisation of new areas (Pechenik 1999). Nevertheless, there are also many disadvantages to dispersal; larvae risk being predated upon or transported to less hospitable environments and in the longer term extensive dispersal can make a species less able to adapt to local conditions (Pechenik 1999).

Most polychaete families exhibit a high degree of diversity in their reproductive modes, despite phylogenetic and morphological constraints (Wilson 1991; Giangrande 1997). Sabellariidae, however, have only ever been observed to undergo free-spawning planktotrophic development (Wilson 1991), considered by many as the most primitive mode of reproduction amongst invertebrates (Jägersten 1972). *Ad-hoc* records of *S. spinulosa* settlement at different times of the year and in different localities (MBA 1957; Wilson 1970b; Garwood 1982; George and Warwick 1985) suggest that *S. spinulosa* either has an extended spawning season or that there is some geographical variation in spawning behaviour. Geographical variation has been observed in the spawning behaviour of the congener, *Sabellaria alveolata* which is reported to have one discrete spawning event in the UK between June and September (Wilson 1971; Culloty et al. 2010) and two extended spawning periods, from March to April and from June to September in the Fromentine tidal delta, France (Gruet and Lassus 1983). The timing and frequency of spawning events will have a significant influence on a species' ability to recover from disturbance events (Newell et al. 1998). This therefore represents a significant gap in our understanding of *S. spinulosa* which will ultimately inhibit our ability to preserve the habitats that they create.

It is not usually possible to observe the spawning behaviour of sublittoral invertebrates directly, but the timing and frequency of spawning events can be determined by tracking gametogenesis within the population (Cotter et al. 2003; Culloty et al. 2010) or by examining the populations structure in terms of body size (Warwick et al. 1978; George and Warwick 1985). Studying the population structure of an organism can also help determine the temporal stability of the population and typical recruitment levels, as well as the longevity and growth rates of the organism (Warwick et al. 1978; George and Warwick 1985; Somers and Kirkwood 1991; Shirose and Brooks 1995; Manjon-Cabeza and Garcia-Raso 1998). To date the size frequency of *S. spinulosa* populations has received little attention in the literature (George and Warwick 1985) and gametogenesis has yet to be studied.

Egg production is another important life history trait, which provides an indication of the energy investment being made per offspring. The egg size of marine invertebrates is strongly correlated with a number of other traits including fertilization mode, sperm structure, developmental mode, fecundity and brood frequency (Olive 1985). The number of eggs produced is also thought to be influenced by ecological factors, such as population size and food availability (Giangrande 1997). Despite the importance of egg production as a life history trait this is not an area of polychaete biology that has been well studied. Egg production has been studied in less than 0.3% of polychaete species (Giangrande 1997). Egg production has not been studied in *Sabellaria spinulosa,* but the sabellariid, *Phragmatapoma lapidosa*, has been found to undergo intra-ovarian oogenesis with blood vessel association (Giangrande 1997).

Elucidating the reproductive cycle of *Sabellaria spinulosa* is not one of the primary aims of this thesis. However, given the paucity of our knowledge in this area and the implications for the management of *S. spinulosa* reefs, additional sampling and analyses have been undertaken in a serendipitous manner, with the following broad aims:

A. Describe the ultrastructure of the gametes of *S. spinulosa*
B. Describe, histologically, the reproductive cycle of *S. spinulosa*
C. Examine the availability of *S. spinulosa* larvae in the water column
D. Refine our understanding of the timing and frequency of *S. spinulosa* spawning events

3.2 Methodology

3.2.1 Gamete Liberation & Examination

Living aggregations of *S. spinulosa* were collected from the East Coast REC site (**Figure 2.11**) in August 2010, for the purpose of investigating gamete ultrastructure. The reef fragments were retained in a marine aquarium for approximately one week prior to examination. Adult worms were carefully extracted from their tubes with tweezers in order to induce the release of gametes, as has previously been reported by Eckelbarger (1976) and Kirtley (1994). Worms were then transferred to vials seawater and allowed to spawn. Gluteraldehyde was later added to the vials as a means of fixing the adults and any gametes that had been released. Adult worms and their reproductive products were dehydrated and dried in a critical point dryer before being coated in a thin layer of gold, in preparation for SEM imaging as described in Eckelbarger and Chia (1976).

3.2.2 Histological Examination

Sabellaria spinulosa specimens were extracted from grab samples collected from the Cutline site in the southern North Sea (**Figure 2.7**) during surveys undertaken in April 2008, July 2008, September 2008, February 2009, March 2009, July 2009, November 2009 and April 2010. Samples collected in April 2010 were not found to be suitable for histological examination due to desiccation during storage. The grab samples had previously been processed for macrofaunal analysis and were stored in industrial methylated spirits (IMS). The hard crown was removed with a sharp blade before each of the extracted worms was dehydrated in ethanol. The dehydrated worms were then mounted in paraffin and sectioned longitudinally at 7 µm intervals using a microtome. The paraffin slices were then mounted on glass slides before being stained with Harris's haematoxylin and counterstained with eosin. Between 3 and 10 replicate sections were taken from each mount, many of which contained several small individuals. Each of the replicate slides were examined using a Leica DMD 108 digital microscope (x400 magnification) and the slide which contained the most complete section of an individual was then used in subsequent analysis. Notes were taken on the stage of gonad development observed in each *S. spinulosa* specimen and these were then categorised according to the descriptions of gametogenesis devised for the congener *Sabellaria alveolata* by Culloty *et al.* (2010).

3.2.3 Larval Availability

Polychaete larvae were extracted from plankton haul samples collected during the eight surveys carried out at the Cutline site, as described above for the plankton haul sampling (April 2008, July 2008, September 2008, February 2009, March 2009, July 2009, November 2009 and April 2010). The identification of polychaete larvae to species level is a difficult and specialist task and there are very few accurate keys in existence. Larvae belonging to the family Sabellariidae were identified using descriptions provided by Wilson (1929) Fauchald (1977), Eckelbarger (1978a) and Bhaud and Fernandez-Alamo (2001). However, most of the drawings and descriptions were based on living specimens, rather than preserved specimens making positive species level identification difficult. This was especially important since the larvae of both *S. spinulosa* and its congener *Sabellaria alveolata* could potentially be present in plankton samples collected from the southern North Sea. A reference collection of lab reared *S. alveolata* larvae, were sourced from Stanislas Dubois (IFREMER) and species level identifications were verified through comparisons of the larval morphology and examination of their provisional bristle morphology using Scanning Electron Microscopy (**Figure 3.1**). The abundance of larvae recorded in each survey was then plotted in a histogram to give an indication of larval availability and the timing of spawning events.

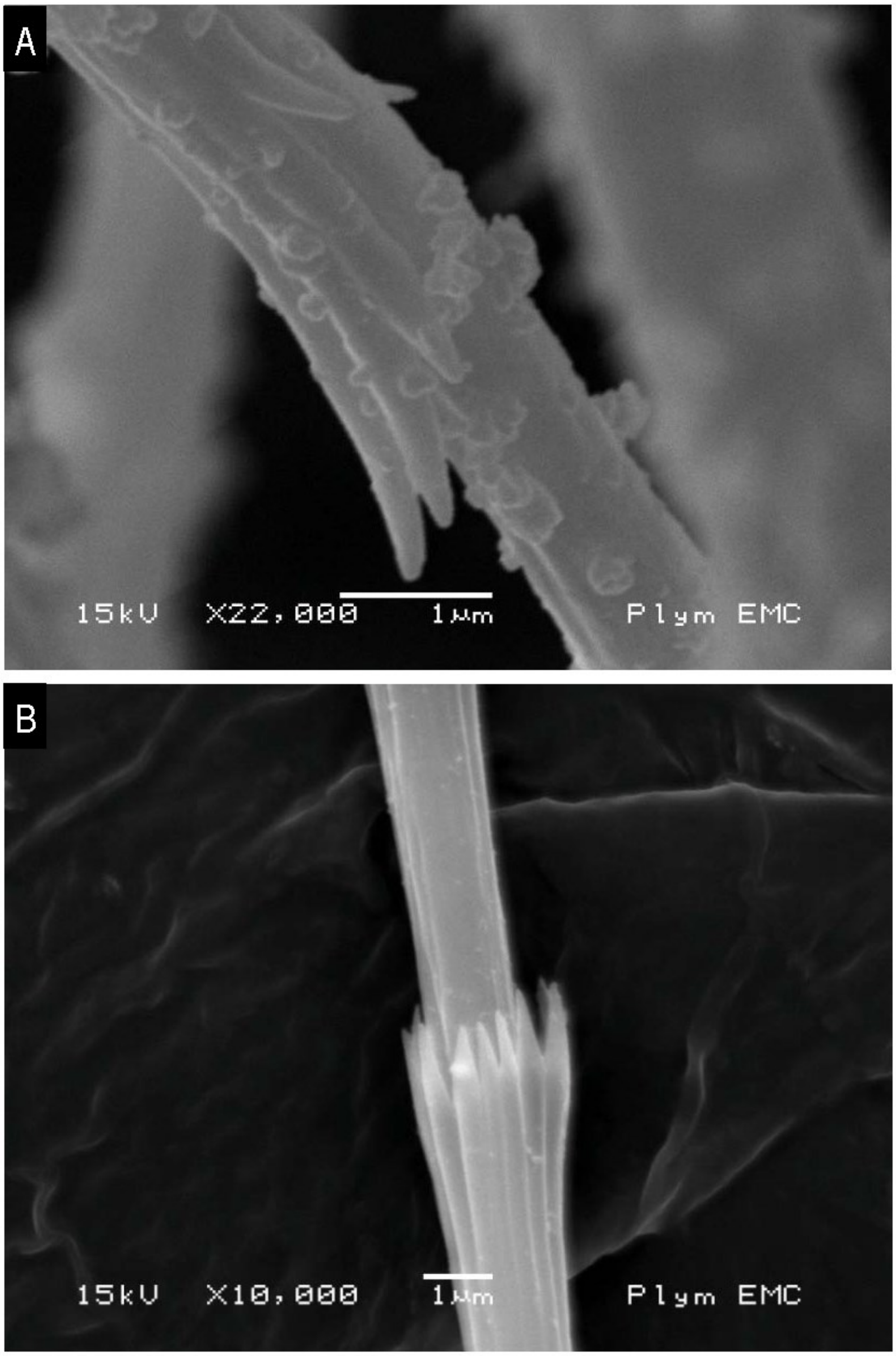


Figure 3.1 Scanning Electron Microscope (SEM) images of A) the asymmetrically ringed provisional bristles of *Sabellaria alveolata* larvae and B) the symmetrically ringed provisional bristles of *Sabellaria spinulosa* larvae.

3.2.4 Size-Frequency Distribution

Biometric measurements (**Figure 3.2**) were recorded for each *Sabellaria spinulosa* extracted from benthic grab samples collected during a single survey undertaken in September 2006 at the Hastings Shingle Bank site in the eastern English Channel (**Figure 2.4**). In order to investigate the age structure of five different areas of reef, measurements were taken from all 4,498 individuals sampled and the data were then pooled according to reef area. Anterior width (**Figure 3.2**) or cephalic trunk width was used as the main measurement of size, with measurements being obtained from the area immediately posterior to the two great lateral lobes (**Figure 3.2**). Anterior width has been found to be the most appropriate measure of sabellariid size since it is not affected by frequently missing posterior regions (Gruet and Lassus 1983; George and Warwick 1985; Hendrick 2007). Total length (anterior + posterior length) and blotted wet weight were also recorded in complete specimens to provide a comparison with anterior width. The resulting data were used to construct size-frequency distribution histograms which were subsequently used to identify different cohorts within each of the five reef areas.

3.3. Results and Discussion

3.3.1 Sexual Dimorphism

Researchers studying the reproductive strategies of sabellariid polychaetes, including *S. spinulosa*, have reported a purple-pink or blueish colouration in gravid females and a white swollen appearance in ripe males, corresponding to the colour of their gametes (Wilson 1929; Kirtley and Tanner 1968; Eckelbarger 1976; Gruet and Lassus 1983). The same dimorphic colouration was observed in the live *S. spinulosa* used in this study. Adults that were removed from their tubes in order to liberate their gametes, were separated on the basis of their colouration and, although some contamination of sex products was unavoidable, eggs were only found in vials that contained adults with a purple hue. Individual eggs were just visible with the naked eye and were observed to have the same purple colouration. The adult males from which sperm were liberated were found to have a milky white appearance corresponding to the semen liberated from them in the laboratory. The sexual dimorphism observed here in *S. spinulosa* is of little significance from a management perspective since their colouration cannot be observed without removing individual worms from their tubes. This observation does nevertheless confirm that the species reproduces sexually and that *S. spinulosa* aggregations contain a mixture of both sexes.

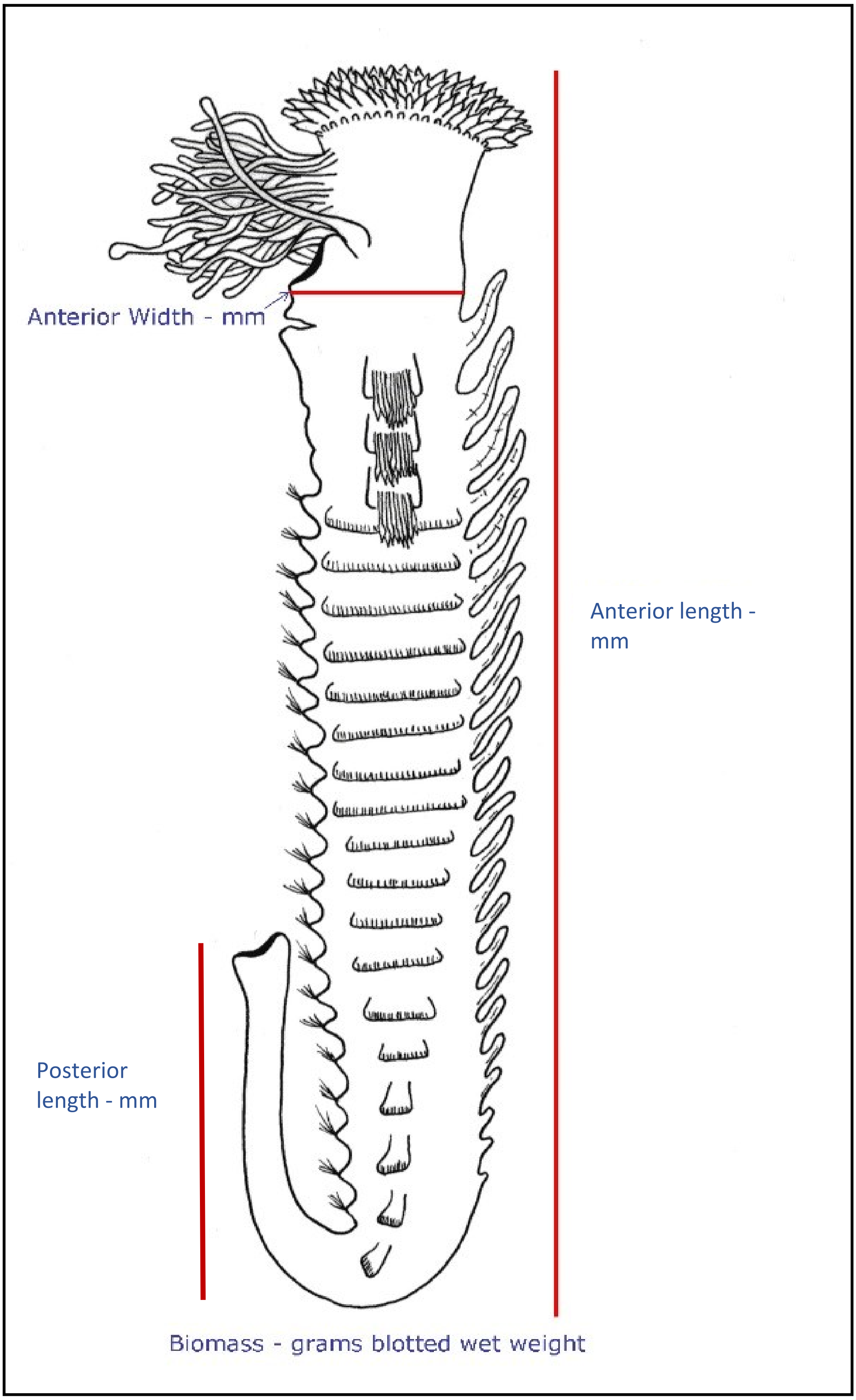


Figure 3.2 Illustration showing where *Sabellaria spinulosa* biometric measurements were taken.

3.3.2 Gamete Ultrastructure

Eggs liberated in the laboratory from adult *Sabellaria spinulosa* ranged in size from 45 µm to 58 µm (**Figure 3.3**). These are some of the smallest eggs recorded for polychaetes, including sabellariids (Thorson 1946; Giangrande 1997). In an extensive review of polychaete reproduction, Giangrande (1997) reports an egg size for *Sabellaria spinulosa* of 150 µm although neither of the quoted source references (Wilson 1929; Kalmus 1931) confirm this observation and hence this is thought to be a typographical error. Wilson (1929) states that the eggs of *S. spinulosa* are smaller than those of *S. alveolata,* which are reported to be between 56 and 90 µm in diameter (Wilson 1929; Robert et al. 1979; Gruet and Lassus 1983), corroborating the results of this study. However, since the eggs were liberated under stress it is possible that they were not fully developed and these measurements should therefore be treated with some caution.

Production of small eggs is most frequently associated with the production of ‘primitive’ sperm in males of the same species. The sperm liberated from these southern North Sea specimens were found to be modified from the primitive sperm type as defined by Franzen (1956), possessing a long tapering tip or acrosome (**Figure 3.4**). The head including the acrosome was approximately 3 µm in length and 2 µm wide. The tail or flagellum was found to reach between 15 and 60 µm. *Sabellaria spinulosa* sperm appear, therefore, to be very similar in size and morphology to those described for *Phragmatopoma lapido*sa (Eckelbarger, 1976) and *S. alveolata* (Robert et al. 1979).

Like other polychaete sperm, *S. spinulosa* sperm have four round protrusions at the base of the head which are assumed to contain the mitochondria which provide energy to the flagellum. The purpose of such a long flagellum, relative to the head, is not clear. It is possible that the flagella become entangled thus promoting clumping, as was evident in the semen liberated in the laboratory (**Figure 3.4**). The elongated flagellum may also serve to keep individual sperm, or clumps, close to the reef structure since such a long appendage is likely to get caught on the tube edges. The release of sperm in clumps which stay loosely associated with the reef has previously been observed in *Phragmatopoma californica* (Thomas 1994b). This species releases eggs in clumps and strings which also get caught on the reef structure, thereby increasing the chances of fertilisation (Thomas 1994a). The majority of the eggs

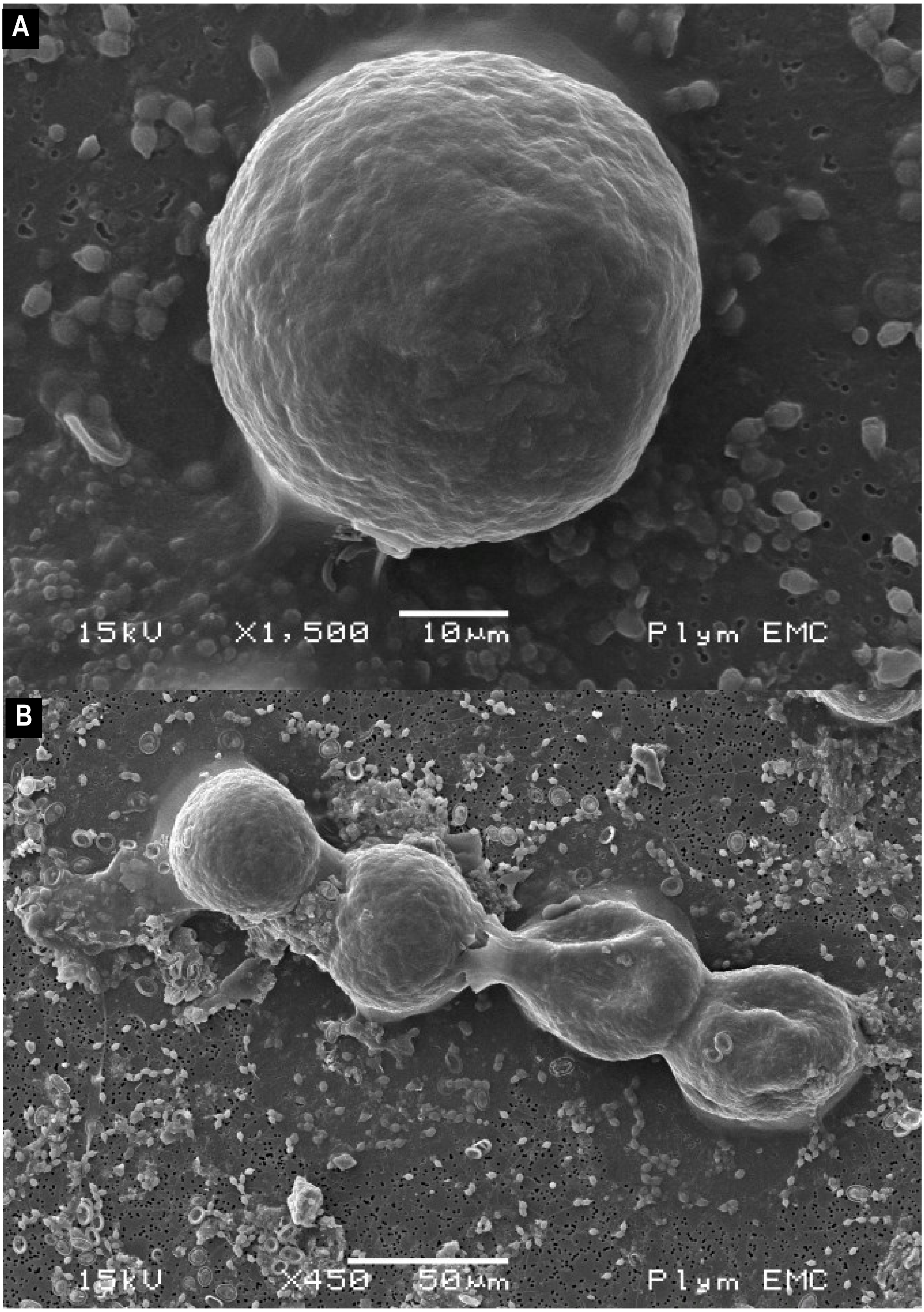


Figure 3.3 SEM images of *Sabellaria spinulosa* eggs liberated from living *Sabellaria spinulosa* collected from the East Coast REC site, in the southern North Sea, in August 2010. A) A single egg with an approximate diameter of 50 μm B) A string of eggs.

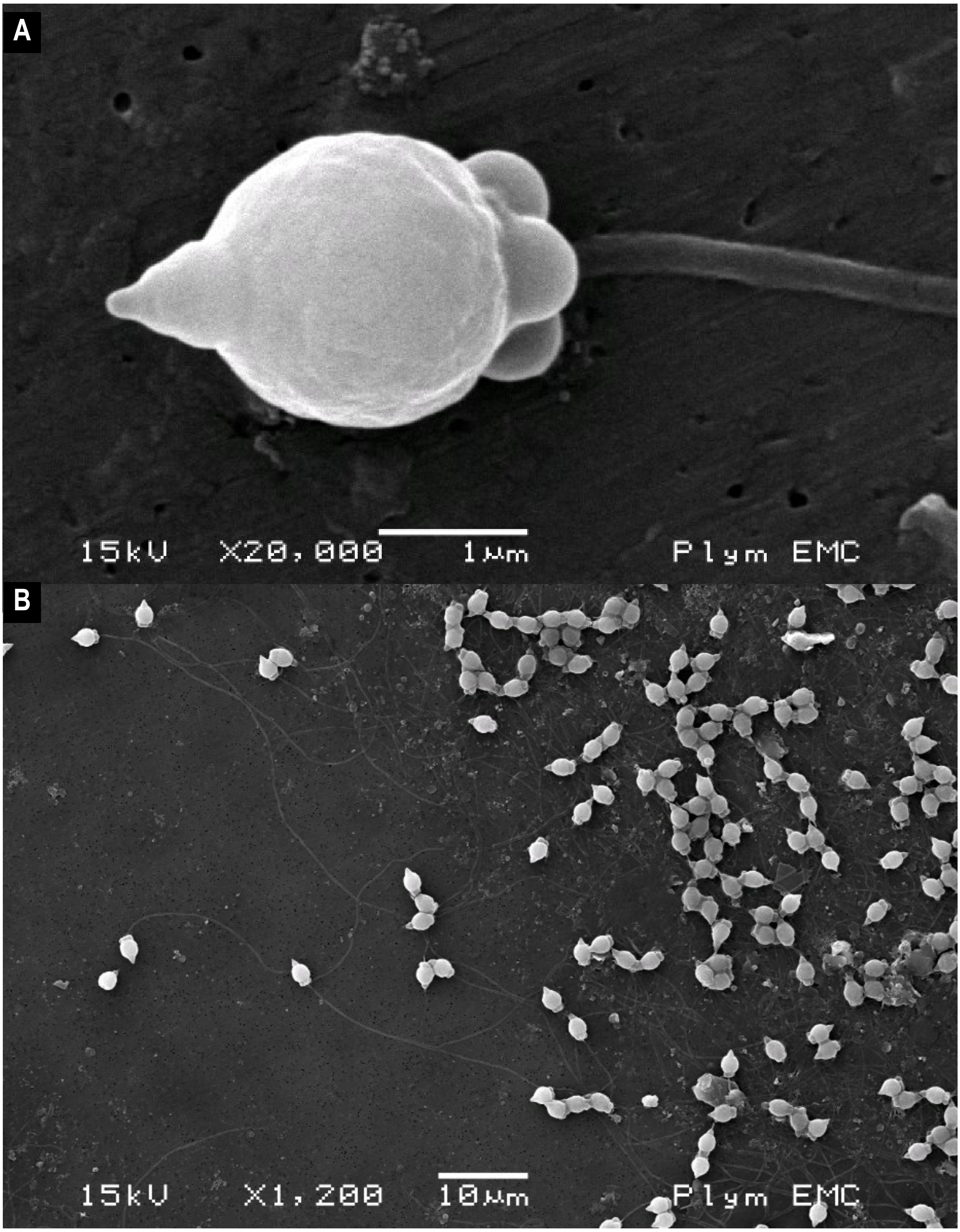


Figure 3.4 SEM images of *Sabellaria spinulosa* sperm liberated from living individuals collected from the East Coast REC study site, in the southern North Sea, in August 2010. A) The head of a single sperm with an approximate diameter of approx. 2 µm B) Multiple sperm illustrating the very long flagella (15-60 µm).

observed in *S. spinulosa* were present in chains (**Figure 3.3**) which may reflect a similar reproductive strategy. If *S. spinulosa* utilise such a strategy, the widely held theory that this species release their gametes in plumes, like most other invertebrate broadcast spawners, would need to be refigured (Ayata et al. 2009). This in turn would have significant implications for our understanding of the fertilisation success and larval dispersion of this species.

3.3.3 Gametongenesis

The stages of gonad development identified through histological examination are shown in **Figure 3.5** and are described in **Table 3.1**. A total of 119 individuals were examined of which 34 were found to be incomplete specimens (IS), missing the posterior region and a further 13 were found to be inactive adults (IA) meaning that they were either immature or were completely spent and their sex could not be determined. Due to the low numbers of specimens examined in each month (**Table 3.2**), a degree of caution should be applied to the results. The following observations should be used to inform future studies in this area rather than as a complete picture of gametogenesis in their own right.

The ratio of males to females was roughly equal (1.12:1) across all of the specimens examined but varied from survey to survey from 3:1 in April 2008 to no females in February 2009. However, these ratios may be an artefact of the low numbers of active adults sampled in these months (n=4). Inactive adults were sampled in most months but were most abundant in September 2008 (n=2) and November 2009 (n=8).

Spermatogenesis

Males exhibiting different stages of gonadal development were evident in all surveys except February 2009, where no active males were sampled, and March 2009 where both of the active males examined were found to be in the early stages of gametogenesis (EA) (**Figures 3.5 and 3.6**). Males that were ripe, partially spent or spent were observed in April, July, September and November, indicating that this species either has a protracted or polytelic spawning season at this site. However, a far greater number of individuals collected at more frequent intervals would be required to unequivocally determine the spawning season of *S. spinulosa*.

Table 3.1 The stages of gametogenesis of female and male *Sabellaria spinulosa* identified through histological examination of specimens collected from Cutline in the southern North Sea. Categories adapted from Culloty et al. (2010).

Abv.	Stage	Female	Male
IA	Inactive (**Figure 3.5A**)	Coelomic cavity empty with no traces of reproductive products.	
EA	Early Active (**Figure 3.5B**)	Oogonia present in clusters arising from stem cells. Very few free oocytes present.	Spermatogonia, spermatids and spermatozoa present in approximately equal numbers
LA	Late Active (**Figure 3.5C**)	All stages of oogenesis present in approximately equal proportions.	Coelomic cavity contains spermatids and spermatozoa in approximately equal proportions.
R	Ripe (**Figure 3.5D**)	Not observed	Coelomic cavity densely packed with spermatozoa.
PS	Partially Spent (**Figure 3.5E**)	Majority of eggs present are mature, significant gaps in the coelomic cavity (>50% empty)	Coelomic cavity largely empty but parapods with spermatozoa.
S	Spent (**Figure 3.5F**)	Coelomic cavity generally empty, remaining oocytes necrotic and / or cytolytic	Coelomic cavity empty with scanty spermatozoa present, usually in the parapods

Table 3.2 Summary of the reproductive state, as outlined in **Table 3.1** and **Figure 3.5**, of male and female *Sabellaria spinulosa* sampled from the Cutline study area in seven different sampling events carried out between April 2008 and November 2011. The number of specimens (n), the ratio of males to females (sex ratio), the number of incomplete specimens (IS) and inactive adults (IA) observed from the survey are also noted.

Survey	n	Sex Ratio (M:F)	IS	IA	Male					Female				
					EA	LA	R	PS	S	EA	LA	R	PS	S
Apr-08	4	3 : 1	1	0	0	2	0	0	1	1	0	0	0	0
Jul-08	48	1.6 : 1	1	1	8	15	0	5	1	0	8	0	8	2
Sep-08	13	0.8 : 1	6	2	3	1	1	0	0	2	0	0	0	4
Feb-09	4	0 : 4	10	0	0	0	0	0	0	2	2	0	0	0
Mar-09	6	0.7 : 1	4	1	2	0	0	0	0	2	1	0	0	0
Jul-09	16	1.5 : 1	5	1	3	5	0	0	1	0	5	0	0	1
Nov-09	28	0.7 : 1	7	8	2	4	2	0	0	2	5	0	2	3
Totals	**119**	**1.12 : 1**	**34**	**13**	**18**	**27**	**3**	**5**	**3**	**9**	**21**	**0**	**10**	**10**

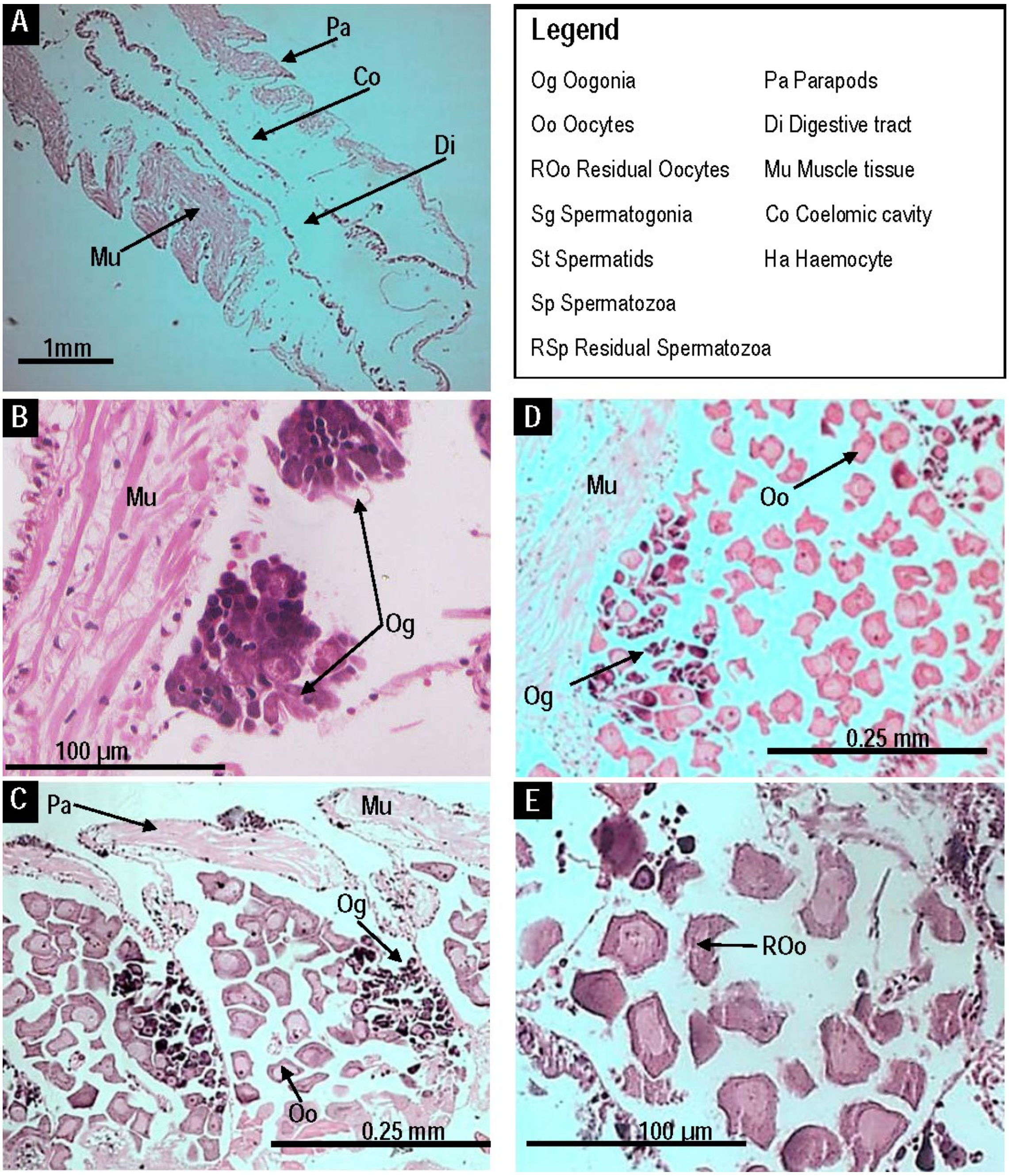
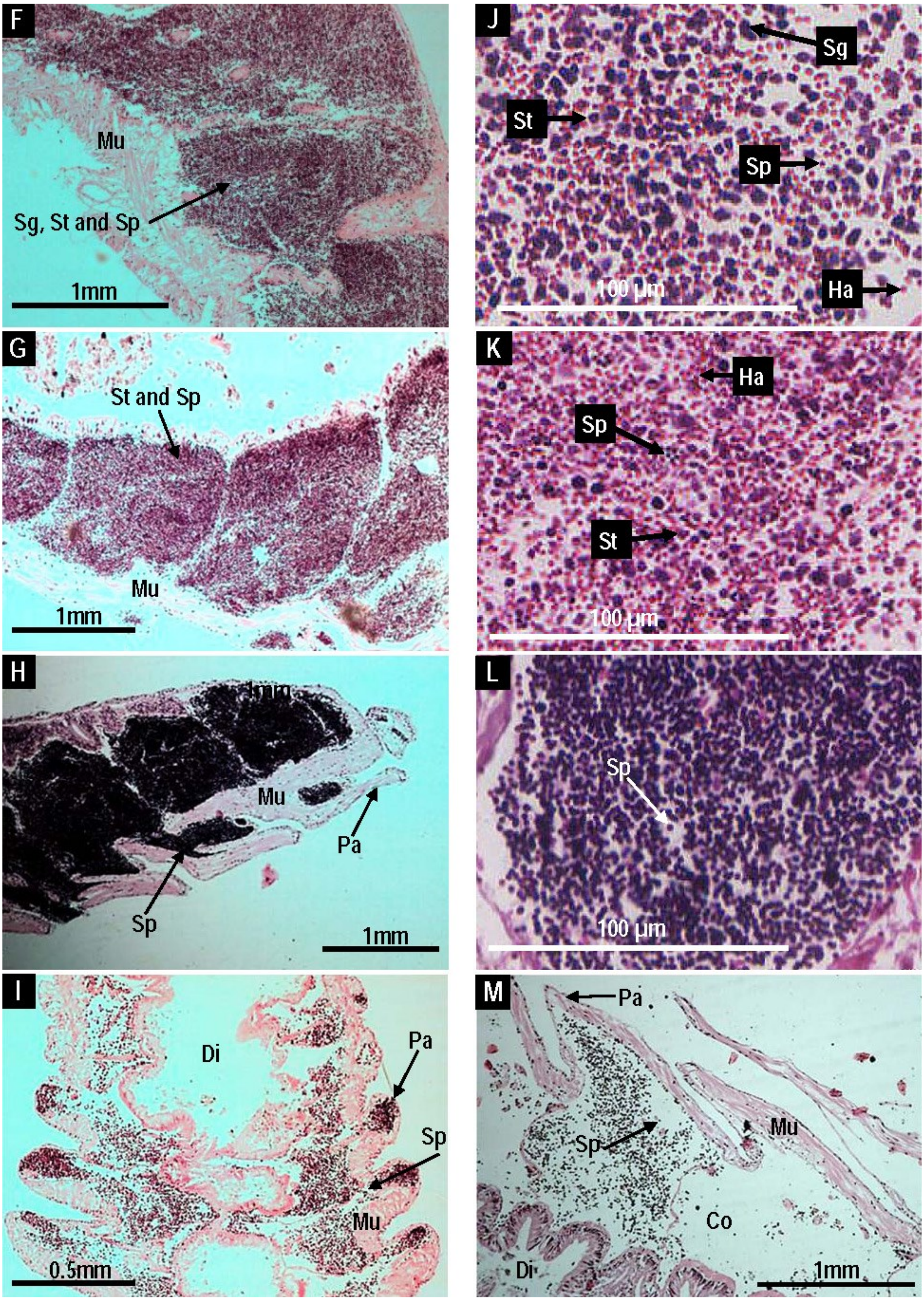


Figure 3.5 Stages of gonad development in male and female *Sabellaria spinulosa*. A) Inactive adult B) Early active female, C) Late active female, D) Partially spent female, E) Spent female F) and J) Early active male, G) and K) Late active male, H) and L) Ripe male, I) Partially spent male and M) Spent male.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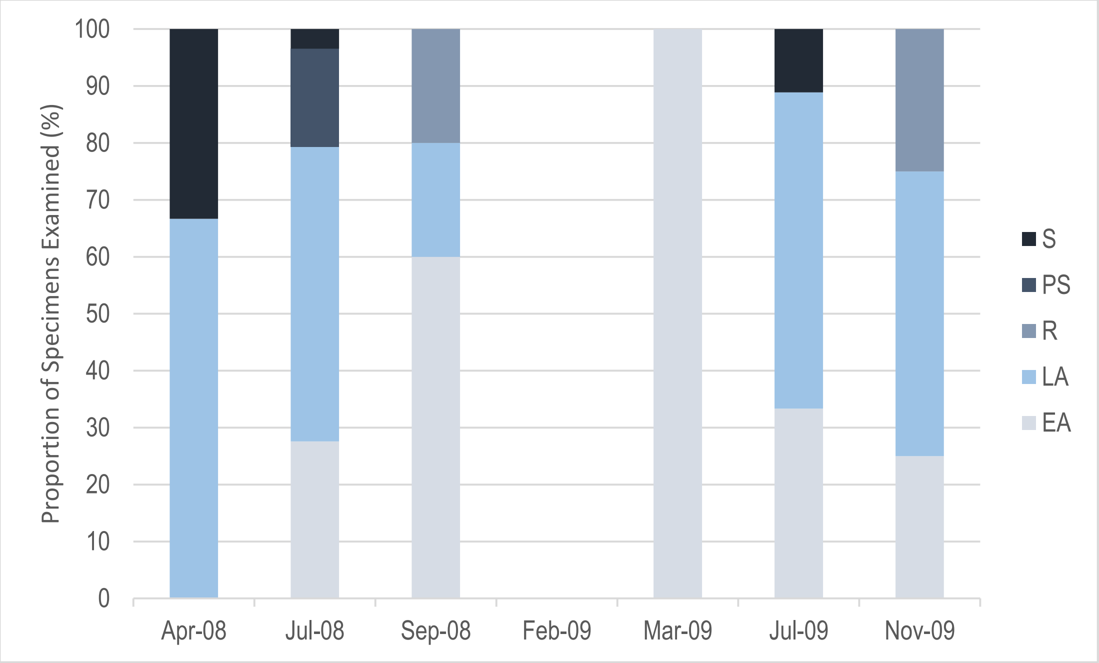


Figure 3.6 Stages of gametogenesis, as outlined in **Table 3.1** and **Figure 3.5**, observed in 56 male *Sabellaria spinulosa* collected Cutline between April 2008 and November 2009.

Oogenesis and ovarian ultrastructure

S. spinulosa gametogenesis was found to be harder to stage in females than in males as all stages of oogenesis were generally evident in the specimens examined (**Figure 3.5**). Based on the specimens examined here it is possible that oogenesis in *S. spinulosa* is different to that observed in its congener *S. alveolata* where the same stage of oogenesis was present throughout each of the individuals examined (Culloty et al. 2010). Furthermore, no females were examined that could be described as ripe using the definitions described for *S. alveolata* by Culloty et al. (2010). It is not clear whether this is an artefact of the limited number of specimens available for examination or whether this species has less well defined stages of development, which would be indicative of semi-continuous or polytelic spawning behaviour.

Oogenesis observed here in *S. spinulosa* was more similar to that reported for the American sabellariid, *Phragmatopoma lapidosa* than its European congener *S. alveolata*. In a study examining the ultrastructure of the ovaries and oogenesis in *P. lapidosa* Eckelbarger (1979) found that all stages of egg development could be found within the ovaries at any one time. The description of the ultrastructure of the ovaries provided by Eckelbarger (1979) closely resembles that observed in *S. spinulosa*, with bunches of follicle cells, presumed to be oocytes in differing stages of development, attached to a genital blood vessel, extending from the intersegmental septum (**Figure 3.8**).

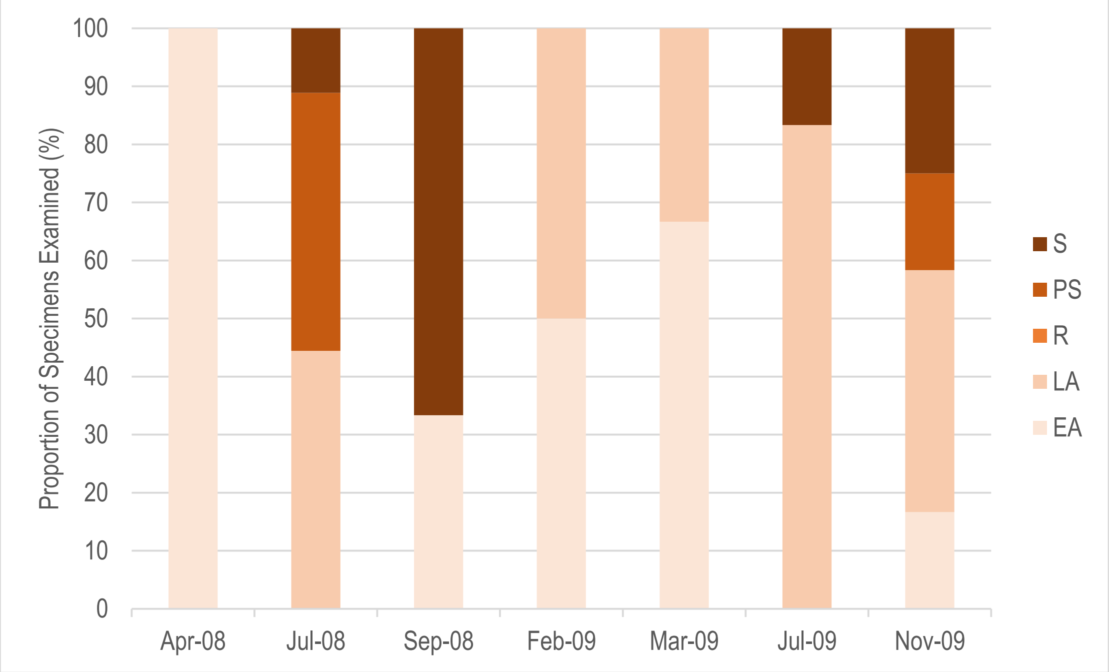


Figure 3.7 Stages of gametogenesis, as outlined in **Table 3.1** and **Figure 3.5**, observed in 50 female *Sabellaria spinulosa* collected from Cutline between April 2008 and November 2009.

Eckelbarger (1979) notes that the role of the follicle cells has yet to be ascertained. Oogenesis in most polychaetes is of the solitary type described by Raven (1961), where each follicle cell develops into an oocyte. However, follicle cells or a sheath of squamous epithelial cells have been reported in some polychaete species such as *Platynereis dumerillii* (Fischer 1974; Fischer 1975), where they are thought to play a mechanically supportive role (Eckelbarger 1979). More detailed examination of the structure of the follicle cells using TEM techniques would be required to further our understanding of the functioning of these cells in *S. spinulosa*. This would also help to determine whether or not the presence of oocytes in different developmental stages means that *S. spinulosa* has the ability to reproduce throughout the year, or for an extended period of time.

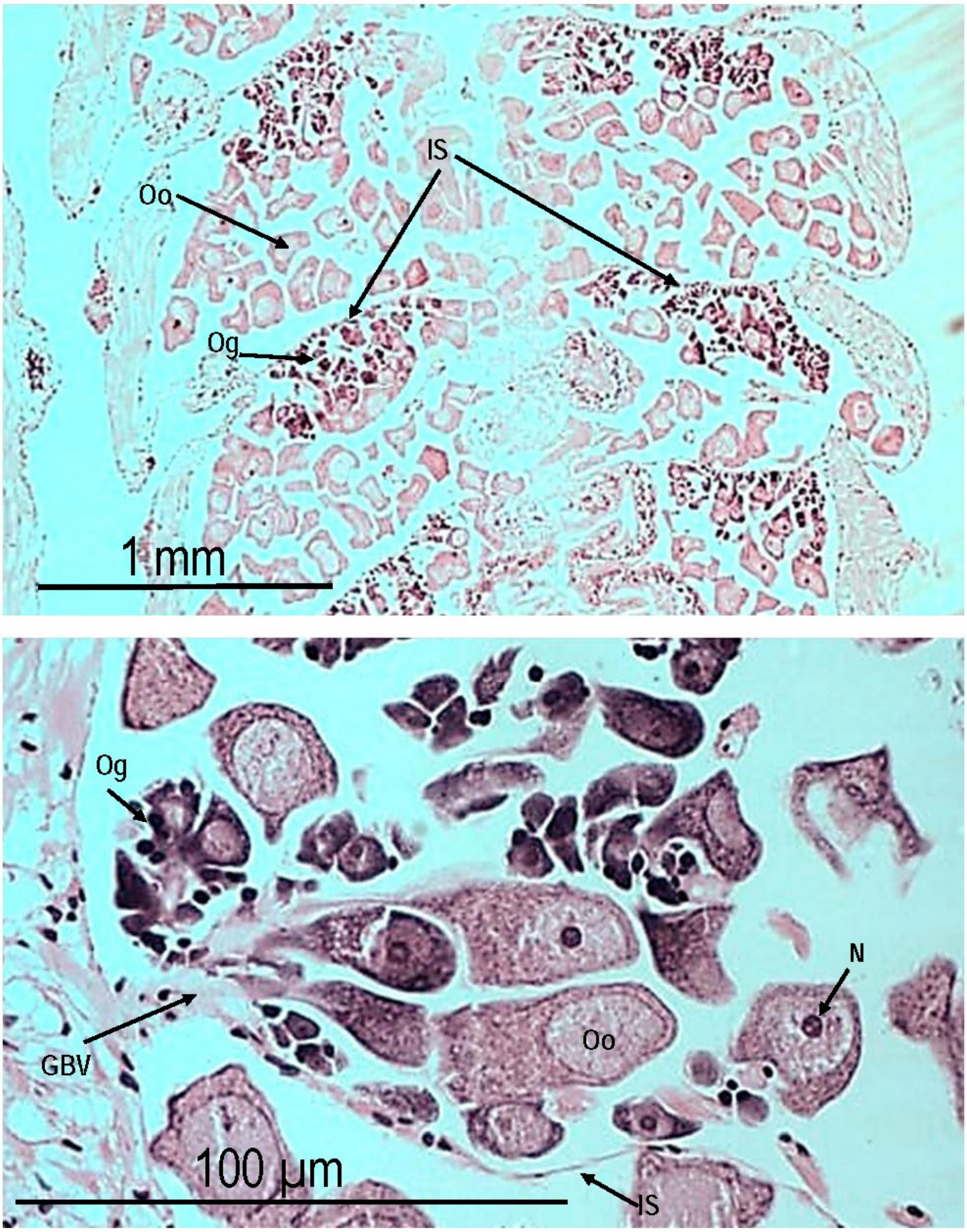


Figure 3.8 Structure and organisation of the ovaries in *Sabellaria spinulosa*. IS, intersegmental septum: GBV, genital blood vessel: Oo, mature oocyte: Og, oogonia: N, Nucleolus.

3.3.4 Larval Availability

The highest abundance of *S. spinulosa* larvae was recorded in the water column in February 2008 (**Figure 3.9**). Since the larvae of *S. spinulosa* typically take between 6 and 8 weeks to metamorphose (Wilson 1970b) we can conclude that the main spawning event occurred between December 2007 and February 2008. That there were no larvae sampled from the water column a month later indicates that settlement had occurred by this time. This corresponds well with the dominance of male and female adults in the later stages of gametogenesis (Late Active, Ripe, Partially Spent & Spent) in November and the dominance of females in the early stages of gametogenesis (early Active) in April (**Table 3.2 and Figures 3.6 and 3.7**). That the only males sampled in April were found to be Spent or Late Active (**Figure 3.6**) is likely to be an artefact of the small numbers examined (n=3).

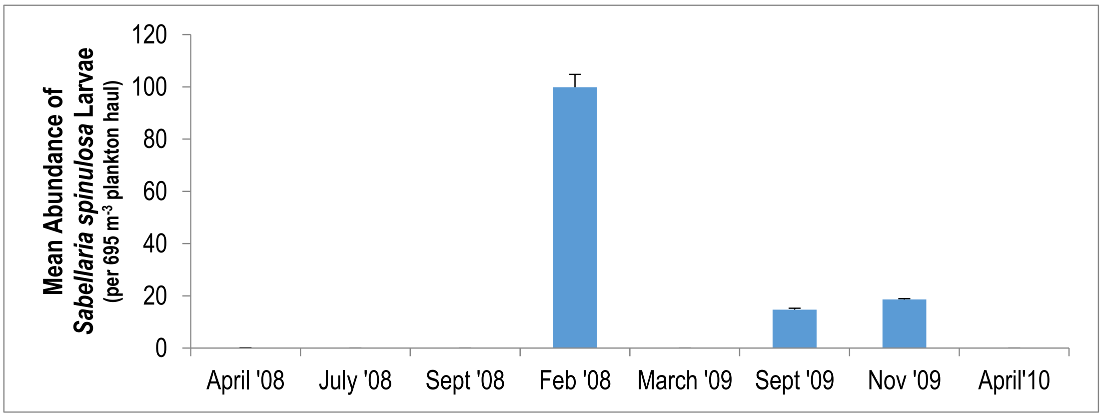


Figure 3.9 Mean abundance (± SE) of *Sabellaria spinulosa* larvae recorded in plankton hauls collected from the Cutline site between April 2008 and April 2010.

A smaller number of larvae were collected in September and November 2009, indicating that there were at least two smaller spawning events between July and September 2008. This again corresponds well with the histological examinations that revealed spent and partially spent females in July, September and November (**Figure 3.7**) and males in the later stages of gametogenesis (Late Active, Ripe, Partially Spent & Spent) at the same times (**Figure 3.6**). Collectively these data indicate a seasonal trend in the spawning behaviour of *S. spinulosa* and it seems likely that this species either has a protracted spawning season extending from July to February or that it has a main spawning event between December and February with some gamete leakage or smaller spawning events in the lead-up to the main event.

The timing of *S. spinulosa* spawning observed here corroborates early observations made by Wilson (1970b) who reported a peak in larval abundance at the beginning of the year when sea temperatures were still cold. Winter spawning is indicative of a species with a boreal distribution, however, *S. spinulosa* is reported to occur along the west coast of India (Achari 1974) as well as southern Africa (Day 1967). Assuming that these are not misidentifications, it would seem likely that *S. spinulosa* will have significantly different spawning times across its geographical range. Wilson (1970b) also noted the presence of *S. spinulosa* larvae in the water column in smaller numbers throughout much of the year. Similarly, Hendrick (2007) observed a secondary recruitment event in a *S. spinulosa* population in the Wash in November. Wilson (1970b) postulates that occasional spawning remote from the main spawning event cannot be ruled out given the capacity of *S. spinulosa* larvae to undergo normal development, in the laboratory, at almost any time of the year. The data presented here, and by Hendrick (2007), support this hypothesis although it has yet to be established whether or not these secondary spawning events are active events making up a protracted spawning season or the result of passive gamete leakage. A more complete time-series data set would be required than that presented here, with the addition of settlement and laboratory experiments. In combination, though, the evidence collected by different authors would suggest that successful recruitment is possible throughout much of the year, although greater recruitment success can be expected in the spring.

3.3.5 Population Structure

The size-frequency distribution data presented in **Figures 3.10-3.12** show that the bulk of the *S. spinulosa* sampled from each of the five reef areas at Hastings Shingle Bank (**Figure 2.4 and Table 2.1**) formed a single cohort. The main cohort peaked at approximately 1.2 mm anterior width, or 9 mm total length in concordance with the size-frequency studies undertaken by George and Warwick (1985) and Hendrick (2007). A smaller cohort of individuals, peaking between 0.3 and 0.5 mm anterior width, was present in all regions except the actively dredged area. In this region only very low numbers of *S. spinulosa* were recorded, although virtually the full size range was present, suggesting that at least some individuals have escaped the impacts of dredging activities. No cohorts have been assigned to the actively dredged area as the occurrence of *S. spinulosa* was very sporadic.

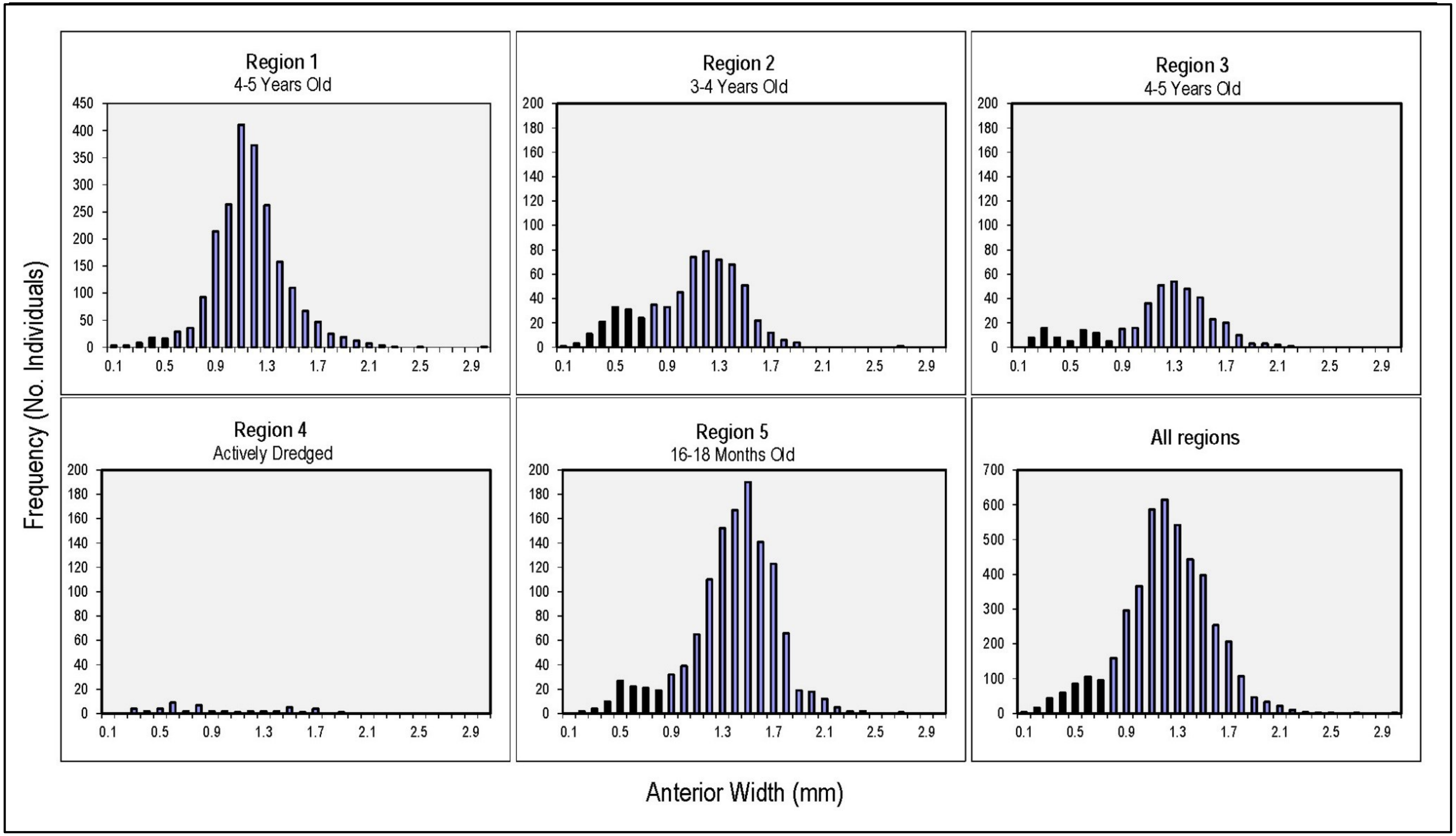


Figure 3.10 Size frequency histograms of the anterior width (mm) of *Sabellaria spinulosa* individuals (n=4498) collected from five regions within Hastings Shingle Bank, in the eastern English Channel, in September 2006. Early developmental cohorts are coloured black and the main adult cohort is coloured purple. No cohorts have been assigned to Region 4 as very few individuals were sampled from this region.

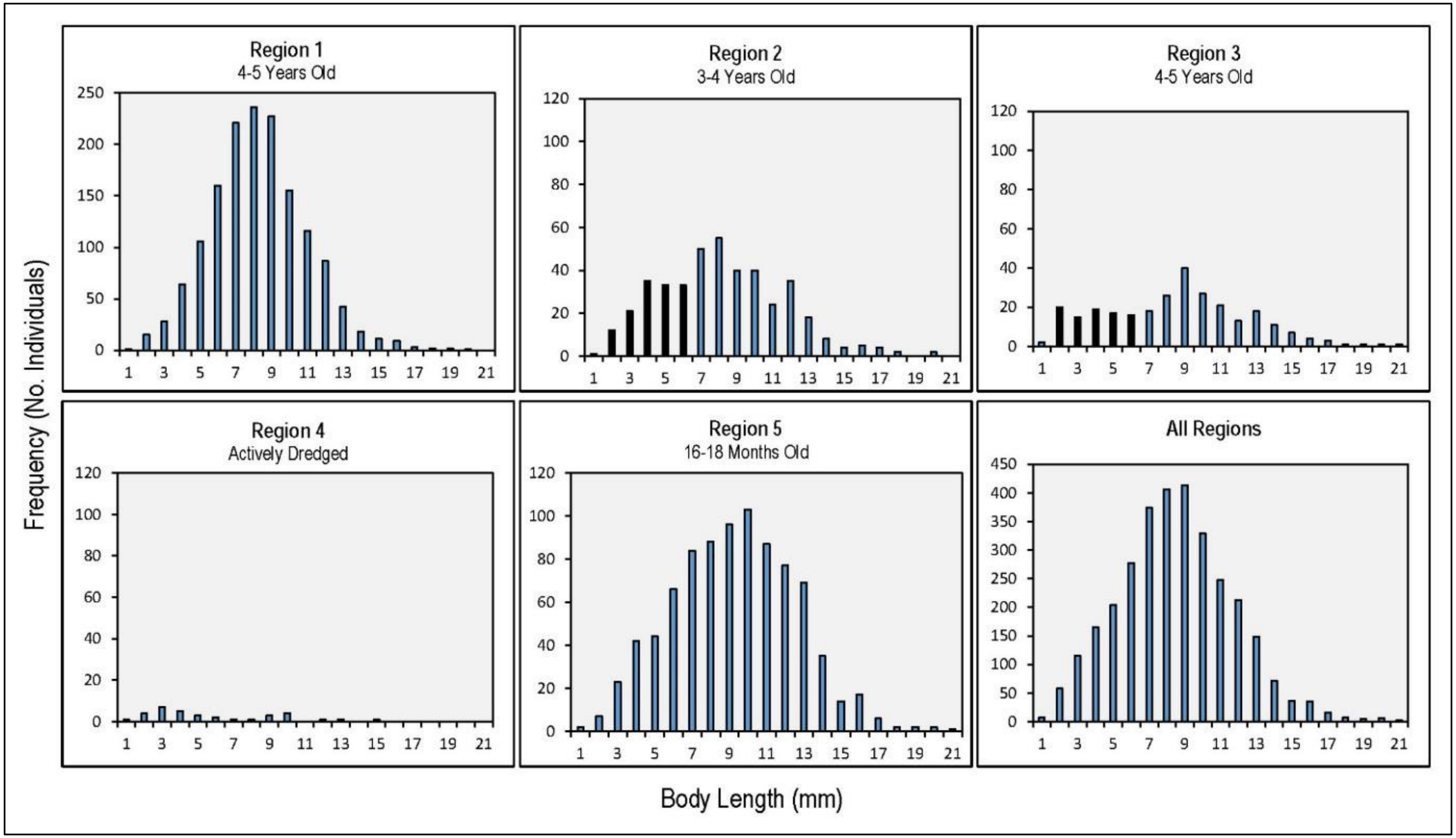


Figure 3.11 Size frequency histograms of total body length (mm) of *Sabellaria spinulosa* individuals (n=4498) collected from five regions within Hastings Shingle Bank, in the eastern English Channel, in September 2006. Early developmental cohorts are coloured black and the main adult cohort is coloured blue. No cohorts have been assigned to Region 4 as very few individuals were sampled from this region.

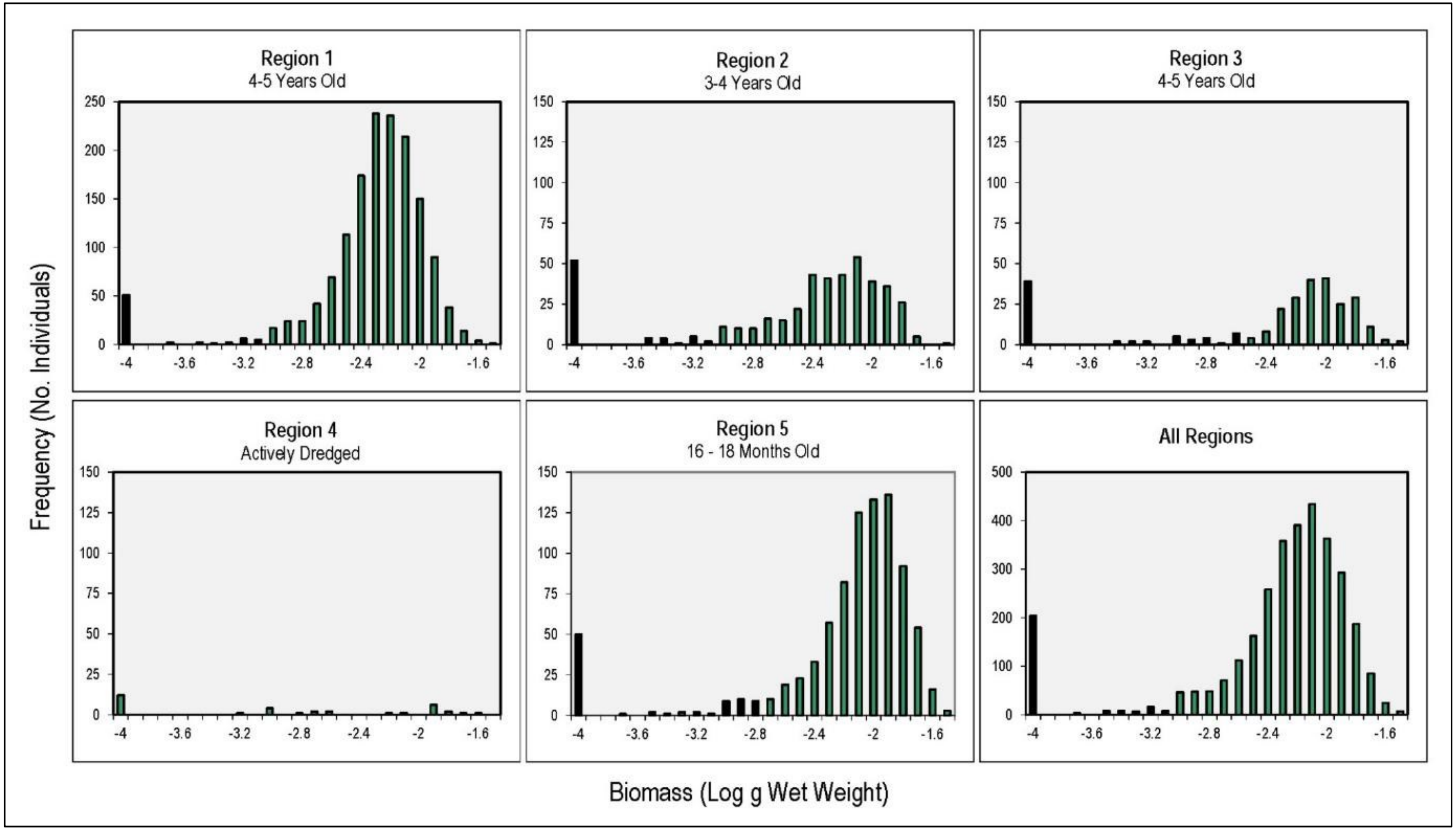


Figure 3.12 Size frequency histograms of total biomass (Log g wet weight) of *Sabellaria spinulosa* individuals (n=4498) collected from five regions within Hastings Shingle Bank, in the eastern English Channel, in September 2006. Early developmental cohorts are coloured black and the main adult cohort is coloured green. No cohorts have been assigned to Region 4 as very few individuals were sampled from this region.

The small proportion of juveniles compared to the main adult cohort across all regions, indicates that the most recent recruitment event was either very small, or that the main cohort is made up of more than one year class. The latter seems most likely given the ratio of newly recruited juveniles to adults (1:10 based on anterior width). This would correspond well with previous observations made by George and Warwick (1985) who found that *S. spinulosa* juveniles grew very quickly, whilst the adults showed little growth after one year, causing the main adult cohorts to merge. *S. spinulosa* reefs are likely therefore to be composed of adults of differing ages. In contrast, *S. alveolata* reefs have a clearly defined age structure (Gruet 1982; Gruet 1984; Gruet 1986b) adding weight to the hypothesis that there are fundamental differences in the reproductive cycle of these congeners. The contrasting age structures of the adult populations of *S. spinulosa* and *S. alveolata* are also likely also to be the cause of the differing appearance of the reef structures formed by these two sabellariids (**See Figure 1.4**). The uniform, honeycomb like structure of *S. alveolata* reefs, in which individuals use the walls of others tubes to complete their own, is indicative of a species which has a very well defined and coordinated reproductive cycle. The main body of a *S. alveolata* reef is made up of adults that have settled and grown synchronously with new recruits being limited to the outer reef edges (Gruet 1982; Gruet and Lassus 1983; Caline et al. 1992). Reefs built by *S. spinulosa* are typically irregular and patchy which is likely to be an artefact of their extended polytelic spawning season. Individual *S. spinulosa* also build complete tubes, which indicates that there is less synchronicity in their reproductive behaviour.

Region 5 represents the newest area of reef which has an approximate age of 16 to 18 months. This area was intensively dredged up to February 2005 when extractive activities were significantly reduced before ceasing completely in March 2005 (Pearce et al. 2007). The reefs sampled in this region were visible on side-scan sonar in August 2005 indicating that there was a significant recruitment event soon after dredging activities ceased. The samples used in the size-distribution analyses presented here were not collected until September 2006 and hence the smallest cohort is likely to represent a March 2006 recruitment. That the main cohort is so much larger than the new recruit cohort in this region, suggests that either the initial recruitment event in 2005 was much more successful and / or that there has been more than one recruitment event between March 2005 and September 2006. A greater proportion of large adults were observed in Region 5 than in the other regions, with cephalic width peaking at 1.5 mm. It is unclear why the adults might be larger in this region, but it is possible that in a younger reef, individuals are less spatially constrained or that there was a greater availability of food, perhaps as a result of nearby dredging activities. That parts of the *S. spinulosa* reef identified in Region 5 were established before the cessation of dredging activities cannot be ruled out either, since extractive activities of this nature are rarely, if ever, 100 % effective.

The size distribution data presented here were collected during a single survey event and it is not therefore possible to determine the longevity of this species with any certainty. However, assuming that the smaller cohort represents a typical recruitment event, and that there are between 1 and 3 recruitment events per year, as observed at the Cutline site (**Figure 3.6, 3.7 and 3.9**), then *S. spinulosa* sampled from the Hastings Shingle Bank reefs are likely to have a maximum age of between 3 and 10 years. This corroborates the earlier observations of George and Warwick (1985), and casts some doubt on the popular belief that *S. spinulosa* is a fast growing annual (Holt et al. 1998; Jones 1998). *S. spinulosa* reefs may appear as annual features, as observed in the Wash by Hendrick (2007), but it seems likely that longevity in this instance is determined by the fragility of the reef structure, rather than by the longevity of the polychaetes that construct them.

3.4 Conclusions

The data presented here were collected in a serendipitous manner, during the course of surveys that were not designed to investigate the reproductive cycle of *Sabellaria spinulosa,* meaning that there are limitations to the conclusions that can be drawn. Nevertheless, it has been possible to use these data to advance our understanding of the reproductive cycle of *S. spinulosa*. These results represent the first description of gamete ultrastructure and gametogenic development in *S. spinulosa* and collectively have furthered our understanding of the timing, frequency and nature of the reproductive cycle of this species.

The eggs liberated from adult *S. spinulosa* in the laboratory were found to be small compared to the eggs other polychaetes (Giangrande 1997) and smaller than the eggs of the congener *S. alveolata* (Wilson 1929; Robert et al. 1979; Gruet and Lassus 1983) ranging in size from 45 µm to 58 µm. The sperm were found to be modified from the primitive sperm type as defined by Franzen (1956), possessing a long tapering tip or acrosome. The head including the acrosome was approximately 3 µm in length and 2 µm wide and the tail or flagellum was found to reach between 15 and 60 µm. Clumping was observed in both the eggs and sperm of *S. spinulosa*, as has previously been described for the related species *Phragmatopoma californica* (Thomas 1994a). This raises the possibility that the gametes of this species may stay loosely associated with the reef structure rather than being broadcast into the water column as had previously been assumed (Giangrande 1997). It will be important to establish the extent to which the gametes clump and catch on the reef structure in the field, as this will influence both the fertilisation success and larval dispersion, or connectivity, of *S. spinulosa* reefs.

Oogensis in *S. spinulosa* was found to be fundamentally different from that observed in its congener *S. alveolata* where the oocytes were present in the same stage of development throughout the coelomic cavity (Culloty et al. 2010). Bunches of follicle cells, presumed to be oocytes in different stages of development, were observed in the majority of the *S. spinulosa* specimens studied here, mirroring oogenesis described for *Phragmatopoma lapidosa* (Eckelbarger 1979). More detailed examination of the structure of the follicle cells using TEM techniques would be required to confirm the function of the follicle cells. However, fully developed oocytes were present in the majority of the females examined indicating that *S. spinulosa* is physiologically able to reproduce throughout much of the year.

Spermatogenesis in *S. spinulosa* was found to be broadly similar to that observed in *S. alveolata*, with some seasonality in the developmental stages present (Culloty et al. 2010). Individuals belonging to several different developmental stages were observed during each month sampled, except for March when all individuals were found to be early active, consistent with a main spawning event having occurred over the winter. *S. spinulosa* larvae were most prevalent in the water column in February with smaller numbers also noted in September and November. No larvae were present in the water column in March indicating that larval recruitment had occurred by this time.

Size-frequency distribution analysis of *S. spinulosa* populations in the eastern English Channel provided further evidence of polytelic spawning with a much greater abundance of adults in the youngest reef than would be expected based on the most recent recruitment. The results of this study corroborate earlier observations of *S. spinulosa* settlement (Wilson 1970b; George and Warwick 1985), indicating that this species either has a protracted spawning period extending from July to February, or that it has a main spawning event between December and February with some secondary spawning events or gamete leakage in the months leading up to the main event as summarised in **Figure 3.13**.

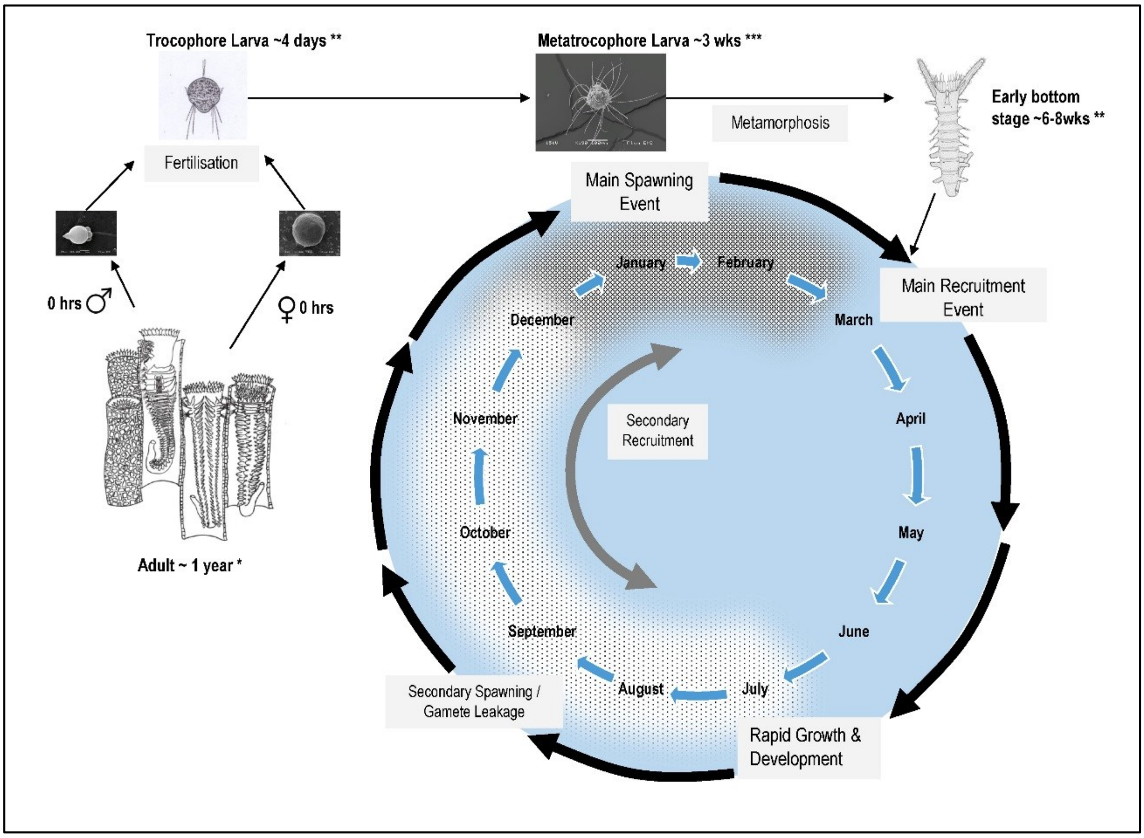


Figure 3.13 Summary of the life cycle of *Sabellaria spinulosa* based on information presented within this thesis and the published literature (Wilson 1929; Wilson 1970b; George and Warwick 1985) * Image redrawn from Schafer (1972), ** images redrawn from (Wilson 1929), *** metatrocophore larva preserved in formaldehyde.

The population structure of *S. spinulosa* reefs in the English Channel showed that the majority of animals belong to one main cohort, which corroborates the results of George and Warwick (1985). There was a relatively abrupt drop in the number of individuals recorded with an abdominal width greater than the modal (most common) width, suggesting that there is a sharp slowing in the growth rate. This accords well with previous work carried out by George and Warwick (1985) in the Bristol Channel, where over the twelve months of the study the main *S. spinulosa* cohort grew from 1.1 mm to 1.2 mm illustrating very slow growth rates of the adult worms. The new settlement of *S. spinulosa* in the Bristol Channel grew approximately 0.8 mm in four months which is over 20 times faster than the growth rate observed in the adult population (George and Warwick 1985). It is therefore likely that the main cohort identified at the

Hastings Shingle Bank site is made up of a number of year classes which have merged due to their slow growth rates. It is possible that the reef structure itself limits the transverse growth of *S. spinulosa*, especially where individuals are tightly packed. Longitudinal growth could not be accurately assessed in this study because of the damage sustained to individuals during standard macrofaunal sample processing. It was not possible to dissolve the tubes using acid as recommended by George and Warwick (1985) since this would dissolve body parts of other species that are necessary for identification. Future work should therefore consider collecting samples dedicated for the purpose of analysis the size-frequency distribution of *S. spinulosa*.

The temporal stability of *S. spinulosa* reefs has traditionally been assumed where reefs have been observed repeatedly in any one location, over time (Gubbay 2007). However, given the potential for these reefs to occur both as annual features (Hendrick 2007) and as more stable habitats, in which individuals are able to realise their maximum longevity, as is indicated by the results presented here and by comparable data collected from the Bristol Channel (George and Warwick 1985), studying the population structure could prove to be a key tool in determining the true temporal stability of *S. spinulosa* reefs. *S. spinulosa* reefs are widespread in the UK (Hiscock 2003) but it is possible that the majority are transient or annual features. More stable reefs may be rarer, and may prove to have a higher ecological value, although this relationship has yet to be investigated. The true stability of a reef feature should therefore be used to determine its relative conservation value, rather than relying on its historic presence as a proxy (Hendrick and Foster-Smith 2006; Gubbay 2007).

The new observations of the reproductive cycle of *S. spinulosa* presented here, indicate that this species has a number of life-history traits typical of an *r*-strategist as summarised in **Table 3.3**. *S. spinulosa* has a protracted spawning season extending from July to February, with several spawning events occurring separately from the main spawning event which occurs between December and February. Fully developed eggs and males in the latter stages of gametogenesis (ripe or late active) were found throughout the year. It is not possible to determine from the data presented here whether individuals are capable of breeding more than once in a year, but *S. spinulosa* populations, as a whole, are certainly capable of breeding more than once in a year, markedly increasing their ability to recover from natural and anthropogenic disturbances.

Table 3.3 Summary of the characteristics of equilibrium (K selected) and opportunistic (*r* selected) species as defined by MacArthur (1960) and the corresponding characteristics of *Sabellaria spinulosa*.

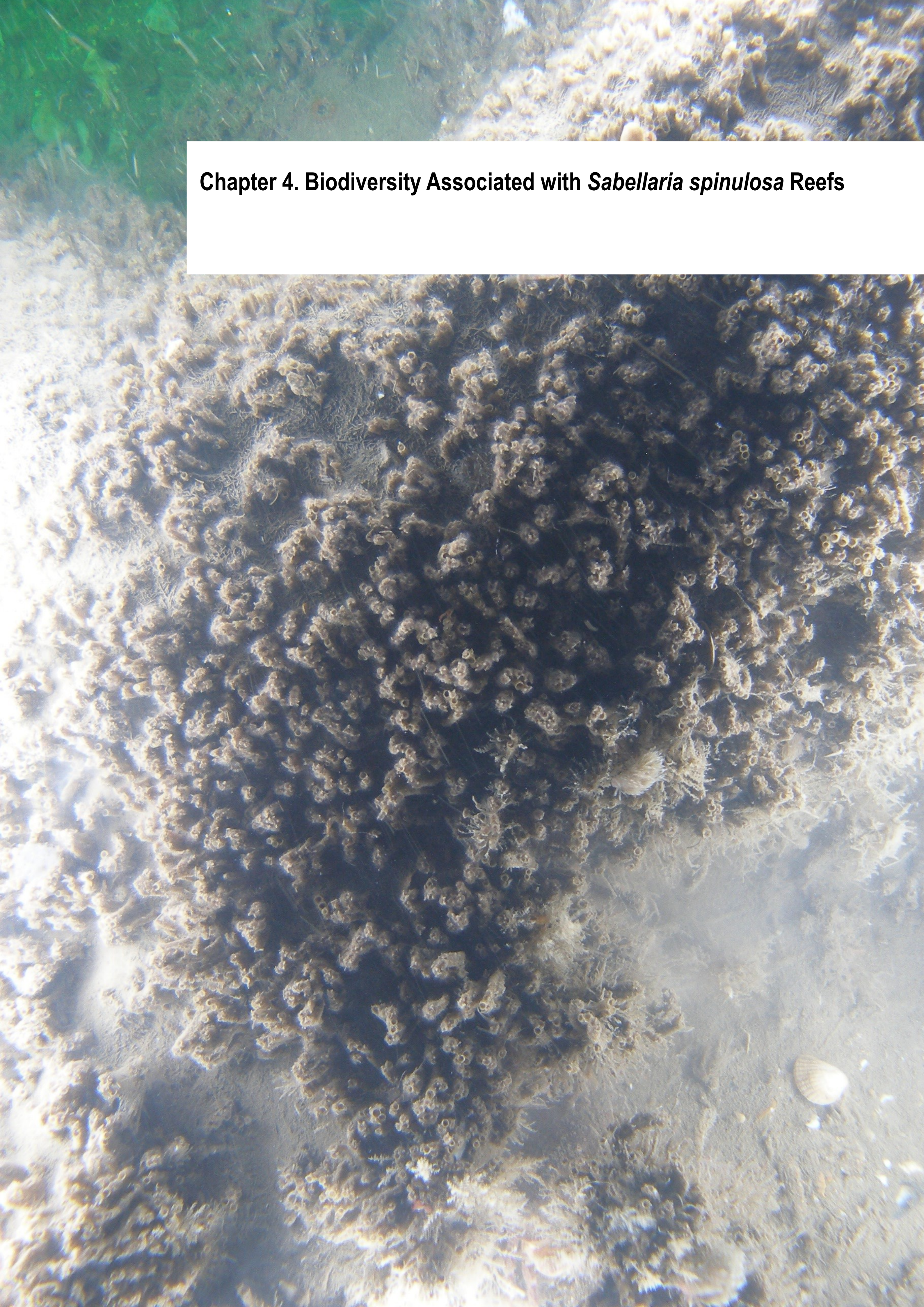
Feature	**Equilibrium (*K*)**	**Opportunistic (*r*)**	***Sabellaria spinulosa***
Reproduction periods	Once per year	Many per year Larvae in the water column most of the year	At least 2-3 times per year Larvae present in the water column in February, September and November Fully developed eggs and males in the latter stages of gametogenesis present throughout the year
Development	Slow growth Delayed reproduction	Rapid growth Early reproduction	Rapid growth Sexual maturity unknown, but presumed to be <1yr
Mortality	Low, Often density dependent	High Often catastrophic Density Independent	Unknown
Recruitment	Low Few large offspring	High Many small offspring	Recruitment levels are unknown High numbers of small offspring (broadcast spawners)
Colonising time	Late	Early	Uncertain, but evidence from the Hastings Shingle Bank site indicates that colonisation occurred within 1-2 months
Adult size	Generally large	Generally small	Moderate amongst polychaetes
Mobility	High	Low Sedentary or sessile	Low Sedentary

Rapid initial growth rates have been observed here and in a study in the Bristol Channel (George and Warwick 1985) which is indicative of a species that also reaches sexual maturity at a young age (Giangrande 1997). The precise age at which *S. spinulosa* reaches sexual maturity is yet to be established but since the adolescent population has been found to merge with the adult cohort within one year (George and Warwick 1985), it can be assumed that sexual maturity has also been reached by one year.

S. spinulosa is a broadcast spawner, producing characteristically high numbers of offspring. The number of eggs per brood has never been quantified although Giangrande (1997) estimates it to be in the order of 100,000. Although high levels of larval mortality are likely temper population numbers this has never been quantified. Successful recruitment has been observed in all studies that have looked at the size-frequency of *S. spinulosa* populations, including this one (George and Warwick 1985; Hendrick 2007). However, recruitment has yet to be formally quantified across years, or interannual spawning events. It is likely though, that recruitment associated with secondary spawning events will reflect the reduced numbers larvae present in the water column, making recovery or colonisation more likely in the spring. Evidence from the eastern English Channel suggests that *S. spinulosa* colonised a previously dredged area within 1 or 2 months indicating that this species can act as an early coloniser although it is likely that there will be some seasonality in this trait.

These findings indicate that *S. spinulosa* have a high reproductive output and fast early growth rates affording them a high capacity to adapt to changes in the environment and to recover from adverse impacts. Many of the life history traits of *S. spinulosa* are typical of *r*-strategists, although not all, hence this species should not be considered as wholly opportunistic. It should also be noted that these traits belong to the species and not necessarily the reef habitats that it creates. It is not yet known how long it takes for a stable *S. spinulosa* reefs to develop, although some of the evidence presented here suggests that reefs can develop in a matter of months in some. Fundamental differences have been identified between the reproductive strategy of *S. spinulosa* and that of its congener *S. alveolata* and what is assumed of broadcast spawners more generally. These differences could have significant implications for the management of this species and once again reiterate the importance of undertaking observational research in this field.

Chapter 4. Biodiversity Associated with *Sabellaria spinulosa* Reefs



4.1 Introduction

The term biodiversity, a compaction of “biological diversity”, refers in general terms to the diversity of life on earth. The term encompasses genetic diversity, organismal diversity and ecological diversity, including functional traits such as body size and feeding behaviours (Harper and Hawksworth 1994; Pearson 2001; Norling et al. 2007). However, the term is often used synonymously with the much narrower community descriptor, species diversity, (Warwick and Clarke 2001). Biodiversity can also be considered at different spatial scales, each of which tells us something different about the system being studied. Sample level diversity, or alpha diversity, is by far the most common scale at which patterns of biodiversity are investigated (Dubois et al. 2002; La Porta and Nicoletti 2009). Measuring and comparing alpha-diversity has obvious uses and advantages from a monitoring and investigative perspective since the data required are easily obtained and there exist numerous methods through which direct comparisons can be made (Magurran 2004; Magurran 2011; Maurer and McGill 2011). The many alpha diversity indices reported in the literature can also be used to make comparisons between different habitat types, locations or time-periods. However, comparisons made on the basis of alpha diversity may not always accurately detect differences or trends in biodiversity, because sample level diversity varies over a small spatial scale (Gray and Elliott 2009).

The biodiversity supported by a given habitat is determined by a complex interplay between environmental variables (both natural and anthropogenic) and biological interactions. One of the key drivers of biodiversity however, is habitat complexity, since more complex habitats provide a greater number of environmental niches which in turn may be occupied by a greater variety of species (Bradshaw et al. 2003; Cranfield et al. 2004; Hewitt et al. 2005; Cosentino and Giacobbe 2006; Skilleter et al. 2006; Gray and Elliott 2009; Buhl-Mortensen et al. 2012). The level of complexity in the benthos depends primarily on the composition of the sediment deposits, with complexity increasing with the range of particle sizes present, and the degree of sorting, with the highest levels of complexity being associated with the lowest levels of sorting or homogeneity (Gray and Elliott 2009; Buhl-Mortensen et al. 2012). The complexity of the benthos is often further enhanced, however, by the presence of hard substrata e.g. cobbles, stones and rocky outcrops (Sheehan et al. 2013; Gatt Støttrup et al. 2014; Trebilco et al. 2015) as well as by marine fauna and the structures which they create (Cranfield et al. 2004; Dame 2005; Hauser et al. 2006; Bouma et al.

2009; Buhl-Mortensen et al. 2012). Some species have profound effects on the seabed, creating conspicuous features which can have a stabilising influence on sediment deposits, particularly in soft-sediment environments (Ragnarsson and Raffaelli 1999; Hall-Spencer and Moore 2000; Bolam and Fernandes 2003; Cranfield et al. 2004) These features are collectively referred to as 'biogenic reefs' or 'biogenic structures', the most prolific examples being coral reefs and seagrass meadows (Nishi and Nishihira 1999; Skilleter et al. 2006; Mellin et al. 2010; Soeffker et al. 2011).

Species capable of creating biogenic reefs exist within most major Phyla, with mussel and oyster beds (Ragnarsson and Raffaelli 1999; Dame 2005), slipper limpet complexes (Thieltges 2005), vermatid reefs (Milazzo et al. 2014) and lesser-known nest-building bivalves (Hall-Spencer and Moore 2000; Trigg et al. 2011) representing the molluscs. High density aggregations of tubiculous polychaetes can also form complex beds (Daro and Polk 1973; Bolam and Fernandes 2003; Rees et al. 2005; Callaway 2006; Godet et al. 2011) as well as more solid reef-like structures (Wilson 1971; Fornos et al. 1997; Dubois et al. 2006). Algae can form mats (Bolam et al. 2000), kelp forests (Anderson et al. 2005) and, in their calcareous forms, maerl beds (Hall-Spencer et al. 2003). Crustacean species do not often form biogenic structures as species belonging to this group are usually free-living and mobile, an exception to this being amphipod tube beds (Sheader 1998). Encrusting animals such as sponges and hydroids do not form biogenic reefs in the truest sense they do increase complexity, and in high abundances can also have a stabilising influence on sediments (Bradshaw et al. 2003; Cranfield et al. 2004).

Of the biogenic reefs mentioned above, most have been identified as priorities for conservation efforts in International and European conservation legislation. This study focusses on reefs formed by the tubiculous polychaete *Sabellaria spinulosa*, which have been identified as a priority for protection under the Habitats Directive (Annex I) and by OSPAR due to their historic losses, sensitivity to anthropogenic disturbance and ability to enhance biodiversity (OSPAR 2003; OSPAR 2008; EC 2013; OSPAR 2013). Despite the emphasis on enhanced biodiversity as a criterion for the inclusion of *S. spinulosa* reefs in the Habitats Directive and the OSPAR list, there is very little empirical evidence to support this assertion. George and Warwick (1985) studied the production of *S. spinulosa* aggregations in the Bristol Channel and noted an increase in the number of species associated with the reefs when compared to the surrounding deposits, although no direct comparisons were made. The sub-tidal communities of the Bristol

Channel are frequently exposed to periods of anoxia and high levels of scouring, meaning that the macrofauna are generally impoverished (Mettam et al. 1994; Warwick and Somerfield 2010). Reefs formed by *S. spinulosa* are more commonly found in association with more stable sedimentary deposits in the eastern English Channel and North Sea which are known to support a more diverse suite of fauna (Heip and Craeymeersch 1995; Rees et al. 1999). It is, therefore, unclear whether the relationship observed between the presence of *S. spinulosa* reefs and enhanced biodiversity in the Bristol Channel extends to reefs that have developed in more stable environmental conditions.

The Wash Zone Report (NRA 1994) found that *S. spinulosa* reefs supported twice as many species and three times as many individuals as the surrounding sediments (excluding the worms themselves), suggesting that sabellariid reefs are exerting a significant structuring influence on benthic communities. However, these figures were derived from comparisons made between samples that contained high abundances of *S. spinulosa* (>100 individuals in 3 Day grab samples) and samples that contained low abundances of *S. spinulosa* (<100 individuals in 3 Day grab samples) with the latter category containing many more sites (n=58) than the former (n=8). These comparisons may not therefore accurately describe the influence of reef presence, particularly as the non-reef / low *S. spinulosa* abundance category included a number of sites known to be negatively influenced by both natural and anthropogenic disturbances (NRA 1994).

Neither of the aforementioned studies were designed specifically to examine the influence that *S. spinulosa* reefs have on macrofaunal communities and both studies are limited to the use of species richness and abundance as a proxy for biodiversity (George, 1985; NRA, 1994). To date no consideration has been given to the influence that *S. spinulosa* reefs have on species equitability (or dominance), taxonomic diversity, functional diversity or beta-diversity, and hence our understanding of this habitats influence on biodiversity is incomplete (Magurran 2011).

In this study we compare the macrofauna (>1 mm) associated with *S. spinulosa* reefs in the eastern English Channel and southern North Sea with macrofauna associated with adjacent sedimentary deposits in order to determine what, if any, influence *S. spinulosa* reef structures have on biodiversity or macrofaunal community composition. Since sediment composition is known to have a significant influence on macrofaunal composition and diversity in these areas (Newell et al. 2001) and to ensure that comparisons were made with the habitat most likely to occur in the absence of specific areas of reef, sedimentary composition was also incorporated into the analysis which tested the following hypothesis:

Hypothesis A

H_{OA}: *S. spinulosa* reef structures have no influence on macrofaunal biodiversity or community composition

H_{1A}: The macrobenthos found in association with *S. spinulosa* reefs is more diverse and abundant that the macrobenthos associated with comparable sedimentary deposits, and the reef support fauna that would not otherwise occur in the area.

It was not possible within the scope of this study to measure all aspects of biodiversity, nevertheless attempts have been made to use a range of indices which measure, or act as proxies for, different aspects of biodiversity, for example, taxonomic distinctness has been used as a proxy measure of ecological diversity (Warwick and Clarke 2001). The focus of this study is the effect that the habitat created by *S. spinulosa* has on biodiversity, and biodiversity must therefore be considered at the habitat scale (beta-diversity) in order to explore the null-hypothesis fully. What follows therefore is an assessment of the influence of *S. spinulosa* reefs on different aspects of alpha-diversity, including species richness, equitability, diversity and taxonomic spread as well as an assessment of the influence that reef presence has on beta-diversity.

4.2 Methodology

4.2.1 Study Site

This study was conducted at Hastings Shingle Bank in the eastern English Channel (0°34E, 50°44.5N; **Figures 2.1-2.3**) in coarse gravel deposits adjacent to an active aggregate extraction site. *Sabellaria spinulosa* aggregations were identified as rough texturing visible on high resolution side-scan sonar data collected during surveys related to the extraction licence. The presence of the structures was confirmed prior to sampling using a towed video courtesy of the National Oceanographic Centre, Southampton. Once the presence of *S. spinulosa* reefs had been confirmed a number of sampling stations were positioned within and closely adjacent (<50 m) to the structures, within a hydrographically linked area (Pearce et al. 2007), in order to test the null hypothesis that the macrofaunal communities are not significantly different on and off the reefs.

4.2.2 Sample collection and processing

A total of 119 samples of the benthos were collected using 0.1m^2 Hamon grab. A small sub-sample (approx. 250 ml) was removed from each grab sample for Particle Size Analysis (PSA). In the case of reef samples this sub-sample was taken from the sediments underlying the reef structure. The remaining material from each grab sample was washed through a 1 mm aperture sieve and the retained material was fixed and preserved in a 4% buffered formaldehyde solution.

4.2.3 Macrofaunal Identification, Enumeration & Biomass

Before processing the grab samples the excess formalin was filtered through a 1 mm mesh sieve. Each sample was gently elutriated with tap water through the same sieve, to extract the low-density components (small crustaceans and annelids). The larger macrofauna were then removed from the elutriated material. Where *S. spinulosa* aggregations were present in the samples, the tubes were elutriated and then gently broken up before being elutriated again to ensure that both the worms themselves and any commensal fauna were retained in the best condition possible. The remaining sediments were sorted under a x40 stereomicroscope to extract the rest of the marine fauna. The entire mixed sample of separated fauna was then preserved in industrial methylated spirit (IMS) for subsequent analysis. Following the initial processing phase, each sample was sorted into major faunal groups before being identified to the highest possible taxonomic resolution (species level in most instances) and the number and blotted wet weight of individuals belonging to each species were recorded. Due to inherent difficulties in quantification, colonial taxa were entered with a nominal value of P=1 (present) in all subsequent statistical analyses.

4.2.4 Sediment Particle Size Analysis

A sub-sample of sediment was taken for Particle Size Analysis (PSA) where possible from each of the grab samples taken. The material was sieved over a range of sieves based on the Wentworth scale as follows: 64 mm, 31.5 mm, 16 mm, 8 mm, 5.6 mm, 4 mm, 2.8 mm, 2 mm, 1.41 mm, 1 mm, 0.710 mm, 0.500 mm, 0.350 mm, 0.250 mm, 0.180mm, 0.125 mm, 0.090 mm and 0.063 mm. The weight of material passing through the finest sieve (0.063 mm) was recorded to give a measure of the silt and clay content.

The results were expressed as cumulative percentage passing and were converted to absolute percentage retained on each sieve size.

The PSA results were then summarised in terms of % gravel, sand and silt and subsequently classified under the Folk classification system (Folk 1954) (**Figure 4.1**) to facilitate the exploration of S. spinulosa reef effects within broad sedimentary habitats.

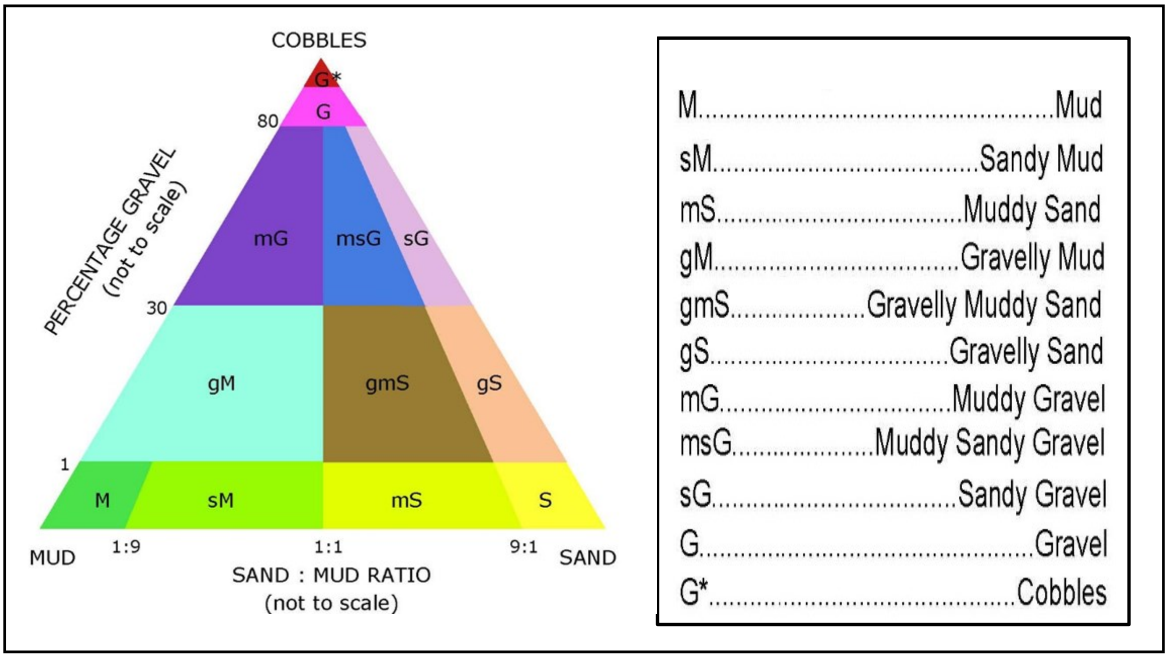


Figure 4.1 Folk classification used to classify sediment sub-samples taken from each grab sample collected from the Hastings Shingle Bank, in the eastern English Channel in 2005. The classification G* was applied to samples that were unsuitable for Particle Size Analysis (PSA) because of the presence of large cobbles.

4.2.5 Data Analysis

As the overarching hypothesis relates to fauna associated with the *S. spinulosa* reefs, *S. spinulosa* itself was excluded from the data in all of the analyses that follow. Samples were grouped according to their position on or off the reefs, as well as the composition of the substratum in accordance with Folk (1954) as summarised in **Table 4.1.** Gravel and muddy sand were not included in the analysis due to the lack of replication. All statistical analyses were undertaken using the PRIMER v6.1 software (Clarke and Warwick 2001; Clarke and Gorley 2006) with the PERMANOVA+ add-on (Anderson and Gorley 2008; Anderson et al. 2008b).

Table 4.1 Summary of grab sample replication (n) within each substratum type (sandy gravel (sG), muddy sandy gravel (msG), gravelly sand, (gS) and sand (S)) and each treatment (reference (ref) and *S. spinulosa* Reef (Sab)).

Substratum	Treatment	n
Gravel (G)	Ref	1
	Sab	1
Sandy gravel (sG)	Ref	41
	Sab	17
Muddy sandy gravel (msG)	Ref	12
	Sab	14
Gravelly sand (gS)	Ref	10
	Sab	3
Gravelly muddy sand (gmS)	Ref	4
	Sab	6
Sand (S)	Ref	4
	Sab	4
Muddy sand (mS)	Ref	0
	Sab	2

Standard community descriptors, number of species (S), abundance (N) and biomass (g wet weight) were calculated for each sample alongside a selection of diversity indices which provide a measure of species richness (Margalef's diversity (d)), species equitability (Pielou's evenness (J')) and diversity, a function of richness and equitability (Shannon-Wiener's diversity (H')) (Magurran 2004; Maurer and McGill 2011). Since all of these diversity indices are sample-size dependent (Warwick and Clarke 2001), Simpson's diversity (1-λ) was also calculated to ensure that any observed patterns in diversity were not artefacts of unequal sampling effort (**Table 4.1**). To complement the more traditional diversity indices, a number of taxonomic distinctness indices (taxonomic distinctness (Δ*), average taxonomic distinctness (Δ+) and variation in taxonomic distinctness (λ+)) were also calculated to test for differences in the taxonomic spread between reef habitats and adjacent sediments as well as the equitability of the taxonomic spread (Warwick and Clarke 2001). Taxonomic distinctness indices were based on hierarchical classifications obtained from the World Register of Marine Species (WoRMs: http://marinespecies.org/).

The relationship between each of the community descriptors and diversity indices and the presence of reef on different substrata was investigated using box and whisker plots and 2- way crossed ANOSIM tests carried out on Euclidean distance resemblance matrices (Clarke 1993), testing for the influence of reef and sediment type. Differences in the variability in species composition, or beta diversity, were compared using a multivariate dispersion (PERMDISP) test carried out on a Jaccard resemblance matrix, based on macrofaunal presence / absence data (Anderson et al. 2006). This test essentially removes the mean effect and tests for differences in dispersion, the equality of which is assumed in the null hypothesis (Fisher 1939). This test uses permutation of the residuals to obtain the P-values making it robust to deviations from normality, negating the need to test data for normality prior to analysis (Anderson 2006; Anderson et al. 2006; Anderson and Gorley 2008; Anderson et al. 2008b). Differences in community composition were investigated using a 2-way crossed ANOSIM test (Clarke 1993; Clarke and Ainsworth 1993) since the assumption of equal dispersion was not fulfilled even after transformation (PERMDISP; Anderson, 2006). The ANOSIM test was carried out on a Bray–Curtis similarity matrix calculated using forth root transformed macrofaunal abundance data. Finally a SIMPER analysis was carried out on the raw abundance data where significant reef effects were detected to explore the composition of fauna on and off the reefs (Clarke et al. 2008).

4.3 Results

The number of species (S), abundance (N) and biomass (g WW) of macrofauna, excluding *Sabellaria spinulosa* itself, were found to be significantly higher in samples taken from within *S. spinulosa* reefs than from adjacent sediments, where the reefs occur on sandy gravel (**Figure 4.2**; **Table 4.2**). Where reefs were sampled from other sediment types there was no significant difference in the number of species (S) or biomass (g WW) that they support although a significant enhancement was observed in the abundance of macrofauna (N) supported by reefs sampled from muddy sandy gravel and gravelly sand habitats.

Margalef's diversity (d) of macrofauna, a measure of species richness, was not found to be significantly different in the presence of *S. spinulosa* reef sampled from any sediment type (**Figure 4.3; Table 4.3**). However, Pielou's J', a measure of species equitability, is significantly lower on *S. spinulosa* reef habitats where they occur in muddy sandy gravel (msG) and sandy gravel (sG) substrata and Shannon-Wiener's diversity (H') and Simpson's diversity (1-λ) were also found to be lower on reefs sampled from muddy sandy gravel (msG) deposits (**Figure 4.3; Table 4.3**) indicating that one or more species has become numerically dominant on reefs that have developed on these sediment types.

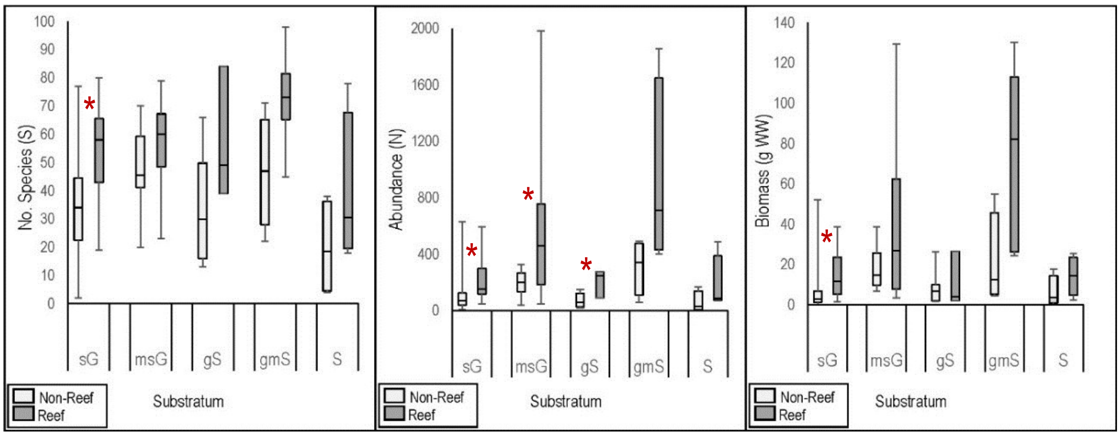


Figure 4.2. Number of species (S), abundance (N) and biomass (g blotted wet weight) per 0.1m^2 Hamon grab sample, from within *Sabellaria spinulosa* reefs (dark grey) and from adjacent sedimentary deposits (pale grey), collected from Hastings Shingle Bank in the eastern English Channel in 2006. Samples have been grouped according to the composition of the substratum (Folk 1954): sandy gravel (sG), muddy sandy gravel (msG), gravelly sand, (gS) and sand (S). *Sabellaria spinulosa* itself was excluded from this analysis. Box plots show the interquartile range and median values whilst the maximum and minimum observed values are represented by the whiskers. An asterisk indicates that there is a significant difference between reef and non-reef habitats (P<5%: see **Table 4.2**).

Table 4.2. Summary of ANOSIM tests carried out on the number of species (S), abundance (N) and biomass (g WW) recorded in 0.1m^2 Hamon grabs collected on and off *Sabellaria spinulosa* reef (identified using high resolution side-scan sonar) in a range of sedimentary deposits in the eastern English Channel: sandy gravel (sG), muddy sandy gravel (msG), gravelly sand (gS), gravelly muddy sand (gmS) and sand (S). Table shows the R statistic (R) and the significance level as a percentage (P). Significant differences (p<5%) are highlighted with bold font.

Community Descriptor	sG		msG		gS		gmS		S	
	R	P	R	P	R	P	R	P	R	P
No. Species	**0.186**	**0.4**	0.074	9.8	0.151	18.9	0.24	10	-0.057	57.1
Abundance	**0.296**	**0.2**	**0.153**	**0.8**	**0.569**	**2.8**	0.063	24.8	0.146	17.1
Biomass	**0.252**	**0.4**	-0.002	43.1	0.035	37.8	0.19	9.5	0	48.6

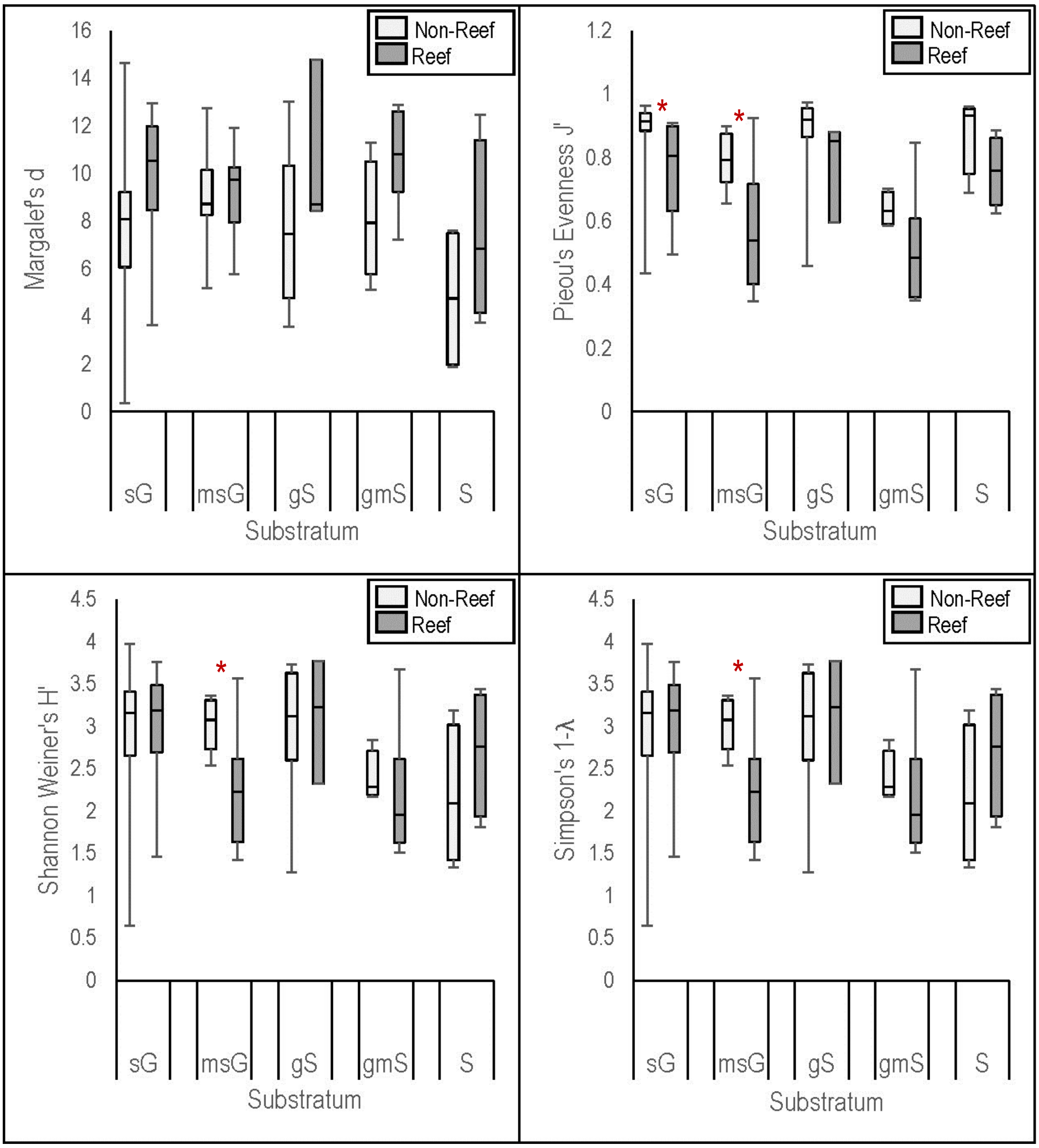


Figure 4.3 Margalef's Diversity (d), Pielou's Evenness (J'), Shannon-Wiener's Diversity (H') and Simpson's Diversity (1-λ) per $0.1m^2$ Hamon grab sample, from within *Sabellaria spinulosa* reefs (dark grey) and from adjacent sedimentary deposits (pale grey), collected from Hastings Shingle Bank in the eastern English Channel in 2006. Samples have been grouped according to the composition of the substratum (Folk 1954): sandy gravel (sG), muddy sandy gravel (msG), gravelly sand, (gS) and sand (S). *Sabellaria spinulosa* itself was excluded from this analysis. Box plots show the interquartile range and median values whilst the maximum and minimum observed values are represented by the whiskers.

Table 4.3 Summary of ANOSIM tests carried out on the alpha diversity measures, Margalef's diversity (d), Pielou's evenness (J'), Shannon-Wiener's diversity (H') and Simpson's diversity (1-λ) of macrofauna recorded in 0.1m^2 Hamon grabs collected on and off *Sabellaria spinulosa* reef (identified using high resolution side-scan sonar) in a range of sedimentary deposits in the eastern English Channel: sandy gravel (sG), muddy sandy gravel (msG), gravelly sand (gS), gravelly muddy sand (gmS) and sand (S). Table shows the R statistic (R) and the probability as a percentage (P). Significant differences (p<5%) are highlighted with bold font.

Alpha Diversity Measures	sG		msG		gS		gmS		S	
	R	P	R	P	R	P	R	P	R	P
Margalef's d'	0.11	5.1	0.011	30.3	0.015	40.2	0.159	19	-0.083	60
Pielou's Evenness	**0.246**	**0.4**	**0.375**	**0.2**	0.146	22.9	0.333	5.2	0.146	22.9
Shannon Weiner's H'	-0.052	78.1	**0.407**	**0.1**	-0.099	58.7	0.063	27.6	-0.125	71.4
Simpson's 1-λ	0.1	9.7	**0.343**	**0.1**	0.093	32.2	0.286	6.2	-0.125	85.7

A small but significant increase in taxonomic distinctness (Δ*) and average taxonomic distinctness (Δ+) was evident on *S. spinulosa* reefs, sampled from muddy sandy gravel habitats (**Figure 4.4; Table 4.4**). No differences in taxonomic distinctness were observed in reefs occurring on other sediment types however indicating that that the taxonomic breadth of macrofaunal communities is not influenced by *S. spinulosa* reefs in this area except where they occur on muddy sandy gravels. In contrast beta diversity, or the variability in macrofaunal composition between samples, was found to be significantly reduced in 3 of the 5 sediment classes studied indicating that species were present more consistently within the reefs than adjacent sediments (**Table 4.5**). No significant difference was identified between the beta diversity of reef macrofauna and sedimentary macrofauna where reefs occur on muddy sandy gravel and gravelly muddy sand however, indicating that these habitats have an equivalent levels of variance in the macrofaunal communities they support.

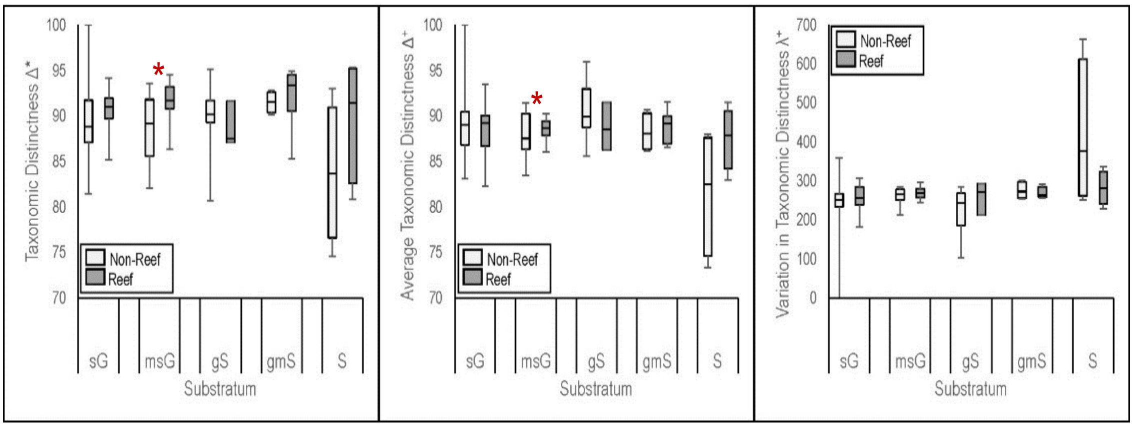


Figure 4.4 Taxonomic distinctness (Δ*), average taxonomic distinctness ($Δ^+$) and variation in taxonomic distinctness ($λ^+$) per 0.1m^2 Hamon grab sample, from within *Sabellaria spinulosa* reefs (dark grey) and from adjacent sedimentary deposits (pale grey), collected from Hastings Shingle Bank in the eastern English Channel in 2006. Samples have been grouped according to the composition of the substratum (Folk 1954): sandy gravel (sG), muddy sandy gravel (msG), gravelly sand, (gS) and sand (S). *Sabellaria spinulosa* itself was excluded from this analysis. Box plots show the interquartile range and median values whilst the maximum and minimum observed values are represented by the whiskers.

Table 4.4 Summary of ANOSIM tests carried out on taxonomic distinctness measures, Taxonomic distinctness (Δ*), average taxonomic distinctness (Δ+) and variation in taxonomic distinctness (λ+) per 0.1m^2 Hamon grab sample collected on and off *Sabellaria spinulosa* reef (identified using high resolution side-scan sonar) in a range of sedimentary deposits in the eastern English Channel: sandy gravel (sG), muddy sandy gravel (msG), gravelly sand (gS), gravelly muddy sand (gmS) and sand (S). Table shows the R statistic (R) and the probability as a percentage (P). Significant differences (p<5%) are highlighted with bold font.

Taxonomic Distinctness Measures	**sG**		**msG**		**gS**		**gmS**		**S**	
	R	**P**	**R**	**P**	**R**	**P**	**R**	**P**	**R**	**P**
Taxonomic Distinctness Δ*	-0.47	74.9	**0.116**	**3.6**	0.076	34.3	0.135	16.7	-0.052	48.6
Avg Taxonomic Distinctness Δ+	-0.013	55.9	**0.126**	**2.6**	-0.106	67.8	-0.103	64.8	-0.222	85.7
Variation in Taxonomic Distinctness λ+	-0.007	48.1	-0.046	85.4	0.108	20.6	-0.012	35.2	-0.357	100

Table 4.5 Results of a PERMDISP, multivariate dispersion test, carried out on a Jaccard resemblance matrix constructed using P/A transformed macrofaunal data recorded in grab samples collected from Hastings Shingle Bank in the eastern English Channel in 2006. Samples have been grouped according to the substratum composition (Folk, 1959) and whether or not the samples were taken from an area identified as *Sabellaria spinulosa* reef using acoustic data. *Sabellaria spinulosa* itself was excluded from this analysis.

F: 10.927, P (perm): 0.001

Pairwise Comparisons (Reef Vs Non-Reef)

Substratum (Folk)	T	P (perm)
Sandy Gravel (sG)	3.7496	0.003*
Muddy Sandy Gravel (msG)	0.5700	0.634
Gravelly Muddy Sand (gmS)	1.4642	0.377
Gravelly Sand (gS)	4.4876	0.005*
Sand (S)	2.4913	0.033*

Means and Standard Errors

Substratum	Non-Reef			Reef		
	n	Average	SE	n	Average	SE
Sandy Gravel (sG)	41	59.10	0.94	17	53.00	1.08
Muddy Sandy Gravel (msG)	12	49.74	2.10	14	48.27	1.58
Gravelly Muddy Sand (gmS)	4	48.26	3.48	6	42.09	2.55
Gravelly Sand (gS)	10	58.46	1.47	3	45.90	0.76
Sand (S)	4	56.50	0.78	4	52.04	1.61

Table 4.6 Summary of ANOSIM tests carried out on a Bray-Curtis similarity resemblance based on fourth root transformed benthic abundance recorded from 0.1m^2 Hamon grab samples collected on and off *Sabellaria spinulosa* reef (identified using high resolution side-scan sonar) in a range of sedimentary deposits in the eastern English Channel: sandy gravel (sG), muddy sandy gravel (msG), gravelly sand (gS), gravelly muddy sand (gmS) and sand (S). Table shows the R statistic (R) and the probability as a percentage (P). Significant differences (p<5%) are highlighted with bold font.

Community Composition	sG		msG		gS		gmS		S	
	R	P	R	P	R	P	R	P	R	P
Macrofaunal Abundance	-0.083	89.8	**0.149**	**1.1**	-0.181	82.9	0.175	11.4	-0.198	85.7

ANOSIM tests carried out on a Bray-Curtis similarity resemblance based on fourth root transformed benthic abundance data revealed that there was no significant difference in the composition of macrofaunal communities associated with *S. spinulosa* reefs, except where they occurred on muddy sandy gravel habitats (**Table 4.6**). A SIMPER test used to explore this difference further (**Table 4.7**) reveals that almost half (46.91%) of the dissimilarity between reef and non-reef habitats in muddy sandy gravel areas is explained by a large increase in the abundance of the porcelain crab *Pisidia longicornis* in the presence of *S. spinulosa* reef. The remaining dissimilarity is explained by much smaller differences in the abundance of macrofaunal taxa for example the barnacle *Balanus crenatus* exhibits a small reduction in its abundance in the presence of the reef falling from an average of 14.92 to 12 individuals per grab sample whilst the tubiculous polychaete, *Spirobranchus triqueter* increases from an average of 4.50 to 5.14 individuals per sample. Such differences are unlikely to represent an ecologically significant difference in the community in isolation. However, the majority (21 of 33) of the taxa, which collectively account for 80 % of the dissimilarity between reef and non-reef communities found in association with muddy sandy gravel deposits, were present on the reef in higher abundance than in adjacent sediments (**Table 4.7**) indicating that the reefs are increasing the overall density of macrofauna in these habitats.

Table 4.7 Summary of species contributing to 75% of the dissimilarity between samples taken from *Sabellaria spinulosa* reefs and adjacent sedimentary deposits, sampled from muddy sandy gravel deposits. The data are derived from a SIMPER test carried out on untransformed benthic abundance data from $0.1m^2$ Hamon grab samples collected from Hastings Shingle Bank in the eastern English Channel. Colonial epifaunal species which cannot be enumerated are included in the data as present “1” or absent “0”. *Sabellaria spinulosa* abundance has been removed from the data. The reef effect on individual species abundance (↑ = enhancement, ↓ = reduction) is also shown.

Taxa	Non- Reef Av. Abund	Reef Av. Abund	Reef Effect	Av.Diss	Diss/SD	Cont%	Cum.%
Pisidia longicornis	47.08	359.50	↑	34.55	1.72	46.91	46.91
Balanus crenatus	14.92	12.00	↓	3.28	0.78	4.46	51.37
Scalibregma inflatum	12.67	5.43	↓	1.61	0.93	2.19	53.56
Crepidula fornicata	1.92	11.29	↑	1.43	0.75	1.94	55.50
Spirobranchus triqueter	4.50	5.14	↑	1.41	0.57	1.91	57.42
Lumbrineris gracilis	8.25	9.79	↑	1.26	0.88	1.71	59.12
Spirobranchus lamarcki	6.08	8.57	↑	1.21	1.07	1.64	60.77
Harmothoe	2.00	11.14	↑	1.12	1.28	1.51	62.28
Phyllodoce maculata	2.00	7.57	↑	1.02	0.81	1.38	63.66
Galathea intermedia	3.75	3.07	↓	0.79	0.89	1.08	64.74
Ampelisca	5.00	3.50	↓	0.78	0.98	1.06	65.80
Mediomastus fragilis	1.83	6.71	↑	0.78	0.86	1.06	66.85
Nemertea	4.08	2.29	↓	0.72	0.97	0.98	67.83
Notomastus latericeus	4.33	1.64	↓	0.67	0.72	0.90	68.73
Abra alba	0.42	4.93	↑	0.60	0.70	0.81	69.55
Ampharete	2.75	1.36	↓	0.58	0.73	0.79	70.34
Aequipecten opercularis	3.08	3.43	↑	0.56	1.07	0.76	71.10
Goniada maculata	3.25	4.57	↑	0.55	0.96	0.74	71.84
Unciola crenatipalma	1.75	3.79	↑	0.54	0.86	0.74	72.58
Poecilochaetus serpens	2.75	0.79	↓	0.54	0.62	0.73	73.31
Pilumnus hirtellus	0.17	4.86	↑	0.50	1.19	0.68	73.99
Lagis koreni	2.83	2.29	↓	0.48	0.73	0.65	74.64
Nephtys	2.17	1.93	↓	0.44	0.51	0.60	75.25
Pholoe inornata	1.17	3.00	↑	0.42	0.90	0.56	75.81
Eunereis longissima	0.75	2.86	↑	0.40	0.86	0.54	76.35
Spirobranchus	1.92	1.64	↓	0.40	0.73	0.54	76.90
Jasmineira elegans	0.75	2.36	↑	0.39	0.69	0.53	77.43
Nassarius reticulatus	0.33	3.14	↑	0.38	0.82	0.51	77.94
Ampharete finmarchica	1.83	0.79	↓	0.36	0.69	0.48	78.42
Nephtys hombergii	0.75	2.36	↑	0.35	0.91	0.47	78.90
Schistomeringos rudolphii	1.92	0.64	↓	0.35	0.74	0.47	79.37
Upogebia deltaura	0.92	1.64	↑	0.32	0.85	0.43	79.80
Myrianida	0.58	2.50	↑	0.32	1.20	0.43	80.23

4.4 Conclusions & Discussion

In their early study of *S. spinulosa* reefs in the Bristol Channel, George and Warwick (1985) recorded a total of 88 taxa from 24 0.07m^2 Day grab samples supplemented by 6 semi-quantitative naturalist dredge samples. The average number of taxa associated with *S. spinulosa* reefs in the North Sea ranges from 22 to 60, based on observations from between 5 and 44 0.1 m^2 grab samples (Rees et al. 1999; Hendrick 2007). An average of 56 taxa, and a total of 336, were identified in association with the Hastings Shingle Bank reefs in this study from 44 0.1m^2 Hamon grab samples, indicating that the species richness documented at this site is broadly comparable to other *S. spinulosa* reefs in the UK.

The gravelly deposits in the Hastings Shingle Bank area are known to support a diverse macrofaunal community with the average number of species typically ranging from 29-71 per 0.1m^2 Day grab sample (Rees et al. 1999). Despite the high richness of sedimentary deposits in this area, species richness (S) was found to be higher, on average, in samples taken from *S. spinulosa* reefs than samples taken from adjacent sedimentary habitats. The increase in species richness was however, only significant where reefs had developed on sandy gravel (sG) deposits, where the average number of species increased by 55 % (**Table 4.8**). Increases of a similar magnitude were observed in reefs sampled from all other sediment types, with the exception of muddy sandy gravel where the average number of species only increased by 18 %, but none of these apparent differences were found to be statistically significant. Like species richness (S), macrofaunal abundance (N), biomass (B) and diversity (Margalef's d') were found, on average, to be higher in grab samples collected from *S. spinulosa* reefs than in those collected from adjacent sedimentary habitats (**Table 4.8**) although these increases were again only statistically significant in a small number of cases. The variance in all of the aforementioned community descriptors is high both on and off the reefs (see **Figures 4.1 – 4.3**) and it is possible that this is masking the true influence that the reefs are having on macrofaunal communities at Hastings Shingle Bank. It is likely that the influence of high variability was further exacerbated by the low sample replication in some sediment classes (**Table 4.1**). Hence any future work in this area would benefit from a more comprehensive sampling regime.

Table 4.8 Summary of the effect of *Sabellaria spinulosa* reefs on macrobenthic community descriptors, showing the average value for each descriptor calculated for reef and non-reef samples taken in different sediment types. Statistically significant reef effects are depicted by upward arrows for enhancements and downward facing arrows for reductions.

Community Descriptor	**Sandy Gravel**			**Muddy Sandy Gravel**			**Gravelly Sand**			**Gravelly Muddy Sand**			**Sand**		
	Non-Reef	**Reef**	**Reef Effect**	**Non-Reef**	**Reef**	**Reef Effect**	**Non-Reef**	**Reef**	**Reef Effect**	**Non-Reef**	**Reef**	**Reef Effect**	**Non-Reef**	**Reef**	**Reef Effect**
No. Species	34.5	53.7	↑	47.7	56.4	~	34.2	57.3	~	46.8	72.8	~	19.75	39.25	~
Abundance	98.2	226.8	↑	194.7	563.4	↑	75.4	204	↑	309	949.8	~	58	181.75	~
Biomass	6.9	14.4	~	17.9	39.5	↑	8.1	11.1	~	21.2	76.7	~	6.4	14.5	~
Margalef's d'	7.5	10	~	8.9	9.2	~	7.7	10.6	~	8.1	10.7	~	4.7	7.5	~
Pielou's Evenness	0.87	0.77	↓	0.79	0.57	↓	0.87	0.77	~	0.64	0.51	~	0.88	0.75	~
Shannon Weiner's H'	2.9	3	~	3	2.2	↓	2.9	3.1	~	2.4	2.2	~	2.1	2.7	~
Simpson's 1-λ	0.90	0.87	~	0.89	0.67	↓	0.91	0.89	~	0.76	0.63	~	0.88	0.84	~
Taxonomic Distinctness Δ*	89.2	90.6	~	88.8	91.5	↑	89.9	88.7	~	91.5	92.3	~	83.7	89.8	~
Avg Taxonomic Distinctness Δ+	88.7	88.5	~	87.9	88.6	↑	90.6	88.8	~	88.2	88.8	~	82.6	87.5	~
Variation in Taxonomic Distinctness λ+	253.4	256.6	~	261.7	269.4	~	251.9	259.4	~	275.3	269.9	~	272.7	282.3	~
Community composition	~	~	Non detected	~	~	Increase in *Pisidia longicornis* abundance	~	~	Non detected	~	~	Non detected	~	~	Non detected
Beta Diversity	59	53	↓	50	48	~	58	46	↓	48	42	~	57	52	↓

Species accumulation curves constructed for all samples taken on and off the reef (**Figure 4.5**) demonstrates that the asymptote of the curves has not been reached in either habitat, and hence more samples will identify more species associated with both reef and sedimentary habitats and it is unclear which habitat supports the greatest diversity of macrofauna. The species accumulation curve for *S. spinulosa* reefs is steeper than that for sedimentary habitats which is indicative of a habitat that supports a higher species richness, however, differences in the underlying species abundance distribution may also be driving this difference in the accumulation curves (Lande et al. 2000). The reduction in between-sample variance, or beta diversity, observed in reef habitats (**Table 4.8**) would explain the difference in the species accumulation curves and furthermore, would suggest that there is a high likelihood of the curves intersecting if more samples were to be added (Lande et al. 2000).

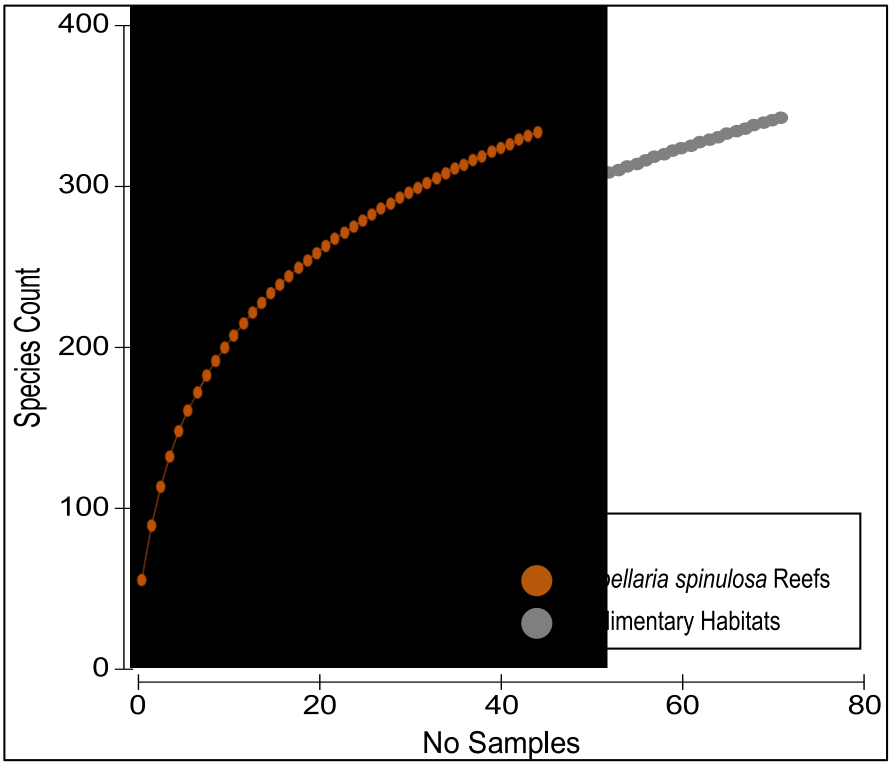


Figure 4.5 Species accumulation curves for samples taken from *Sabellaria spinulosa* reefs (red) and from adjacent sedimentary habitats (grey), across all substratum types included in these analyses (sG, msG, gS, smS and S).

Despite the high variance and low replication in some sediment types, significant reef effects were detected, most notably in reefs occurring on muddy sandy gravels. The abundance and biomass of associated macrofauna was found to be enhanced significantly by the presence of the reefs, whilst species richness remained unchanged and species equitability and diversity were found to decrease in the presence of the reefs. The composition of the macrofaunal community associated with *S. spinulosa* reefs occurring on muddy sandy gravels was also found to be significantly different, leading to a small increase in taxonomic distinctness. All of these reef effects can be explained by the very high dominance of the long clawed porcelain crab, *Pisidia longicornis* which was present at nearly eight times the density found in adjacent sediments. The ecological significance of such high abundances of this species are as yet unclear, although *P. longicornis* is known to be a favoured prey item of many demersal fish species (Lopezjamar et al. 1984; Reubens et al. 2013c). That the influence of *S. spinulosa* reefs has such a pronounced effect on *P. longicornis* where the reefs occur on muddy sandy gravel is in part a reflection of the preferred environmental niche of this species. *P. longicornis* is a crevice dwelling species often found in mixed sediments and bryozoan turfs where there are numerous suitable refugia. It should be noted that increases in the abundance of this species were observed across all sediment types in the presence of *S. spinulosa* (**Table 4.9**) and it is likely such increases would be statistically significant if the study were to be repeated with a greater degree of sample replication.

Table 4.9 The average abundance of the long clawed porcelain crab, *Pisidia longicornis*, on and off *Sabellaria spinulosa* reefs sampled from a range of sediments in the eastern English Channel.

	Sandy Gravel		Muddy Sandy Gravel		Gravelly Sand		Gravelly Muddy Sand		Sand	
	Non-Reef	Reef	Non-Reef	Reef	Non-Reef	Reef	Non-Reef	Reef	Non-Reef	Reef
Average *Pisidia longicornis* abundance ($0.1m^2$)	16	47	47	360	3	32	133	613	2	28

An increase in the overall macrofaunal abundance was observed on reefs sampled from sandy gravel, muddy sandy gravel and gravelly sand habitats (**Table 4.8**). A similar enhancement of macrofaunal abundance, or macrofaunal density, has been observed in the presence of *Lanice conchilega* beds (Rabaut et al. 2007), dense aggregations of *Pygospio elegans* (Bolam and Fernandes 2003), kelp holdfasts (Hauser et al. 2006) and *Modiolus modiolus* beds (Ragnarsson and Burgos 2012) indicating that this type of biological enhancement is fairly common amongst biogenic habitat modifiers. Although enhancing macrofaunal abundance may not trigger the same conservation response as enhancing biodiversity, the ecological significance is likely to be as important, if not more so. That macrofaunal species including, predation-prone mobile taxa, are able to inhabit *S. spinulosa* reefs in higher densities than adjacent sedimentary habitats indicates that the reefs provide additional refugia, protecting these macrofaunal species from predation. It is also possible however, that the increased abundance of macrofauna is linked to an increase in the availability of food. The polychaetes themselves produce faecal matter which may contribute to the diet of some members of the community and the reef structures may also be acting to trap further particulate matter and plankton, by exerting a degree of drag on the surrounding water. It is perhaps most likely though, that the reefs are increasing the volume of available habitat. Generally, macrofaunal species only inhabit the top 5-10 cm of sedimentary deposits (Thorson 1957; Holme 1964; Barnett and Hardy 1967) and since the reefs in this area are estimated to be at least 5-10 cm in height (Pearce et al. 2007) their presence could feasibly double the habitat available to macrofaunal species. Whatever the cause of the increased density of macrofaunal species, is can be surmised that the reefs are acting as spatially efficient concentrations of species that would otherwise occur across a wider area, and in some instances this translates to an increase in biomass and productivity and the associated ecosystem services that this brings (Norling et al. 2007).

Beta-diversity is arguably the most appropriate measure of biodiversity at the habitat level, since we would anticipate a more biodiverse habitat having a higher level of variation between samples than a less biodiverse habitat (Anderson et al. 2006; Bevilacqua et al. 2012). This study has shown that the beta-diversity of *S. spinulosa* reefs is comparable to muddy sandy gravel and gravelly sand habitats but that it is significantly lower than sandy gravel, gravelly muddy sand and sand habitats. This again points to a stable and consistent habitat which supports a rich macrofaunal community that is very similar in many respects to that found in association with mixed substrata in the eastern English Channel (Rees et al. 1999).

Dense polychaete aggregations have generally been found to support a different macrofaunal community to that found in adjacent sedimentary habitats, and the presence of the polychaete tubes stabilises and enhance species diversity (Bolam and Fernandes 2003; Rabaut et al. 2007; Van Hoey et al. 2008). It has long been assumed that *S. spinulosa* reefs have a similar structuring effect on the macrobenthos (Holt et al. 1998; Jones et al. 2000; Hendrick and Foster-Smith 2006). Where *S. spinulosa* reefs occur on impoverished sediments of the Bristol Channel, there is evidence that they significantly alter the macrofaunal community composition and dramatically increase species richness (George and Warwick 1985). In contrast, this study has demonstrates that the *S. spinulosa* reefs on Hastings Shingle Bank have no discernible effect on the composition of the macrofauna, although they do influence the relative abundance of species where they occur on muddy sandy gravels. *S. spinulosa* reefs have not been found to increase biodiversity and in fact have been found to decrease beta-diversity where they occur on certain sediment types. Overall the effect of *S. spinulosa* reefs on sedimentary habitats can be surmised as an increase in the density of macrofaunal species that would otherwise be present over a wider area, leading to a significant increase in macrofaunal abundance and / or species richness where they occur on certain habitat types.

The six-fold increase in the abundance of the invasive American slipper limpet, *Crepidula fornicata*, in the presence of *S. spinulosa* reefs, at Hasting Shingle Bank, is particularly noteworthy. This is the first record of this association, and the first indication that this habitat could potentially be vulnerable to the impacts of this invasive non-native species (Tillin et al. 2010). *Crepidula fornicata* have caused significant mortalities on *Mytilus edulis* and *Ostrea edulis* beds where their presence caused a fundamental change in the substratum (Barnes et al. 1973; Thieltges et al. 2006). Faeces and pseudofaeces rapidly accumulate where *C. fornicata* is found in high densities, turning a hard substratum into a soft sediment one. This change in the nature of the substratum has been found to inhibit the settlement of native oysters (Barnes et al. 1973) and could have a similar effect on *S. spinulosa*.

This study presents a snapshot of a *S. spinulosa* reef community at one location at one point in time. There are likely to be spatial variations in the influence that *S. spinulosa* reefs have on macrofaunal communities and the relationships identified here may also vary over-time. The Hastings Shingle Bank is an active aggregate extraction site, and whilst the reefs included in this study were not being impacted directly by extraction activities at the time of sampling, they all have been impacted by these activities in the past and are likely to be influenced by increased turbidity associated with the dredging activities at the site on an ongoing basis. The prevalence of *S. spinulosa* reefs around the perimeter of the active dredge area indicates that the impacts of heightened turbidity levels are unlikely to be having a detrimental impact on *S. spinulosa* itself. However, it is possible, if not likely, that the high turbidity levels associated with aggregate extraction are having some influence on the fauna associated with the reefs. That the influence of *S. spinulosa* reefs on macrofauna described in this study is contrary to many earlier assertions suggests that further work is necessary to clarify the ecosystem functions of this habitat fully. The incorporation of sampling from a reef that is not subject to anthropogenic disturbance, or extreme levels of natural disturbance, should be a priority for future work in this field.

This study raises questions about the perceived link between *S. spinulosa* reefs and enhanced biodiversity which represents a very real challenge to biodiversity protection legislation. *S. spinulosa* reefs can be considered as concentrations of species, often in elevated densities, that would likely be present in the wider area without them. It would be spatially efficient to protect these habitat types if the aim of conservation efforts was to preserve the range of species typically found in sedimentary habitats. However, the highest value of *S. spinulosa* reefs to humans probably lies in the enhancement of biomass and productivity that *S. spinulosa* reefs provide where they occur in certain habitat types but the legislative structures to support these arguments, as well as the scientific evidence base, remains poorly developed.

Chapter 5. *Sabellaria spinulosa* reefs as a food source for fish

5.1 Introduction

Biogenic habitats supporting rich faunal assemblages have been found to have an influence on the feeding behaviour of local fish populations and to provide important food resources (Jiang and Carbines 2002; Bender et al. 2013; Rabaut et al. 2013). Similarly, there are indications that *Sabellaria spinulosa,* and the fauna associated with the habitat it creates, may provide an important food source for higher trophic levels. The association between the pink shrimp, *Pandalus montagui,* and *S. spinulosa* reefs reported by Warren and Sheldon (1967) is thought to be based on a predator-prey relationship as has been observed in their Russian congeners (Chuhukalo and Shebanova 2008). The shore crab, *Carcinus maenus*, and the shanny, *Lipophrys pholis,* have been found to prey on sabellariids in the UK (Taylor et al. 1962; Bamber and Irving 1997) although the importance of *S. spinulosa* in the diet of these species has never been formally investigated. Holt et al. (1998) also suggest that flatfish are likely to feed on *S. spinulosa* which could explain the association between commercially important fisheries and *S. spinulosa* reefs (personal communications with fishermen) although this also has yet to be confirmed by empirical evidence. Fauna known to be associated with *S. spinulosa* reefs such as the long clawed porcelain crab, *Pisidia longicornis* (**Chapter 4**) can also be an important prey item in the diets of some demersal fish species (Lopezjamar et al. 1984).

A considerable amount of research has been carried out on the diet of individual fish species, although efforts have primarily focused on species targeted by commercial fisheries (Hamerlynck and Hostens 1993; Burke 1996; Bromley et al. 1997; Greenstreet et al. 1998; Cabral 2000; Darnaude et al. 2001; Pinnegar et al. 2003; Mollmann et al. 2004; Andersen et al. 2005; Carruthers et al. 2005; Trenkel et al. 2005; Stafford et al. 2007; De Raedemaecker et al. 2011). Much less is known about the diet of demersal fish that have no commercial value (Creutzberg and Witte 1989; Van der veer et al. 1990; King et al. 1994; Power and Attrill 2002; Vasconcelos et al. 2004). The aim of this chapter is to investigate the diet of demersal fish associated with *S. spinulosa* reefs and to determine whether the fauna associated with the reef habitats, including *S. spinulosa* itself, are important prey items for this component of the marine food web.

Sabellaria spinulosa reefs are listed under Annex I of the EU Habitats Directive (EC 2013) and in the OSPAR list of threatened and declining habitats (OSPAR 2008), and hence targeted destructive sampling of this habitat is not permissible in the UK (Gubbay 2007). A limited amount of incidental trawl sampling of *S. spinulosa* reefs was carried out during the East Coast Regional Environmental Characterisation (REC) surveys, where new reefs were identified in areas where there were previously no records of them occurring (Limpenny et al. 2011). Fish were retained from all trawls containing a large volume of *S. spinulosa* tubes (>20 l) and the stomach contents were analysed in order to assess the importance of this habitat in the diet of demersal fish. It was not possible to retain fish from trawl samples taken from adjacent habitats as this sampling was not part of the planned survey cruise and hence the time and resources needed to process and store the samples were very limited. These samples nevertheless can provide important insights into the feeding behaviour of fish associated with *S. spinulosa* reefs, especially in the absence of any possibility of a targeted survey.

The aim of this chapter is to investigate the diet of demersal fish associated with S. spinulosa reefs and to determine whether the fauna associated with the reef habitats, including S. spinulosa itself, are important prey items for this component of the marine food web.

The aim of this chapter is to determine whether or not demersal fish feed on *S. spinulosa* reefs and to investigate the commonalities between the diets and feeding behaviours of fish species associated with the reefs. To that end, the following hypotheses have been tested:

Hypothesis B

H_{0B}: *Sabellaria spinulosa* and abundant reef fauna (e.g. *Pisidia longicornis*) are not present in the guts of demersal fish sampled from *S. spinulosa* reefs.

H_{1B}. *S. spinulosa* and abundant reef fauna (e.g. *Pisidia longicornis*) are dominant in the guts of demersal fish sampled from *S. spinulosa* reefs.

Hypothesis C

H_{0B}: The diet of demersal fish sampled from *S. spinulosa* reefs is comparable to published records

H_{1B}. The diet of demersal fish sampled from *S. spinulosa* reefs is markedly different from published records

Hypothesis D

H_{0C}: There is no structure in the diets of demersal fish associated with *S. spinulosa* reefs

H_{1C}: There are distinct feeding groups or guilds amongst the demersal fish associated with *S. spinulosa* reefs

5.2 Methodology

5.2.1 Sample Collection and Processing

Scientific beam trawl (2 m) samples were collected from 21 locations within the *Sabellaria spinulosa* reefs identified in the East Coast REC study area (**Figure 2.11**). From these trawl samples a total of 287 fish, belonging to 16 species, were retained. A separation between the stomach and the intestine of fish is often difficult to distinguish and in many species is entirely absent (Beyst et al., 1999), therefore their entire gastrointestinal tract was removed and opened before being fixed in a formal-saline solution and preserved in 70% Industrial Methylated Spirit (IMS). All food items in the entire gastrointestinal tract were identified to the highest level of taxonomic distinction possible, counted and weighed. Owing to the varying degrees of digestion, not all prey items could be identified to species level. Consequently, some taxa were recorded at genus level or lower, and heads of prey were used to determine the abundance of prey items. Despite the varying taxonomic resolution of prey taxa, the data were not aggregated so as to retain sufficient resolution to facilitate comparisons with *S. spinulosa* reef fauna.

Ontogenetic shifts in diets are frequently reported in fish species that have been well studied (Cardinale 2000; Shaheen et al. 2004). However, the diet of many of the species sampled here have not been comprehensively documented, if at all. Fish were therefore categorised according to their developmental stage (juvenile or adult) based on published records of length at maturity (L_m) as detailed in **Table 5.1**. As no record of the length at maturity could be identified for the long-spined sea scorpion, *Tauralus bubalis*, the developmental stage of individuals included in this study was estimated based on the maximum length reported for this species (**Table 5.1**).

Table 5.1 Length at maturity (L_m) of demersal fish used in this study to separate juveniles and adults and the associated source. Where length at maturity ranges were reported rather than single values, the middle value was used and ranges are reported below in parentheses.

Common Name	Scientific Name	L_m (mm)	Source
Butterfish	*Pholis gunnellus*	95 (90-100)	(Cattrijsse and Hampel 2000)
Dover Sole	*Solea solea*	303	(Froese and Pauly 2011)
Dab	*Limanda limanda*	260	(Froese and Pauly 2011)
Northern Rockling	*Ciliata septentrionalis*	62	(Froese and Pauly 2011)
Pogge	*Agonus cataphractus*	100	(Cattrijsse and Hampel 2000)
Dragonet	*Callionymus lyra*	174	(Froese and Pauly 2011)
Lesser Weever	*Echiichthys vipera*	95	(Creutzberg and Witte 1989; Vasconcelos et al. 2004)
Bull rout	*Myoxocephalus scorpius*	225 (150-300)	(Froese and Pauly 2011)
Whiting	*Merlangius merlangus*	29 (28-30)	(Froese and Pauly 2011)
Sea scorpion	*Taurulus bubalis*	N/A*	
Sand Eel	*Hyperoplus lanceolatus*	130 (110-150)	(Froese and Pauly 2011)
Poor Cod	*Trisopterus minutus*	134	(Froese and Pauly 2011)
Bib	*Trisopterus luscus*	216	(Froese and Pauly 2011)
Plaice	*Pleuronectes platessa*	308	(Froese and Pauly 2011)
Dogfish	*Scyliorhinus canicula*	570	(Froese and Pauly 2011)
Flounder	*Platichthys flesus*	223	(Froese and Pauly 2011)

*Specimens assumed to be adults based on their large size (100-140mm) relative to maximum size (175mm) reported by (Wheeler 1978)

5.2.2 Dietary Description

To evaluate the importance of each prey taxon in the diet, a number of standard prey metrics were calculated, each of which provides a different insight into the feeding habits of the fish (Hyslop 1980; Marshall and Elliott 1997). Numerical abundance (N) provides information regarding feeding behaviour whilst weight (W) is thought to reflect the dietary nutritional value and occurrence (O) provides insights into the population-wide feeding behaviour (Hyslop 1980; Macdonald and Green 1983; Cortes 1997). Each prey taxa was counted, and weighed, and expressed as a percentage of the total number, or weight, of prey in the individual. From this the total percentage dietary composition was calculated, which removes some of the bias associated with fish size (Cortes 1997). The index of relative importance (IRI) also known as the food importance index, was also calculated in accordance with Pinkas et al. (1971):

$$IRI = (\%\,N + \%\,W)\,\%O$$

The index of relative importance calculates the number of stomachs that contained the prey taxa relative to the total number of stomachs that contained prey items and in this way, the importance of small prey items taken in large numbers is not overestimated. Because of the difficulties experienced when comparing IRI values among prey types (Cortes 1997), the IRI values for each specific prey category (IRIi) were then converted to % IRI:

$$\%IRI = \left(\frac{IRIi}{\sum^{n}_{i=1} IRI_i} \right) 100$$

where n is the total number of food categories considered. This index provides a single comprehensive measure of diet, is less biased than weight, frequency or number alone, and facilitates comparisons to other studies (Cortes 1997). Finally, the Shannon-Wiener prey diversity index (H') and Pielou's J', an evenness measure, were computed to provide an indication of niche breadth (Marshall and Elliott 1997).

5.2.3 Dietary Trend Analysis

Multivariate analysis of the gut content data were used to investigate the trends in feeding which exist amongst the fish species sampled from *Sabellaria spinulosa* reefs in the southern North Sea, using the PRIMER v6 software package (Clarke and Warwick 2001; Clarke and Gorley 2006). The gut content data (abundance) was standardised and averaged by fish species before being used to construct a resemblance matrix based on Bray-Curtis similarity. The resulting resemblance matrix was used to construct a group average sorting dendrogram and a SIMPROF test was applied to identify statistically significant clusters within the data, testing the null-hypothesis that there is no structure in the diets of these fish species (Clarke et al. 2008). A SIMPER test was then carried out on the same data to ascertain the prey items contributing most to the similarities within the feeding groups identified using the SIMPROF test and the differences between them.

5.3 Results & Discussion

5.3.1 Prey Choice of Demersal Fish Species Associated with Sabellaria spinulosa Reefs

It is evident from **Table 5.2** and **Figure 5.1** that there is a significant positive correlation between the number of individuals examined and the number of prey items identified for each fish species. Whilst no formal assessment of sampling sufficiency has been carried out as part of this study, it is very unlikely that sufficient samples have been taken to fully assess the prey choices of all 16 species. However, since targeted destructive sampling of *S. spinulosa* reefs is not permissible due to its conservation status serendipitous sampling, as was undertaken here, is the only possibility of assessing the trophic interactions related to this habitat. For this reason, all fish retained from *S. spinulosa* reefs in the East Coast REC study site have been subjected to gut content analysis and, where possible, all of the data are included in the subsequent analyses.

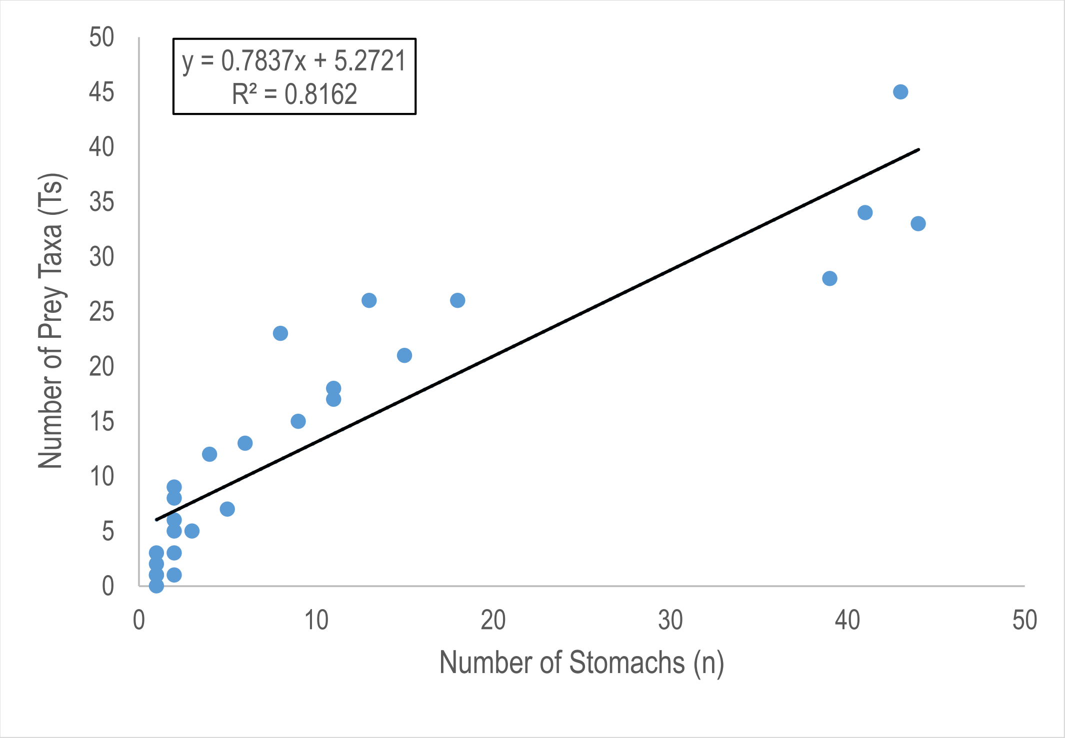


Figure 5.1 Regression plot showing the relationship between the numbers of stomachs examined (n) and the total number of prey taxa (Ts) identified for each fish species.

Table 5.2 Number of each fish (n) sampled from *Sabellaria spinulosa* reefs in the East Coast REC study site, in the southern North Sea in 2009, with an indication of the fish size interval classes (total length, L_T) and the developmental stages based on published records of length at maturity (L_m) as listed in **Table 5.1**. Also shown are a range of feeding indices calculated from gut content data: Total prey taxa (Ts), mean prey taxa (S) abundance (N) and weight (W) in g Wet weight per fish and two measures of niche breadth (Shannon-Wieners diversity H' and Pielou's J' an evenness measure).

Species	Common Name	Developmental Stage	n	L_T Range (mm)	Total Prey Taxa (Ts)	Mean Prey / Individual			Niche Breadth	
						S	N	W	H'	J'
Pholis gunnellus	Butterfish	Adult	44	100-180	33	3.3	7.1	0.15	2.14	0.61
		Juvenile	2	70	5	3.5	8	0.01	1.32	0.82
Solea solea	Dover Sole	Adult	4	310-340	12	4	20.3	0.53	1.6	0.67
		Juvenile	41	120-300	34	2.7	8	0.34	2.24	0.63
Limanda limanda	Dab	Adult	2	260-370	6	3	22.5	2.72	1.29	0.72
		Juvenile	43	90-250	45	3.7	12.8	0.61	2.3	0.6
Ciliata septentrionalis	Northern Rockling	Adult	39	70-120	28	2.6	3.5	0.09	2.47	0.74
		Juvenile	1	60	3	3	3	0.01	~	~
Agonus cataphractus	Pogge	Adult	13	100-140	26	3.3	6.8	0.14	2.7	0.83
		Juvenile	15	70-90	21	3.3	8.1	0.14	2.57	0.84
Callionymus lyra	Dragonet	Adult	6	180-210	13	2.8	4.2	0.26	2.23	0.87
		Juvenile	18	70-160	26	2.9	7.3	0.15	2.73	0.84
Echiichthys vipera	Lesser Weever	Adult	9	100-140	15	4	11.3	0.24	2.18	0.79
		Juvenile	11	80-90	17	3.3	9.4	0.16	2.1	0.74
Myoxocephalus scorpius	Bull rout	Adult	1	270	0	0	0	0	~	~
		Juvenile	11	60-210	18	3.4	4.5	1.15	2.57	0.89
Merlangius merlangus	Whiting	Adult	1	310	1	1	4	0.01	~	~
		Juvenile	8	130-250	23	4.9	12.5	0.36	2.54	0.81
Tauralus bubalis	Sea scorpion	Adult	5	100-140	7	2	3.2	0.45	1.59	0.82
Hyperoplus lanceolatus	Sand Eel	Adult	2	170-190	3	1.5	7	0.09	0.83	0.75
		Juvenile	2	80-100	1	1	400	0.1	~	~
Trisopterus minutus	Poor Cod	Adult	3	140-160	5	2.3	9	0.22	1.51	0.94
Trisopterus luscus	Bib	Juvenile	2	140-160	9	5.5	34.5	0.81	1.5	0.68
Pleuronectes platessa	Plaice	Juvenile	2	190-220	8	4	11	0.69	1.87	0.9
Scyliorhinus canicula	Dogfish	Juvenile	1	120	2	2	4	0.22	~	~
Platichthys flesus	Flounder	Adult	1	250	1	1	7	2.68	~	~

Pholis gunnellus – Butterfish

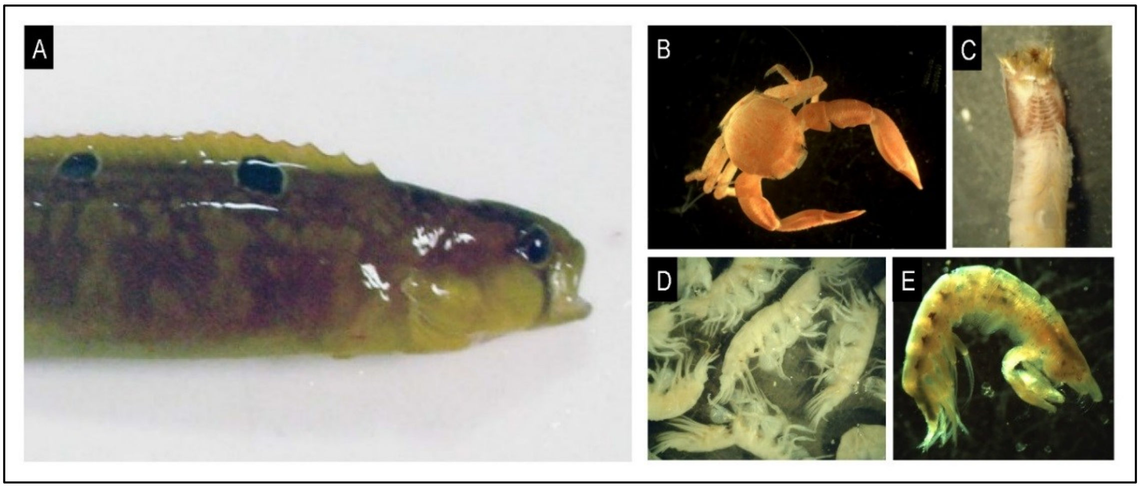


Figure 5.2 Photographs of the butterfish, *Pholis gunnellus* (A) and four of the main prey items identified in the stomach contents of 46 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) The long clawed porcelain crab, *Pisidia longicornis*, C) the Ross worm, *Sabellaria spinulosa*, D) various amphipods and E) the amphipod *Gammaropsis maculata.*

The butterfish*, Pholis gunnellus*, is a small eel-shaped fish (**Figure 5.2**) most commonly reported from rocky shores but also found at depths of up to 100 m (Dipper 2001; Kay and Dipper 2009; Shorty and Gannon 2013). *P. gunnellus* has been reported in high densities in association kelp beds and reef habitats where it is thought they seek refuge from predators, such as the grey Heron *Ardea cinerea* and the otter, *Lutra lutra* (Sawyer 1967; Carss and Elston 2003; Kay and Dipper 2009). The butterfish has a small head with a protruding lower jaw, an upturned mouth and small conical teeth (Sawyer 1967). It has been postulated that the diet and feeding behaviour of fish can, to some extent, be predicted based on their morphology (Elliott et al. 2002). The upturned mouth and conical teeth of *P. gunnellus* indicate that it has a manipulative mode of feeding and is most likely an ambush predator (Wootton 1990; Elliott et al. 2002). The small mouth of *P. gunnellus* will nevertheless mean that this species is restricted to small prey items.

There is very little published data on the diet of *P. gunnellus* but this species has previously been reported to feed primarily on amphipod crustaceans and isopods (Sawyer 1967). However, some fish guides report a more generalist diet including a variety of small invertebrates and fish eggs (Wheeler 1978; Dipper 2001). The diet of *P. gunnellus* individuals included in this study is summarised overleaf in **Table 5.3**.

Table 5.3 The relative importance of all prey taxa averaged across adult *Pholis gunnellus* (n=44) and juvenile *P.gunnellus* (n=2) in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	%N	%W	%O	IRI	%IRI
Pisidia longicornis	45.19	58.70	73	7556	67.96
Sabellaria spinulosa	16.67	17.02	75	2527	22.73
AMPHIPODA	7.69	6.31	32	445	4.01
CRUSTACEA	3.53	9.35	23	293	2.63
DECAPODA	3.85	3.37	14	98	0.89
Podoceridae	4.81	0.28	16	81	0.73
Gammaropsis maculata	3.53	0.38	9	36	0.32
GASTROPODA	1.28	0.07	9	12	0.11
Galathea intermedia	1.28	1.33	5	12	0.11
Melitidae	1.28	0.13	7	10	0.09
Caprellidae	1.28	0.10	7	9	0.08
Galathea	0.64	0.89	5	7	0.06
POLYCHAETA	0.96	0.08	5	5	0.04
Stenothoidae	0.64	0.06	5	3	0.03
Mytilidae	0.64	0.02	5	3	0.03
OSTRACODA	0.64	0.00	5	3	0.03
Amphilochidae	0.96	0.06	2	2	0.02
Polynoidae	0.32	0.63	2	2	0.02
Sthenelais	0.32	0.44	2	2	0.02
Eualus pusiolus	0.32	0.35	2	2	0.01
Cancer	0.32	0.17	2	1	0.01
Iphimedia minuta	0.32	0.08	2	1	0.01
Plumulariidae	0.32	0.07	2	1	0.01
Stenothoe marina	0.32	0.03	2	1	0.01
NEMERTEA	0.32	0.02	2	1	0.01
OPHIUROIDEA	0.32	0.02	2	1	0.01
Pseudoprotella phasma	0.32	0.02	2	1	0.01
Hydroides norvegica	0.32	0.01	2	1	0.01
Pleustidae	0.32	0.01	2	1	0.01
Dyopedos monacanthus	0.32	0.00	2	1	0.01
Polinices	0.32	0.00	2	1	0.01
Corophiidae	0.32	0.00	2	1	0.01
Pomatoceros lamarcki	0.32	0.00	2	1	0.01

Juveniles

Prey Taxa	%N	%W	%O	IRI	%IRI
Podoceridae	50.00	10.65	100	6065	36.09
Abludomelita obtusata	25.00	50.46	100	7546	44.90
AMPHIPODA	12.50	17.59	50	1505	8.95
Sabellaria spinulosa	6.25	18.06	50	1215	7.23
Gammaropsis	6.25	3.24	50	475	2.82

Crustaceans made up the majority of the prey consumed by *P. gunnellus*, in terms of both biomass (%W) and abundance (%N) by both adults and juveniles with polychaetes accounting for most of the remainder of the diet (**Table 5.3**). An ontogenetic shift is evident in the diet of this species with adults feeding primarily on the long clawed porcelain crab (67.96 IRI%) whilst the juveniles feed on amphipods including *Abludomelita obtusata* (44.90 IRI%) and species belonging the family Podeceridae (36.09 IRI%). *Sabellaria spinulosa* was an important prey item in the diet in all of the *P. gunnellus* examined, although the relative importance was much higher in the diet of adults (22.73 IRI%) than in juveniles (7.23 IRI%).

Sabellaria spinulosa has not previously been recorded as a prey item for *P. gunnellus* (Sawyer 1967; Pinnegar 2009). The importance of *S. spinulosa* in the diet of *P. gunnellus* sampled from these southern North Sea reefs may therefore indicate that this habitat is providing a more accessible food source or one that provides a superior source of nutrition. Previous records of the diet of *P. gunnellus* also indicated a more restricted diet than is reported here (Sawyer 1967; Pinnegar 2009) indicating that *S. spinulosa* reefs could also be increasing the variety of prey items available to this species.

Both adult and juvenile *P. gunnellus* were found to be homogenous feeders with the two most important prey items occurring in the stomach contents of c.75% of adults and 100% of juveniles sampled from the *S. spinulosa* reefs. Alongside the two dominant prey items, a high number of rare prey items were identified in the diet of adult *P. gunnellus*, which is typical of a species exhibiting specialist feeding behaviour (Cortes 1997). Juveniles of the same species appear to have a more generalist diet with a more even spread of abundance across the prey items identified (J’ = 0.82). However, given the small number of stomachs examined (n=2) it is very likely that rare prey items will have been under sampled.

Solea solea – Dover Sole

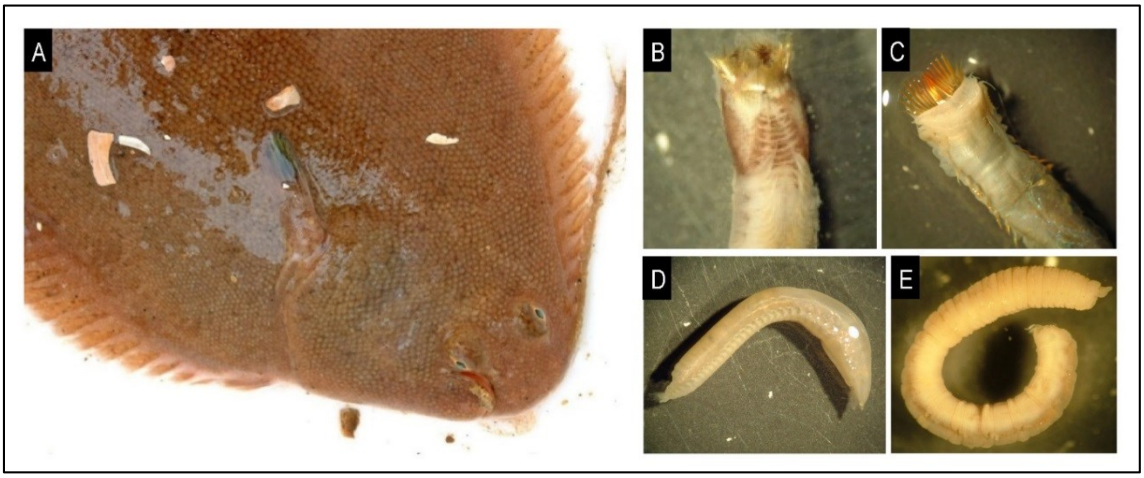


Figure 5.3 Photographs of the Dover sole, *Solea solea* (A) and four of the main prey items identified in the stomach contents of 45 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the Ross worm, *Sabellaria spinulosa*, C) the Pectinariid worm *Lagis koreni* D) the Opheliid worm *Ophelia borealis* and E) the Capeteliid worm *Notomastus latericeus.*

The Dover sole, *Solea solea,* is a large, distinctive flatfish with a smooth body and rounded head (**Figure 5.3**). It is widespread around UK coasts and prefers muddy/sandy areas where it buries itself during the day and where its preferred prey, nereid polychaetes or rag worms, are most abundant (Cabral 2000; Kay and Dipper 2009). Dover sole have also been reported to feed on other polychaetes, molluscs and crustaceans (Cabral 2000; Darnaude et al. 2001; Rijnsdorp and Vingerhoed 2001; Amezcua et al. 2003; De Raedemaecker et al. 2011). *S. solea* has a sub-terminal mouth which helps it find prey within the sediments (El Bakery 2014). Both the upper and lower jaws of *S. solea* are edentulous, a feature normally only observed in herbivorous fish (Gerking 1994). However, *S. solea* have teeth on both the upper and lower surface of the buccal cavity which they use to hold, grasp and tear their food (El Bakery 2014). Dover sole have a small mouth relative to their head and this is reflected in the size of the preferred prey of infaunal polychaetes.

Table 5.4 The relative importance of all prey taxa averaged across all specimens of *Solea solea* studied (n=45) in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	%N	%W	%O	IRI	%IRI
Lagis koreni	37.04	62.13	25	2479	34.35
Pectinariidae	17.28	24.00	50	2064	28.60
ACTINIARIA	24.69	6.52	50	1560	21.62
POLYCHAETA	6.17	2.47	50	432	5.99
Sabellaria spinulosa	6.17	1.37	50	377	5.23
Ampharetidae	1.23	1.54	25	69	0.96
Crangon crangon	1.23	0.88	25	53	0.73
Ampelisca spinipes	1.23	0.41	25	41	0.57
Crangonidae	1.23	0.26	25	37	0.52
DECAPODA	1.23	0.20	25	36	0.50
Mysella bidentata	1.23	0.14	25	34	0.48
Corophiidae	1.23	0.06	25	32	0.45

Juveniles

Prey Taxa	%N	%W	%O	IRI	%IRI
Sabellaria spinulosa	30.79	29.80	66	3990	66.39
POLYCHAETA	5.18	21.02	32	831	13.83
Pectinariidae	5.49	10.30	17	270	4.49
AMPHIPODA	22.87	1.12	20	468	7.79
Sthenelais boa	0.61	11.91	5	61	1.02
CRUSTACEA	4.27	3.03	10	71	1.19
Opheliidae	4.27	3.96	5	40	0.67
Notomastus	0.91	4.16	5	25	0.41
Atylus swammerdamei	8.54	0.54	12	111	1.84
Nereididae	0.61	3.33	5	19	0.32
Eunicidae	1.22	2.28	5	17	0.28
Sthenelais	0.30	3.02	2	8	0.13
MYSIDACEA	1.22	0.48	10	17	0.28
Crangon crangon	0.91	0.67	7	12	0.19
Gastrosaccus spinifer	1.22	0.48	7	12	0.21
Crangonidae	1.52	0.43	7	14	0.24
Echinocyamus pusillus	1.22	0.87	2	5	0.08
OPHIUROIDEA	1.52	0.10	7	12	0.20
Lagis koreni	0.61	0.55	2	3	0.05
Galathea intermedia	0.30	0.57	2	2	0.04
Crangon	0.61	0.23	5	4	0.07
Ophiura albida	0.61	0.37	2	2	0.04
Ampeliscidae	0.30	0.34	2	2	0.03
DECAPODA	0.61	0.05	5	3	0.05
Atylus	1.52	0.03	2	4	0.06
Schistomysis spiritus	0.30	0.11	2	1	0.02
Gammarellus homari	0.30	0.09	2	1	0.02
Gammarellus	0.30	0.08	2	1	0.02
Unciola crenatipalma	0.30	0.03	2	1	0.01
Pholoe baltica (sensu petersen)	0.30	0.01	2	1	0.01
Anaitides	0.30	0.01	2	1	0.01
GASTROPODA	0.30	0.01	2	1	0.01
Urothoe	0.30	0.00	2	1	0.01
Eumida	0.30	0.00	2	1	0.01

Juvenile *S. solea* consumed a diverse range of prey (n=34, H' = 2.24) including polychaetes, crustaceans, echinoderms and molluscs (**Table 5.4**). The majority of the prey taxa were rare, and the diet of juvenile *S. solea* was dominated by *S. spinulosa* (66.39 %IRI). The diet of adult *S. solea* showed similarities with the diet of juveniles, although the dominant prey was different. *Sabellaria spinulosa* was still an important prey in the diet of adults (5.23 IRI%) but there appears to be an ontogenetic shift towards pectinariid polychaetes including *Lagis koreni* (28.60 IRI% and 34.35 IRI% respectively).

The dominance of *S. spinulosa* in the diet of juvenile *S. solea* is reflected in the low evenness value (J' =0.63) and is indicative of specialist feeding behaviour (Cortes 1997). These results differ from earlier records of the diet of juvenile *S. solea* made by Dolbeth et al. (2008) who reported a smaller niche breadth (H' = 1.2) and a diet dominated by errant polychaetes, and Cabral (2000) who identified only 15 prey species in a much larger sample of stomachs (n=609), of which the amphipod crustacean *Corophium* spp. was most numerically dominant (I_N=56.8) and the nereid, *Hediste diversicolor* was most abundant in terms of biomass (I_W=57.9). This disparity in the feeding behaviour and prey preferences of juvenile *S. solea* indicates the presence of a behavioural shift in individuals associated with the *S. spinulosa* reefs in the East Coast REC study area.

The dominance of polychaetes in the diet of *S. solea* is consistent with other reports of the dietary preferences of this species (Cabral 2000; Rijnsdorp and Vingerhoed 2001; Dolbeth et al. 2008; De Raedemaecker et al. 2011) although this is the first record of this species feeding on *S. spinulosa.* Errant polychaetes such as nereids and nephtyds are typically reported as being the dominant prey of *S. solea* (Cabral 2000; Dolbeth et al. 2008) although as these records of the diet of *S. solea* are from estuarine environments it is possible that there is a nearshore / offshore shift in feeding behaviour reflecting prey abundances and availability.

***Limanda limanda* – Dab**

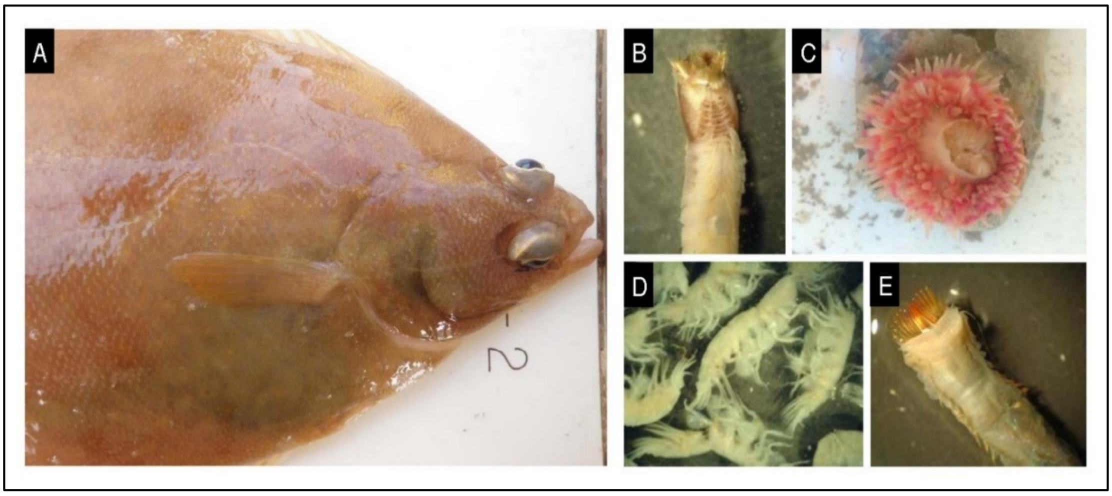


Figure 5.4 Photographs of the Dab, *Limanda limanda* (A) and four of the main prey items identified in the stomach contents of 45 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the Ross worm, *Sabellaria spinulosa*, C) a sea anemone, Actiniaria spp. D) some amphipod crustaceans and E) the pectinariid worm, *Lagis koreni.*

The dab*, Limanda limanda,* is the most abundant flatfish species in the North Sea (Daan et al. 1990). Its large eyes, small mouth gape (**Figure 5.4**) and ability to move quickly, reflect its visual feeding habits (Hinz et al. 2005). Dab has an unusual hunting behaviour, pouncing on and biting off parts of invertebrates protruding from the substratum such as mollusc siphons and polychaetes (Dipper 2001; Kay and Dipper 2009). *Limanda limanda* has also been found to be a highly opportunistic feeder, consuming a wide variety of fauna including echinoderms, fish, polychaetes and molluscs (Amezcua et al. 2003; Hinz et al. 2005; De Raedemaecker et al. 2011; Schueckel et al. 2011). The opportunistic nature of *L. limanda* is thought to have contributed to its success in the North Sea, where it adapts its feeding behaviour to capitalise on prey that have been exposed by bottom trawling (Kaiser and Ramsay 1997). Dab have small terminal mouths which do not protrude, limiting the size of prey they are able to catch and consume (Wheeler 1978; Dipper 2001)

Adult *L. limanda* utilized a small number of prey items (6 taxa) and showed a small niche breadth (H' = 1.29) in comparison to juveniles of the same species (H' =2.3), although this is likely to be at least partly attributable to the differing number of stomachs in each class (n = 2 and 43 respectively) (**Table 5.2**).

Table 5.5 The relative importance of all prey taxa averaged across adult (n=2) and juvenile (n=43) *Limanda limanda* in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*)), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	%N	%W	%O	IRI	%IRI
Ophiura ophiura	80.00	97.34	50	8867	88.67
Crangon crangon	6.67	0.37	50	352	3.52
Pisidia longicornis	4.44	1.14	50	279	2.79
ACTINIARIA	4.44	0.65	50	255	2.55
Crangon allmanni	2.22	0.49	50	136	1.36

Juveniles

Prey Taxa	%N	%W	%O	IRI	%IRI
Sabellaria spinulosa	40.62	29.69	68	4802	59.63
ACTINIARIA	20.22	27.52	46	2212	27.48
AMPHIPODA	11.48	0.99	22	274	3.40
Pectinariidae	4.01	5.78	20	191	2.37
DECAPODA	1.82	5.78	20	148	1.84
POLYCHAETA	1.82	3.73	22	122	1.51
Pisidia longicornis	2.55	1.48	22	88	1.10
Atylus swammerdamei	3.28	0.14	10	33	0.41
CRUSTACEA	1.46	0.39	17	31	0.39
OPHIUROIDEA	1.28	1.62	10	28	0.35
Ophiothrix	0.91	8.05	2	22	0.27
LEPTOLIDA	0.36	3.38	5	18	0.23
Crangon allmanni	0.55	1.13	7	12	0.15
OSTEICHTHYES	0.36	1.71	5	10	0.13
Ophiothrix fragilis	0.18	3.68	2	9	0.12
PELECYPODA	0.73	0.46	7	9	0.11
Ampharetidae	0.91	0.61	5	7	0.09
Crangon crangon	0.36	0.26	5	3	0.04
Sertulariidae	0.55	0.00	7	4	0.05
Nereididae	0.18	1.61	2	4	0.05
Atylidae	1.28	0.06	2	3	0.04
Pomatoceros lamarcki	0.36	0.02	5	2	0.02
Campanulariidae	0.36	0.01	5	2	0.02
Marphysa bellii	0.18	0.56	2	2	0.02
NEMERTEA	0.18	0.45	2	2	0.02
Philocheras fasciatus	0.18	0.34	2	1	0.02
Crangonidae	0.36	0.11	2	1	0.01
Stenothoe marina	0.36	0.00	2	1	0.01
Haleciidae	0.18	0.14	2	1	0.01
Plumulariidae	0.18	0.09	2	1	0.01
MYSIDACEA	0.18	0.08	2	1	0.01
Gammarellus homari	0.18	0.05	2	1	0.01
Phyllodocidae	0.18	0.03	2	1	0.01
Abludomelita obtusata	0.18	0.02	2	0	0.01

Juvenile *L. limanda* exploited the widest range of prey fauna (45 taxa) of all the fish groups studied (**Table 5.2**) reflecting the opportunistic nature of their feeding. The diet of the juvenile dab was dominated by

Sabellaria spinulosa (59.63 IRI%) although sea anemones, Actiniaria spp. also made an important contribution (27.43 IRI%) (**Table 5.5**). Although juvenile dab have a broad dietary niche (H' = 2.3), most prey taxa were rare in the diet with 38 of the 45 prey items having a relative importance index (IRI %) of less than 1.This shows good agreement with the dietary records held in the Integrated Database and Portal for Fish Stomach Records[1] (DAPSTOM) (Pinnegar 2009) which also shows that *L. limanda* has a broad diet including polychaetes, echinoderms, crustaceans and molluscs. However, *S. spinulosa* was only present sporadically in previous records, indicating that this species is able to modify its feeding behaviour in order to capitalise on the high density of prey present in these reef habitats. This opportunistic feeding behaviour has been reported previously by Kaiser and Ramsay (1997), where dab were found to switch their prey to capitalise on fauna released into the environment during the process of bottom trawling.

Ciliata septentrionalis – Northern Rockling

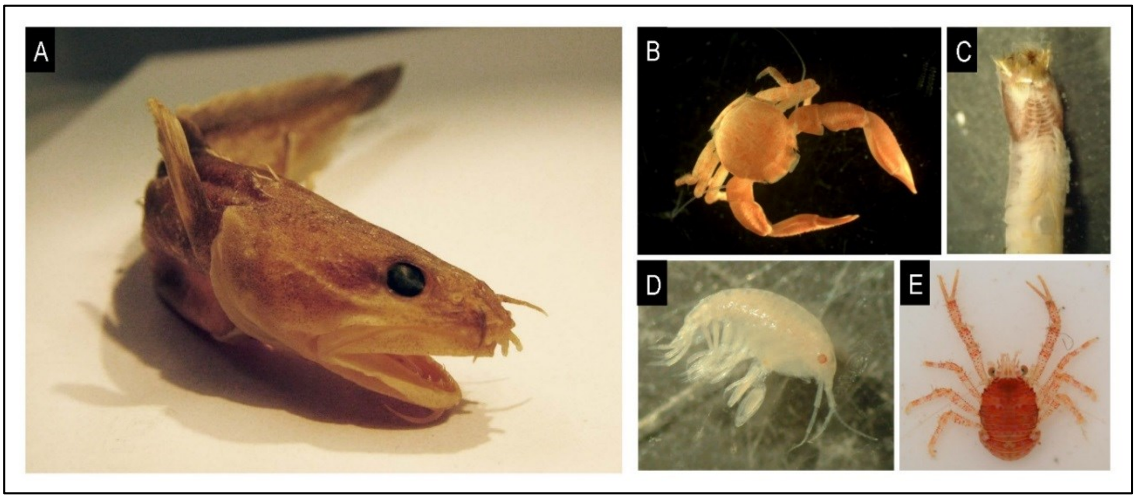


Figure 5.5 Photographs of the Northern Rockling, *Ciliata septentrionalis* (A) and four of the main prey items identified in the stomach contents of 40 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the long clawed porcelain crab*, Pisidia longicornis*, C) the Ross worm, *Sabellaria spinulosa*, D) the amphipod *Stenothoe marina* and E) the squat lobster *Galathea intermedia.*

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[1] https://data.gov.uk/dataset/dapstom

The northern rockling, *Ciliata septentrionalis*, is similar in appearance to the five-bearded rockling, *Ciliata mustela*, but has a distinctive frill of papillae above the top lip and the large mouth that reaches back behind the eyes (**Figure 5.5** & Kay and Dipper 2009). As a small demersal fish it shows a preference for benthic invertebrates, particularly the decapods *Galathea* sp. and *Pisidia* sp., as well as some mysids and polychaetes (Wheeler 1978). It is considered to be relatively rare in comparison to the five-bearded rockling, and is not usually found as far offshore as in the present study. No published records or studies including the diet of this species have been identified in the peer reviewed literature, making this one of the first formal assessments of the diet of this species.

Adult *C. septentrionalis* were found to have a broad diet (H'=2.47) consuming a total of 39 prey taxa (**Table 5.2**). Unidentified crustaceans and decapods were the most important prey overall (27.82 %*IRI* and 23.12 %*IRI* respectively) occurring in a large proportion of the guts (41.03 %*O*, 33.33 %*O*) as was the porcelain crab, *Pisidia longicornis* (18.42 %*IRI*) (**Table 5.6**). These findings show good agreement with records contained in DAPSTOM (Pinnegar 2009) which also indicate a preference for crustacean prey including *P. longicornis*. The diet of the single juvenile *C. septentrionalis* was very similar to the diet of the adults although this individual showed a greater reliance on polychaetes (**Table 5.6**).

Table 5.6 The relative importance of all prey taxa averaged across adult (n=39) and juvenile (n=1) *Ciliata septentrionalis* in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	**%N**	**%W**	**%O**	**IRI**	**%IRI**
CRUSTACEA	16.06	17.04	41	1358	28.72
DECAPODA	12.41	20.38	33	1093	23.12
Pisidia longicornis	13.14	17.74	28	871	18.42
POLYCHAETA	12.41	6.48	33	630	13.32
Thoralus cranchii	5.11	10.86	18	287	6.06
AMPHIPODA	8.03	0.80	21	181	3.83
Galathea intermedia	3.65	6.47	10	104	2.20
Hippolytidae	2.19	4.43	5	34	0.72
Sabellaria spinulosa	2.92	0.10	10	31	0.65
Polynoidae	1.46	2.83	5	22	0.47
Pariambus typicus	5.11	0.12	3	13	0.28
Stenothoe marina	2.19	0.20	8	18	0.39
Pandalina brevirostris	0.73	3.62	3	11	0.24
Praunus	1.46	2.54	3	10	0.22
Gammaridae	2.19	0.27	5	13	0.27
Galathea	0.73	2.62	3	9	0.18
Gammaropsis maculata	1.46	0.34	5	9	0.19
Caprella linearis	1.46	0.02	5	8	0.16
Cancer	0.73	0.96	3	4	0.09
Crangon crangon	0.73	0.82	3	4	0.08
Pandalidae	0.73	0.63	3	3	0.07
Ampelisca diadema	0.73	0.44	3	3	0.06
GASTROPODA	0.73	0.18	3	2	0.05
Unciola crenatipalma	0.73	0.09	3	2	0.04
Lysianassidae	0.73	0.01	3	2	0.04
Amathia lendigera	0.73	0.00	3	2	0.04
Amphilochidae	0.73	0.00	3	2	0.04
Podoceridae	0.73	0.00	3	2	0.04

Juveniles

Prey Taxa	**%N**	**%W**	**%O**	**IRI**	**%IRI**
POLYCHAETA	33.33	46.32	100	7965	39.82
CRUSTACEA	33.33	44.21	100	7754	38.77
AMPHIPODA	33.33	9.47	100	4281	21.40

Agonus cataphractus – Pogge

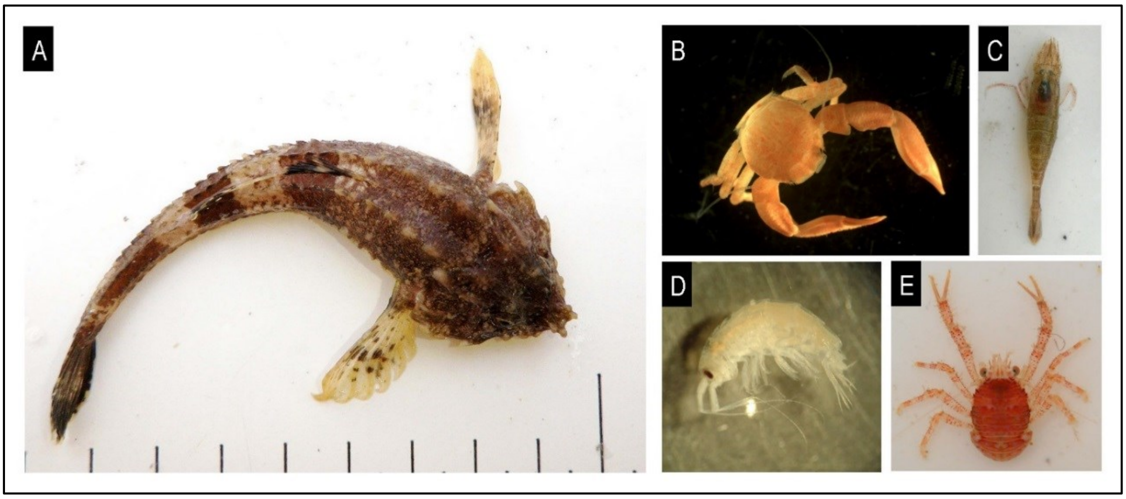


Figure 5.6 Photographs of the Pogge, *Agonus cataphractus* (A) and four of the main prey items identified in the stomach contents of 28 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the long clawed porcelain crab*, Pisidia longicornis*, C) the brown shrimp, *Crangon allmanni* D) the amphipod, *Atylus swammerdami* and E) the squat lobster *Galathea intermedia.*

The pogge or armoured bullhead, *Agonus cataphractus* (**Figure 5.6**) is normally found on soft substrata in coastal and estuarine areas (Wheeler 1978; Dipper 2001; Power and Attrill 2002; Kay and Dipper 2009). Pogge have an inferior or sub-terminal mouth, where the lower jaw is shorter than the upper jaw, surrounded by sensory barbels, indicating that it is a bottom feeder. It is one of the smallest fish in this study and as it has no commercial importance it has received very little attention in the peer reviewed literature (Marshall and Elliott 1997; Power and Attrill 2002; Klimpel et al. 2003). Based on limited observations *A. cataphractus* has been found to feed primarily on crustaceans, including juvenile crabs, shrimp and amphipods (Wheeler 1978; Power and Attrill 2002; Klimpel et al. 2003). Power and Attrill (2002) found that the abundance of Pogge in the Thames estuary was influenced by the abundance of age-0 dab, *Limanda limanda*, indicating that these may also be important prey items for this species.

The dietary niche breadth of adults and juveniles belonging to this species were broadly similar in terms of both diversity (H’ = 2.7 and H’ =2.57 respectively) and evenness (J’ = 0.83 and 0.84 respectively) and composition (**Tables 5.2 and 5.7**) indicating that there is no ontogenetic shift in terms of dietary breadth, at least between these two categories.

Table 5.7 The relative importance of all prey taxa averaged across adult (n=15) and juvenile (n=13) *Agonus cataphractus* in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	%N	%W	%O	IRI	%IRI
Pisidia longicornis	21.59	22.95	31	1371	34.74
CRUSTACEA	6.82	11.74	46	857	21.71
Crangon allmanni	6.82	13.06	15	306	7.75
AMPHIPODA	12.50	4.59	15	263	6.66
Crangonidae	2.27	12.21	15	223	5.65
Stenothoe marina	7.95	0.49	15	130	3.29
POLYCHAETA	3.41	1.76	23	119	3.02
Galathea intermedia	3.41	4.03	15	114	2.90
Gammarellus homari	6.82	5.82	8	97	2.46
DECAPODA	3.41	2.37	15	89	2.25
Thoralus cranchii	1.14	5.64	8	52	1.32
Soleidae	2.27	4.39	8	51	1.30
Sabellaria spinulosa	2.27	0.76	15	47	1.18
Polynoidae	2.27	3.43	8	44	1.11
Pilumnus hirtellus	1.14	3.82	8	38	0.97
Isaeidae	2.27	0.96	8	25	0.63
Abludomelita obtusata	2.27	0.48	8	21	0.54
Lysianassidae	2.27	0.12	8	18	0.47
Schistomysis spiritus	1.14	0.38	8	12	0.30
Atylus swammerdamei	1.14	0.33	8	11	0.29
Hippolytidae	1.14	0.23	8	11	0.27
OSTEICHTHYES	1.14	0.18	8	10	0.26
Gastrosaccus spinifer	1.14	0.10	8	9	0.24
Podoceridae	1.14	0.07	8	9	0.24
Gammaropsis	1.14	0.05	8	9	0.23
OPHIUROIDEA	1.14	0.03	8	9	0.23

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
Pisidia longicornis	15.57	31.30	33	1563	32.70
DECAPODA	8.20	11.75	47	931	19.47
AMPHIPODA	13.93	2.11	33	535	11.19
Crangon crangon	4.92	10.22	27	404	8.45
POLYCHAETA	5.74	2.97	33	290	6.08
Galathea intermedia	3.28	8.32	20	232	4.85
Crangon allmanni	3.28	10.48	13	183	3.84
Atylus swammerdamei	19.67	3.99	7	158	3.30
CRUSTACEA	2.46	4.22	20	134	2.79
Podoceridae	7.38	0.26	13	102	2.13
CUMACEA	4.10	0.07	13	56	1.16
Pandalina brevirostris	0.82	5.53	7	42	0.89
Abludomelita obtusata	2.46	0.66	13	42	0.87
MYSIDACEA	2.46	1.24	7	25	0.52
Dyopedos monacanthus	0.82	2.02	7	19	0.40
Ampelisca spinipes	0.82	2.01	7	19	0.39
Lepidonotus squamatus	0.82	1.70	7	17	0.35
Gastrosaccus spinifer	0.82	1.05	7	12	0.26
Ampeliscidae	0.82	0.06	7	6	0.12
Phtisica marina	0.82	0.04	7	6	0.12
Tanaopsis graciloides	0.82	0.03	7	6	0.12

Both adult and juvenile *Agonus cataphractus* consumed a broad array of prey (26 taxa and 21 taxa respectively), and exhibited a relatively high level of heterogeneity in their diets with *Pisidia longicornis,* the most important prey taxon in both groups, only being present in around a third of the stomachs analysed. Most of the crustaceans identified as being important in the diet of *A. cataphractus* were small, mobile, and predominantly crevice-dwelling animals including a number of amphipod and shrimp species. This corresponds well with previous records of *A. cataphractus* diet (Pinnegar, 2009, Power & Attrill, 2002, Wheeler, 1978) and suggests that *A. cataphractus* may be utilising the high abundance of *P. longicornis* and other small decapods taking refuge in the reef crevices.

Callionymus lyra – Dragonet

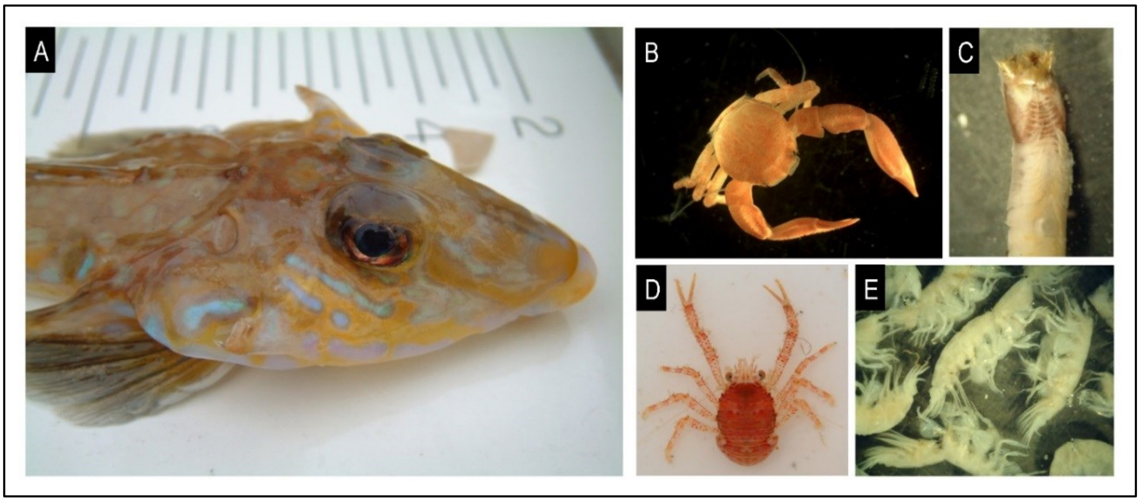


Figure 5.7 Photographs of the common Dragonet, *Callionymus lyra (*A) and four of the main prey items identified in the stomach contents of 24 specimens collected in association with *Sabellaria spinulosa* reefs in the East Coast REC study site: B) the long clawed porcelain crab*, Pisidia longicornis*, C) the ross worm, *Sabellaria spinulosa*, D) the squat lobster *Galathea intermedia* and E) some amphipod crustaceans.

The common dragonet, *Callionymus lyra* (**Figure 5.7**) is widely distributed in coastal regions of the UK (Van der veer et al. 1990; King et al. 1994; Dolbeth et al. 2008). Like *A. cataphractus*, the mouth of *C. lyra* is inferior or sub-terminal meaning the lower jaw is shorter than the upper jaw. *C. lyra* however, lacks the sensory barbels of *A. cataphractus* and has large fleshy lips and a strongly extensible jaw indicating that whilst both species are bottom feeders, the precise nature of their feeding behaviour may be very different. Divers have observed puffs of muddy water being blown out of the gills of *C. lyra* which could indicate that this species sucks up sediments and filters out the fauna living within it (Dipper 2001). Although this species has not received much attention in the literature a small number of studies have reported its dietary preferences (Davis 1966; Lopezjamar et al. 1984; Van der veer et al. 1990; King et al. 1994; Klimpel et al. 2003; Dolbeth et al. 2008). *Callionymus lyra* has a varied diet, feeding on polychaetes, crustaceans, molluscs and echinoderms (Davis 1966; Lopezjamar et al. 1984; Van der veer et al. 1990; King et al. 1994; Dolbeth et al. 2008). Considerable variations have been noted in the relative importance of these groups in the diet of *C. lyra* and this species is therefore assumed to have a high degree of dietary adaptability.

Table 5.8 The relative importance of all prey taxa averaged across adults (n=6) and juvenile (n=18) *Callionymus lyra* in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	%N	%W	%O	IRI	%IRI
OPHIUROIDEA	20.00	23.33	17	722	17.30
AMPHIPODA	12.00	7.33	33	644	15.43
Nereididae	4.00	29.70	17	562	13.45
Sabellaria spinulosa	8.00	5.70	33	457	10.93
Pisidia longicornis	4.00	16.49	17	342	8.18
POLYCHAETA	8.00	1.08	33	303	7.25
CRUSTACEA	8.00	0.41	33	280	6.71
Paguridae	4.00	11.85	17	264	6.33
Ampeliscidae	8.00	1.60	17	160	3.83
Atylus swammerdamei	8.00	0.16	17	136	3.26
Atylidae	8.00	0.04	17	134	3.21
GASTROPODA	4.00	2.20	17	103	2.48
DECAPODA (juv)	4.00	0.12	17	69	1.64

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
Sabellaria spinulosa	11.36	31.14	56	2361	45.60
AMPHIPODA	25.76	4.22	33	999	19.29
Pisidia longicornis	9.85	22.23	28	891	17.21
Galathea	3.03	15.80	17	314	6.06
CRUSTACEA	3.79	3.96	22	172	3.32
COPEPODA	20.45	0.02	6	114	2.20
Sthenelais	1.52	12.85	6	80	1.54
DECAPODA	2.27	2.10	17	73	1.41
Gammarellus homari	2.27	1.84	6	23	0.44
PELECYPODA	1.52	0.19	11	19	0.37
Crangon allmanni	0.76	2.18	6	16	0.32
Atylus swammerdamei	2.27	0.30	6	14	0.28
Pectinariidae	2.27	0.16	6	14	0.26
Podoceridae	2.27	0.04	6	13	0.25
POLYCHAETA	0.76	1.02	6	10	0.19
Melitidae	1.52	0.08	6	9	0.17
Atylidae	1.52	0.07	6	9	0.17
Cancer pagurus	0.76	0.78	6	9	0.17
Gammaropsis maculata	0.76	0.48	6	7	0.13
Lumbrineridae	0.76	0.15	6	5	0.10
DECAPODA (juv)	0.76	0.13	6	5	0.10
Phoxichilidium femoratum	0.76	0.12	6	5	0.09
Isaeidae	0.76	0.10	6	5	0.09
Atylus guttatus	0.76	0.02	6	4	0.08
GASTROPODA	0.76	0.02	6	4	0.08
Glyceridae	0.76	0.01	6	4	0.08

The dietary niche breadth of adults and juveniles belonging to this species were broadly similar in terms of both diversity (H' = 2.23 and H' =2.73 respectively) and evenness (J' = 0.87 and 0.84 respectively) although differences were observed in the prey composition and relative importance (**Tables 5.2 and 5.8**). Juvenile *C. lyra* fed on a wider range of prey than adults (**Table 5.8**) although their diet was more dominated by *Sabellaria spinulosa* which accounted for over 45% of the diet in terms of relative importance (IRI%). An ontogenetic shift is evident in this species, with brittle stars, Ophioroidea, being the most numerically important (20 N%) and relatively important (17.30 IRI%) prey item in the adult diet, whilst being absent from the diet of juveniles. The importance of polychaetes in the diet of both adults and juveniles corroborates the findings of Klimpel et al. (2003) although this is the first reported record of *S. spinulosa* in the diet of this species. That *C. lyra* of both developmental stages are feeding on *S. spinulosa* and fauna associated with the reefs such as *Pisidia longicornis* and *Gammarus homari* (**Chapter 4**) demonstrates that this habitat is providing an important prey source for this species.

Echiichthys vipera – Lesser Weever Fish

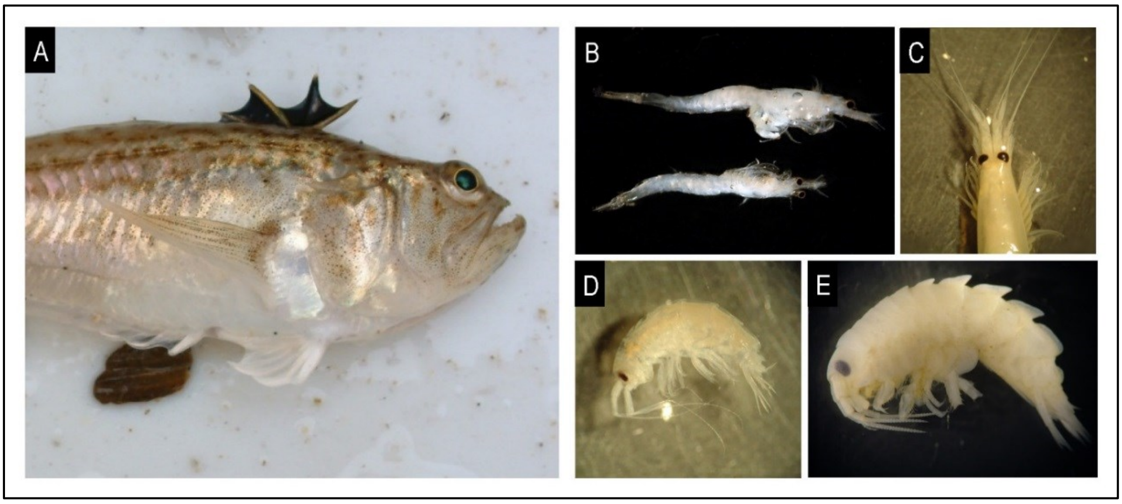


Figure 5.8 Photographs of the Lesser Weever Fish, *Echiichthys vipera* (A) and four of the main prey items identified in the stomach contents of 20 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the ghost shrimp, *Schistomysis spiritus*, C) the mysid shrimp *Gastrosaccus spinifer*, D) the amphipod *Atylus swammerdami* and E) the amphipod *Gammarellus homari.*

The lesser weever fish, *Echiichthys vipera,* is a common demersal fish in sandy sediments where it buries itself during the day (Vasconcelos et al. 2004). The upturned or superior mouth of *E. vipera* (**Figure 5.8**) reflects its carnivorous nature (Creutzberg and Witte 1989; Vasconcelos et al. 2004). A limited number of studies on the diet of *E. vipera* have shown that its diet is dominated by crustaceans, particularly mysid shrimps and amphipods, in keeping with the burrowing behaviour observed in this species (Vasconcelos et al. 2004). Both adults and juveniles observed in this study, consumed a moderate number of prey taxa (15 and 17 respectively) and this was reflected in the niche breadth indices (**Table 5.2:** H' = 2.18, J'=0.79 and H' = 2.1, J' =0.74 respectively). The ghost shrimp, *Schistomysis spiritus,* was the most important prey taxa in the diet of juvenile *E. vipera* (54.16 IRI%) occurring in 83 % of the guts studied (**Table 5.9**). This is indicates a very homogenous and specialist diet (Cortes 1997). In contrast the amphipod *Gammarellus homari* was the most important prey taxa in the diet of adult *E. vipera* (32.8 IRI%) although this prey taxon was only present in 44% of the guts studied and unidentified amphipods, mysids and crustaceans were also identified as important prey items (13.50-17.88 IRI%), indicating a more generalist diet. An ontogenetic shift in the diet of *E. vipera* has previously been reported by Vasconcelos et al. (2004) who found that this species consumed an increasing proportion of fish prey with increasing size.

Table 5.9 The relative importance of all prey taxa averaged across adult (n=9) and juvenile (n=11) *Echiichthys vipera* in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	%N	%W	%O	IRI	%IRI
Gammarellus homari	31.63	37.46	50	3455	36.61
AMPHIPODA	16.33	13.02	63	1834	19.44
MYSIDACEA	13.27	16.08	50	1467	15.55
CRUSTACEA	10.20	8.28	63	1155	12.24
Schistomysis spiritus	11.22	11.50	38	852	9.03
Gastrosaccus spinifer	4.08	7.80	25	297	3.15
Atylus swammerdamei	5.10	0.35	38	205	2.17
Crangon	2.04	3.29	13	67	0.71
Gammarellus	2.04	0.40	13	30	0.32
Eurydice pulchra	1.02	0.93	13	24	0.26
DECAPODA (juv)	1.02	0.62	13	21	0.22
Jassa	1.02	0.19	13	15	0.16
POLYCHAETA	1.02	0.08	13	14	0.15
DECAPODA	0.00	0.00	0	0	0.00
Gadidae	0.00	0.00	0	0	0.00

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
Schistomysis spiritus	21.36	25.20	83	3880	54.16
MYSIDACEA	21.36	27.50	33	1629	22.74
Atylus swammerdamei	14.56	2.46	25	426	5.94
Gammarellus homari	9.71	11.71	17	357	4.98
DECAPODA (juv)	13.59	3.87	17	291	4.06
DECAPODA	3.88	0.96	17	81	1.13
CRUSTACEA	2.91	2.70	25	140	1.96
OSTEICHTHYES	0.97	12.25	8	110	1.54
AMPHIPODA	3.88	1.06	17	82	1.15
Philocheras trispinosus	0.97	5.93	8	58	0.80
Gastrosaccus spinifer	1.94	3.93	8	49	0.68
POLYCHAETA	0.97	1.67	8	22	0.31
Eurydice	0.97	0.40	8	11	0.16
Bathyporeia	0.97	0.29	8	11	0.15
Dyopedos monacanthus	0.97	0.05	8	8	0.12
Atylus	0.97	0.02	8	8	0.12

Fish (Osteichtyes) was recorded in the diet of a single juvenile but were otherwise absent from the diet of *E. vipera* sampled from the *S. spinulosa* reefs in the East Coast REC study area. This perhaps indicates that amphipods and mysids are present in high enough numbers in this habitat, to make them a more energetically favourable prey item compared to the more typical prey of sand eels (Pinnegar, 2009).

Myoxocephalus scorpius – Bull Rout

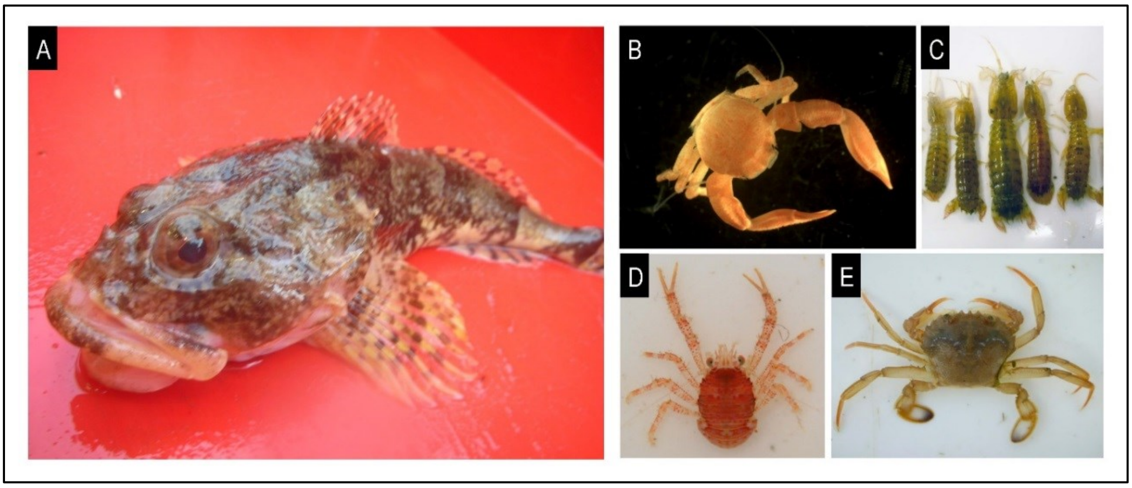


Figure 5.9 Photographs of the Bull Rout, *Myoxocephalus scorpius* (A) and four of the main prey items identified in the stomach contents of 12 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the long clawed porcelain crab, *Pisidia longicornis*, C) the mantis shrimp, *Rissoides desmaresti*, D) the squat lobster, *Galathea intermedia* and E) the swimming crab, *Liocarcinus depurator*.

The short-spined sea scorpion or bull rout, *Myoxocephalus Scorpius* (**Figure 5.9**) is a commonly encountered sea scorpion very similar in appearance to its relative, the long-spined sea scorpion, *Taurulus bubalis*. Both species are ambush predators with large, sub-terminal, protractible mouths and they have been reported to consume a range of amphipods, isopods, decapods and fish (Cardinale 2000; Kay and Dipper 2009). The large mouth size in *M. scorpius* means that it is far less limited in the prey it can consume than many of the other species included in this study.

Juvenile *M. scorpius* consumed a moderate range of prey (18 taxa) and had a broad diet (H’=2.57, J’=0.89). Many of the important prey taxa were crustaceans, although polychaetes, fish and nemerteans were also contributed to the diet (**Table 5.10**). This result is in general concordance with the data stored in DAPSTOM (Pinnegar 2009) and to the results of previous studies (Cardinale 2000) which also show the diet of *M. scorpius* is dominated by crustaceans. It is interesting to note the occurrence of the mantis shrimp, *Rissoides desmaresti*, in in the same gut as the mud shrimp, *Callianassa subterranea*. These two species live in burrows in cohesive muddy sediments (Vansteenbrugge et al. 2012), a habitat which could be provided by the accumulation of silt between the *S. spinulosa* reef structures, although no such association has previously been recorded.

Table 5.10 The relative importance of all prey taxa averaged across juvenile *Myoxocephalus scorpius* (n=11) in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
CRUSTACEA	11.36	17.72	45	1322	26.21
Pisidia longicornis	20.45	1.79	45	1011	20.04
DECAPODA	11.36	9.94	45	968	19.19
POLYCHAETA	9.09	2.30	36	414	8.21
Liocarcinus depurator	2.27	21.02	9	212	4.20
Rissoides desmaresti	2.27	20.63	9	208	4.13
Galathea intermedia	9.09	1.40	18	191	3.78
OSTEICHTHYES	4.55	4.94	18	172	3.42
Thoralus cranchii	4.55	1.12	18	103	2.04
Sabellaria spinulosa	4.55	0.01	18	83	1.64
Crangon crangon	2.27	5.77	9	73	1.45
Crangon	4.55	2.25	9	62	1.22
Callianassa subterranea	2.27	4.17	9	59	1.16
Pilumnus hirtellus	2.27	4.10	9	58	1.15
Crangon allmanni	2.27	2.67	9	45	0.89
MYSIDACEA	2.27	0.10	9	22	0.43
NEMERTEA	2.27	0.06	9	21	0.42
Corophiidae	2.27	0.01	9	21	0.41

***Merlangius merlangus* – Whiting**

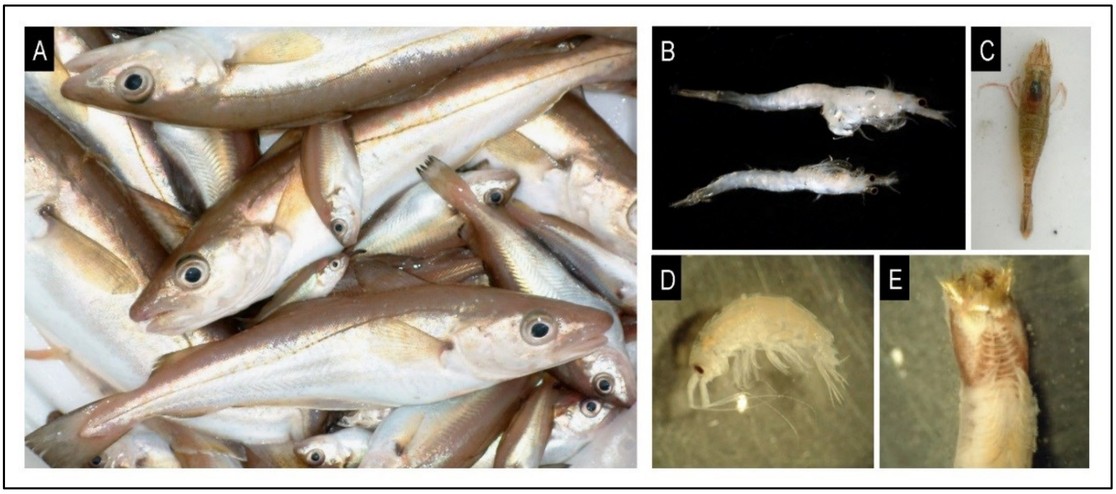


Figure 5.10 Photographs of the Whiting, *Merlangius merlangus* (A) and four of the main prey items identified in the stomach contents of 9 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the ghost shrimp, *Schistomysis spiritus*, C) the brown shrimp, *Crangon allmanni*, D) the amphipod, *Atylus swammerdami* and E) the Ross worm, *Sabellaria spinulosa*.

The whiting, *Merlangius merlangus* (**Figure 5.10**), is a commercial species of gadoid, common on all UK coasts. It has a sub terminal mouth with a shorter lower than upper jaw and numerous small conical teeth. The mouth of the whiting is moderate in size relative to its body meaning that it is able to utilise a wide range of prey. Juvenile whiting generally eat small crustaceans, such as copepods and mysids, switching to larger crustaceans and fish as they grow (Hamerlynck and Hostens 1993; Bromley et al. 1997; Hostens and Mees 1999; Pinnegar et al. 2003; Stafford et al. 2007). Large adult whiting are almost entirely piscivorous, feeding mainly on sand eels, clupeids and gadoids, including other whiting (Bromley et al. 1997; Greenstreet et al. 1998).

Unidentifiable mysid shrimps were found to be the only prey item present in the single adult stomach included in this study (**Table 5.11**), but as only 4 individuals were present, equating to 0.01g Wet Weight, it seems likely that this individual had not eaten very recently and this is unlikely to represent the diet of this predator group. Juvenile whiting were found to have a relatively broad diet made up of 23 taxa (H' =2.54; **Table 5.2**) dominated by crustaceans, although fish, polychaetes and hydroids were also present (**Table 5.11**). The relative importance of prey was fairly equitable amongst the five most important prey taxa (Amphipoda, Osteichthyes, *Atylus swammerdamei,* Mysidacea and Crustacea: 10.12 - 18.53 IRI%), indicating a generalist, heterogenous diet (Cortes 1997). The diet of *M. merlangus* described in this study is in general agreement with gut content data held in DAPSTOM (Pinnegar, 2009). Whilst there is no evidence of a radical shift in the feeding behaviour or diet of *M. merlangus* associated with the presence of the *S. spinulosa* reef, this predator is clearly feeding on reef fauna, including *S. spinulosa* itself.

Table 5.11 The relative importance of all prey taxa averaged across adult (n=1) and juvenile (n=8) *Merlangius merlangus* in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	%N	%W	%O	IRI	%IRI
MYSIDACEA	100.00	100.00	100	20000	100.00

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
AMPHIPODA	13.00	2.81	63	988	18.53
OSTEICHTHYES	3.00	28.24	25	781	14.64
Atylus swammerdamei	11.00	0.91	50	596	11.17
MYSIDACEA	10.00	5.71	38	589	11.05
CRUSTACEA	5.00	5.80	50	540	10.12
Schistomysis spiritus	8.00	6.41	25	360	6.76
POLYCHAETA	2.00	7.83	25	246	4.61
Sabellaria spinulosa	2.00	6.35	25	209	3.92
Crangon	1.00	13.63	13	183	3.43
Dyopedos monacanthus	14.00	0.46	13	181	3.39
Tubularia	1.00	9.98	13	137	2.57
Atylidae	9.00	0.15	13	114	2.14
Gastrosaccus spinifer	4.00	1.97	13	75	1.40
Podoceridae	5.00	0.32	13	67	1.25
Crangon allmanni	1.00	3.44	13	55	1.04
Nephtys	1.00	3.34	13	54	1.02
DECAPODA	3.00	0.23	13	40	0.76
LEPTOLIDA	1.00	2.18	13	40	0.75
Stenothoe marina	2.00	0.18	13	27	0.51
Sertularia	1.00	0.02	13	13	0.24
CUMACEA	1.00	0.01	13	13	0.24
Haleciidae	1.00	0.01	13	13	0.24
Campanulariidae	1.00	0.00	13	13	0.24

Taurulus bubalis – Sea Scorpion

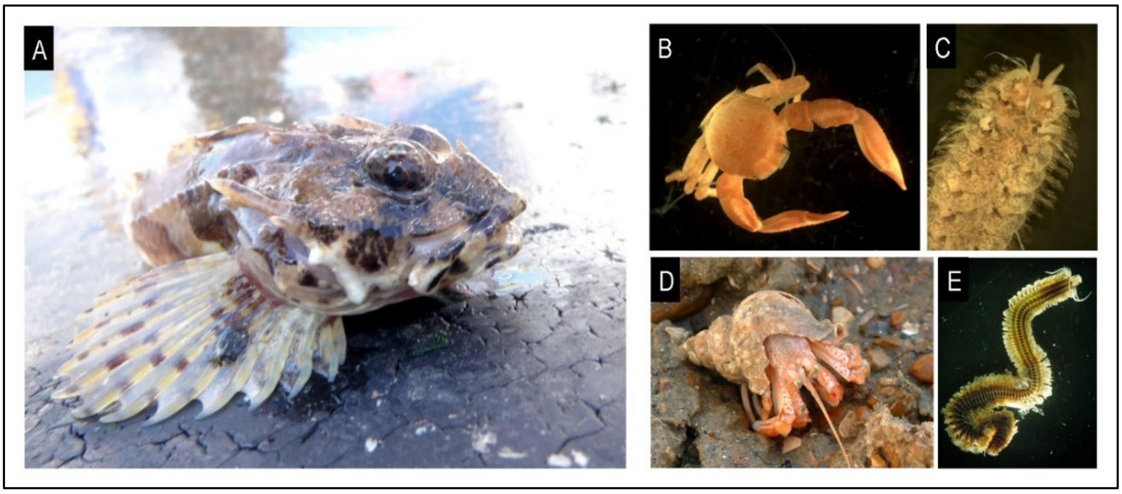


Figure 5.11 Photographs of the Sea Scorpion, *Taurulus bubalis* (A) and four of the main prey items identified in the stomach contents of 5 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the long clawed porcelain crab, *Pisidia longicornis*, C) the scale worm, *Harmothoe antilopes* (Polynoidae), D) the hermit crab, *Pagurus bernhardus* and E) the Phyllodociid worm, *Anaitides lineata*.

The long-spined sea scorpion*, Taurulus bubalis* (**Figure 5.11**) is a common demersal fish species, very similar in appearance to the bull rout, *Myoxocephalus scorpius*. It is more commonly found on rocky shores in pools with seaweed, but can also be found down to depths of 30 m (Kay and Dipper 2009). Like *M. Scorpius*, *T. bubalis* is an ambush predator with a large, sub-terminal, protractible mouth which would allow it to predate a wide range of prey. A total of 5 *T. bubalis* guts were analysed, all of which are assumed to be adults based on their size relative to the maximum reported size (Wheeler 1978) (**Table 5.2**). *T. bubalis* consumed a relatively low diversity of prey (7 taxa) which was reflected in its niche breadth (H' =1.59). This is likely, however, to be an influenced by the very small sample size analysed (n=5).

The diet of *T. bubalis* has not been the subject of any formal assessment and there are very few records held in DAPSTOM (Pinnegar 2009). However, the few records that do exist, indicate that fish and molluscs are the most important prey items for this species, in contrast to the results of this study which indicate that crustaceans and polychaetes are important prey for *T. bubalis* (**Table 5.12**). The disparity between DAPSTOM records and the results of this study indicate that *T. bubalis* may demonstrate some trophic adaptability. The dominance of *P. longicornis* in the diet of *T. bubalis* sampled from the *S. spinulosa* reefs in the southern North Sea indicates that this species may be taking advantage of highly abundant prey species associated with this habitat, although examination of more specimens would be required to make any firm conclusions about their feeding behaviour.

Table 5.12 The relative importance of all prey taxa averaged across adult *Taurulus bubalis* (n=5) in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*) and rank. Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	% N	% W	% O	IRI	%IRI
Pisidia longicornis	50.00	16.86	80	5349	66.76
Paguridae	6.25	68.92	20	1503	18.76
DECAPODA	12.50	11.66	20	483	6.03
Polynoidae	12.50	1.95	20	289	3.61
POLYCHAETA	6.25	0.37	20	132	1.65
Phyllodocidae	6.25	0.20	20	129	1.61
AMPHIPODA	6.25	0.04	20	126	1.57

Hyperoplus laceolatus – Sand Eel

Figure 5.12 Photographs of the Sand Eel, *Hyperoplus lanceolatus* (A) and three of the prey items identified in the stomach contents of 4 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the nereid worm, *Nereis zonata*, C) some copepods and D) some decapod crustaceans (Pink shrimp, *Pandalus montagui*).

The greater sand eel, *Hyperoplus lanceolatus* (**Figure 5.12**) is a shoaling fish that is heavily fished for commercial purposes and also provides a significant food source for a number of fish and sea bird species (Wanless et al. 1998). This species is often associated with sand banks where it is able to dive down into the sand to avoid predation (Wanless et al. 1998). Like other sandeel species, *H. lanceolatus* has a long slender body and a sharply protuberant lower jaw. *H. lanceolatus* however, lacks the protusible upper jaw that other sandeel species have and has a pair of conspicuous teeth in the roof of its mouth (Wheeler 1978). The significance of the teeth in the roof of its mouth, for feeding, is not yet fully understood but it is possible that they help *H. lanceolatus* to hold a grip on their larger prey, which can include other sandeel species (Dipper 2001). *H. lanceolatus* is classified as both a pelagic and a demersal fish, and is known to have a varied diet reflecting the habitats it frequents, feeding on small planktonic fauna and fish, as well as benthic invertebrates (Dipper 2001; Kay and Dipper 2009).

The two juvenile sand eels included in this study were found to be feeding exclusively on calanoid copepods (**Table 5.13**) and had consumed an average of 400 individuals each, indicating that this food source is abundant in this area. Calanoid copepods were also identified as being the most important prey item for the two adult sand eels although these contributed very little to the biomass found in the stomachs (0.79 %W). Nereid polychaetes and unidentifiable crustaceans were also present in the adults diet and contribute most in terms of biomass, 75.29 %W and 23.92 %W respectively.

Table 5.13 The relative importance of all prey taxa averaged across adult (n=2) and juvenile (n=2) *Hyperoplus lanceolatus* in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	% N	% W	% O	IRI	%IRI
COPEPODA	85.71	0.79	50	4325	43.25
Nereididae	7.14	75.29	50	4122	41.22
CRUSTACEA	7.14	23.92	50	1553	15.53

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
COPEPODA	100.00	100.00	100	20000	100.00

The diet of *Hyperoplus lanceolatus* is very different from all other fish species analysed during this study. This species consumed a high abundance of very small pelagic prey (Calanoid Copepods) and their diet included a very narrow range of prey items (3 taxa), reflected in their low niche breadth (H' = 0.83 and H' = 0 for adults and juveniles respectively). This is, in part, a reflection of the taxonomic discrimination afforded to copepods but also indicates that this species is a very specialist feeder. The importance of small copepods in the diet of *H. lanceolatus* corresponds with data held in DAPSTOM, where nearly two thirds of the biomass of identifiable material was found to be copepods (Pinnegar 2009). Polychaetes were not recorded in the diet of *H. lanceolatus* from previous studies in the southern North Sea (Pinnegar 2009) although this species is noted as feeding on benthic invertebrates in a number of other sources (Dipper 2001). It is unlikely that the presence of nereids in the diet of sand eels is directly attributable to the presence of the reef habitat since they would be unable penetrate its hard structure. It is, however, possible that the sand eels were feeding in sand patches between the reef structures, which may be influenced by an overspill of benthic species from adjacent *S. spinulosa* reef, or they may be feeding on pelagic stages of the worm, including reproductive epitokes.

Trispoterus minutus **– Poor Cod**

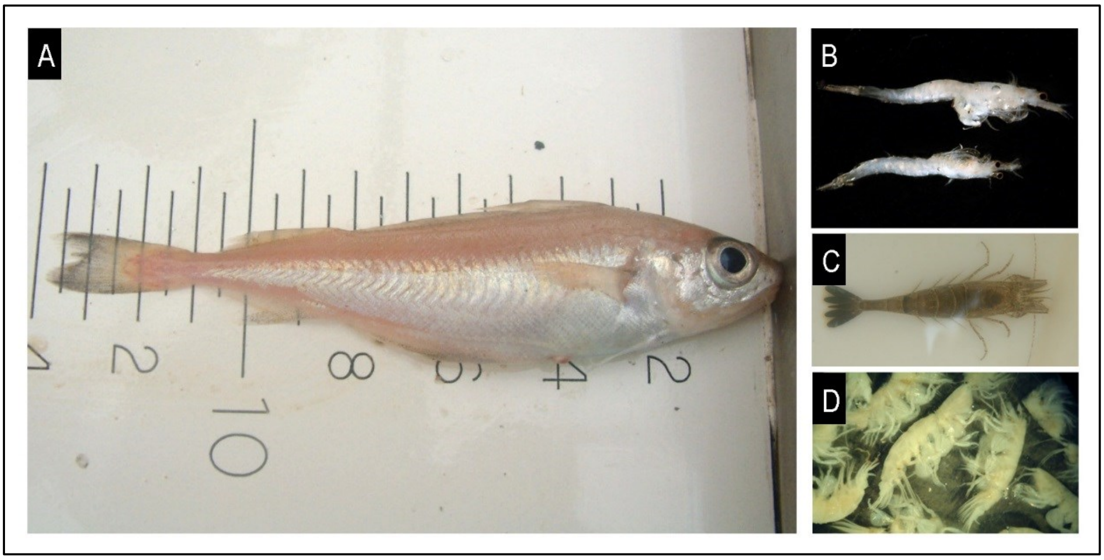


Figure 5.13 Photographs of the Poor Cod, *Trisopterus minutus* (A) and three of the prey items identified in the stomach contents of 3 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the ghost shrimp, *Schistomysis spiritus*, C) the brown shrimp, *Crangon crangon* and D) some amphipods.

The poor cod, *Trisopterus minutus* (**Figure 5.13**) is a shoaling fish found on all UK coasts. It is a member of the Gadoid family and has a broadly similar body and mouth shape to other species belonging to this group. Like whiting, poor cod has a terminal mouth, although in this case the upper jaw overlaps the lower jaw which is indicative of a fish that feeds primarily on the seabed. *T. minutus* has been the subject of a number of feeding studies and has been found to have considerable overlap in its diet with fellow gadoids including bib, *Trisopterus luscus,* and cod, *Gadus morhua* (Armstrong 1982). *T. minutus* exhibits dietary partitioning based on size with smaller individuals (70-90mm) feeding on small crustaceans such as mysids and shrimps whilst larger individuals (100-190mm) feed on larger crustaceans including crabs and small fish (Armstrong 1982; Morte et al. 2001). Polychaetes have also been recorded in the diet of poor cod although they were generally not as prolific or abundant in their stomach contents (Armstrong 1982).

The three adult *T. minutus* included in this study fed exclusively on crustaceans (**Table 5.14**) with *Schistomysis spiritus* dominating the diet (47.40 %IRI) alongside unidentified crustaceans (37.42 %IRI) and mysid shrimp (10.44 *%IRI)* (**Table 5.14**). This is in strong agreement with records in DAPSTOM (Pinnegar 2009) as well as published records of *T. luscus* diet (Armstrong 1982).

Table 5.14 The relative importance of all prey taxa averaged across adult *Trisopterus minutus* (n=3) in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Adults

Prey Taxa	% N	% W	% O	IRI	%IRI
Schistomysis spiritus	70.37	55.95	33	4211	47.40
CRUSTACEA	11.11	22.13	100	3324	37.42
MYSIDACEA	11.11	16.70	33	927	10.44
Crangon crangon	3.70	4.40	33	270	3.04
AMPHIPODA	3.70	0.82	33	151	1.70

Trisopterus luscus – Bib

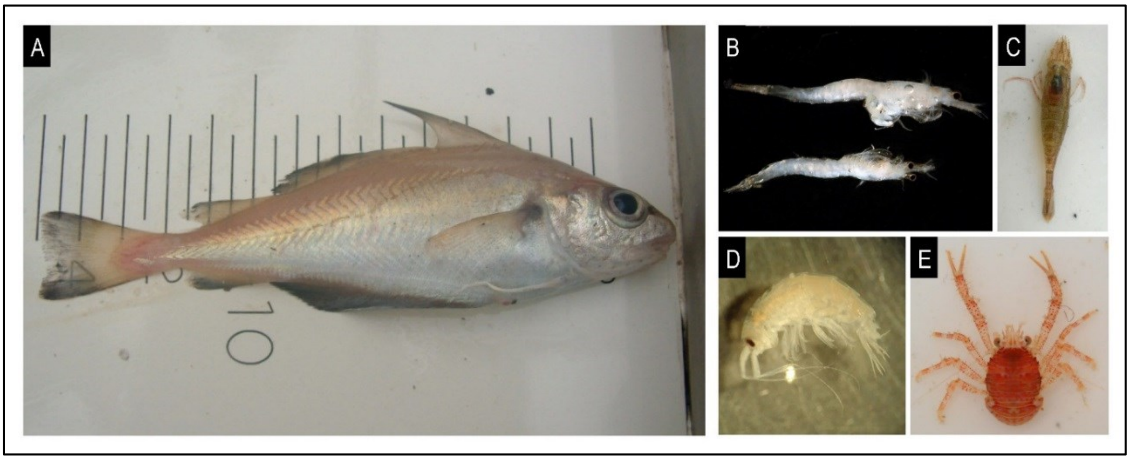


Figure 5.14 Photographs of the Bib, *Trisopterus luscus* (A) and four of the prey items identified in the stomach contents of 2 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the ghost shrimp, *Schistomysis spiritus*, C) the brown shrimp *Crangon allmanni, D)* the amphipod *Atylus swammerdami* and E) the squat lobster *Galathea intermedia*.

The diet of bib, *Trisopterus luscus* (**Figure 5.14**), shows considerable overlaps with that of its congener *T. minutus* of the same size (Armstrong 1982). Bib ultimately reach a larger size than *T. minutus* as adults and at this point there is some divergence in their diet with *T. luscus* as they are able to feed on larger prey including crustaceans and fish (Armstrong 1982). The two *T. luscus* specimens examined here were both juveniles and in the same size range as the *T. minutus* examined (**Table 5.2**). They were found to have a narrow niche breadth (H' = 1.27) in comparison to the other fish species studied and fed primarily on mysid crustaceans with *Schistomysis spiritus* being the dominant prey (66.19 %*IRI*) (**Table 5.15**). This shows good agreement with published records on the diet of juvenile bib (Armstrong 1982; Hamerlynck and Hostens 1993; Hostens and Mees 1999; Dolbeth et al. 2008).

Table 5.15 The relative importance of all prey taxa averaged across juvenile *Trisopterus luscus* (n=2) in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O*), index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
Schistomysis spiritus	57.97	59.46	100	11743	66.19
MYSIDACEA	20.29	17.11	100	3740	21.08
AMPHIPODA	13.04	1.07	50	705	3.98
DECAPODA	1.45	10.24	50	584	3.29
Galathea intermedia	1.45	5.07	50	326	1.84
Crangon allmanni	1.45	4.16	50	280	1.58
Nereididae	1.45	2.03	50	174	0.98
CRUSTACEA	1.45	0.63	50	104	0.58
Atylus swammerdamei	1.45	0.24	50	85	0.48

Pleuronectes platessa – Plaice

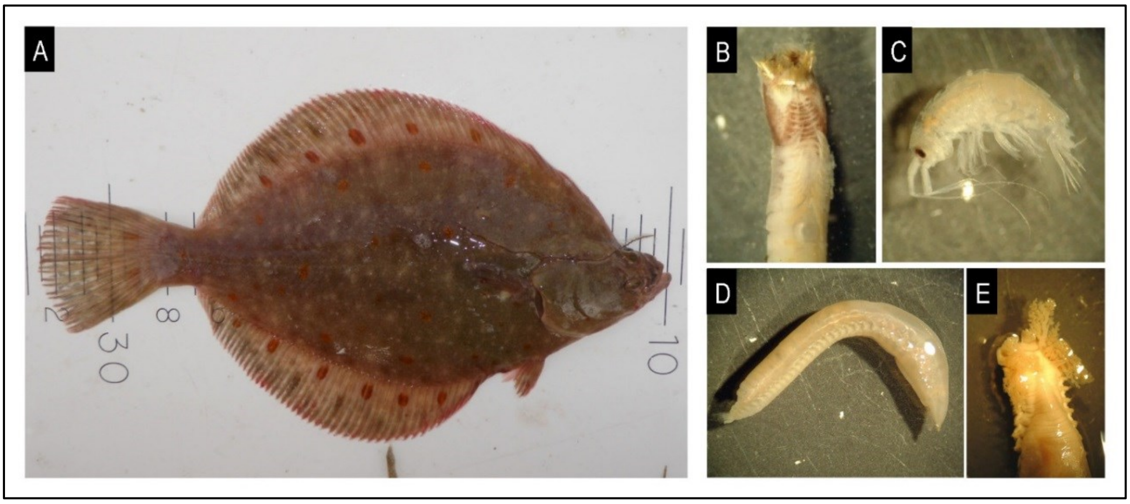


Figure 5.15 Photographs of the Plaice, *Pleuronectes platessa* (A) and four of the prey items identified in the stomach contents of 2 specimens collected in association with *Sabellaria spinulosa* reefs at the East Coast REC study site: B) the ross worm, *Sabellaria spinulosa*, C) the amphipod *Atylus swammerdami,* D) the opheliid worm, *Ophelia borealis* and E) the terebellid worm, *Lanice conchilega*.

The plaice, *Pleuronectes platessa,* is a particularly distinctive flatfish with orange-red spots on skin that is smooth to the touch (**Figure 5.15**). *P. platessa* is associated with sandy substrata where it partially buries itself to provide camouflage. *P. platessa* is an ambush predator but is limited in its prey choices by its comparatively small mouth. Plaice have been noted as being experts in nipping off the protruding siphons of buried bivalves (Wheeler 1978; Dipper 2001) and the fact that they have larger teeth on their lower jaws makes them well adapted for this feeding method. Adult plaice also consume whole molluscs, crushing them with their strong pharyngeal teeth (Dipper 2001; Amezcua et al. 2003; Kay and Dipper 2009). Plaice known to feed on polychaetes, crustaceans, brittle stars and sand eels (Wheeler 1978; Amezcua et al. 2003).

The two adult *P. platessa* included in this study exploited a small range of prey (8 taxa) and their diet was dominated by the polychaetes *S. spinulosa* (39.37 %IRI) and Opehlia (20.81 %IRI) and mysid shrimp (17.77 %IRI) (**Table 5.16**). These results are consistent with records in DAPSTOM (Pinnegar, 2009) and those in the peer reviewed literature (Amezcua et al., 2003) although molluscs are notable in their absence. Whilst it is impossible to draw any firm conclusions from the analysis of two fish guts, the dominance of *S. spinulosa* in the diet of these individuals does indicate that this species will utilise the reefs as a source of food and that this species may be capable of crushing up the reef structures to expose the worms as was previously postulated by Holt et al. (1998).

Table 5.16 The relative importance of all prey taxa averaged across adult *Pleuronectes platessa* (n=2) in terms of abundance (%N), biomass (%W), frequency of occurrence (%O), index of relative importance (IRI) and overall importance (%IRI). Unidentifiable gut content and parasites were excluded from this analysis.

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
Sabellaria spinulosa	36.36	42.38	50	3937	39.37
Ophelia	13.64	27.99	50	2081	20.81
MYSIDACEA	9.09	26.45	50	1777	17.77
CRUSTACEA	13.64	2.37	50	800	8.00
Atylus falcatus	9.09	0.25	50	467	4.67
Terebellidae	9.09	0.19	50	464	4.64
POLYCHAETA	4.55	0.24	50	239	2.39
OSTEICHTHYES	4.55	0.13	50	234	2.34

***Scyliorhinus canicula* – Lesser Spotted Dogfish**

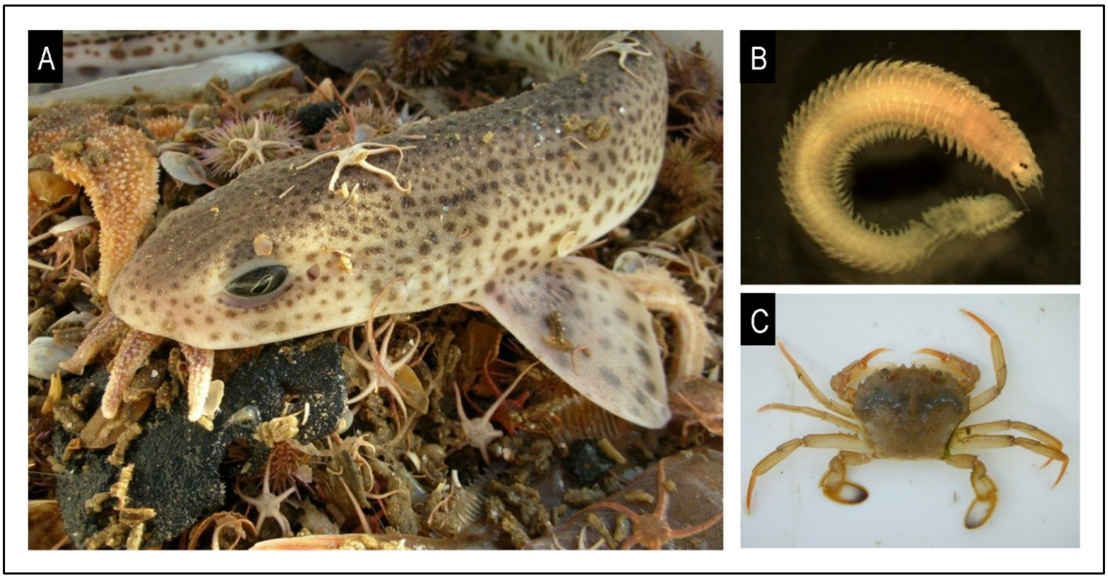


Figure 5.16 Photographs of the Lesser Spotted Dogfish, Scyliorhinus canicula (A) and two of the prey items identified in the stomach contents of 1 specimen collected in association with Sabellaria spinulosa reefs at the East Coast REC study site: B) the nereid worm, Nereis zonata and C) the swimming crab *Liocarcinus depurator* (a decapod crustacean). Note that this specimen was dead upon retrieval of the trawl.

The dogfish, *Scyliorhinus canicula* (**Figure 5.16**) is a small shallow water shark with an inferior or sub-terminal mouth, set quite far back on underside of body, indicative of a bottom feeder. Nine different tooth types have been recorded from the Smallspotted Catshark. These range from strongly oblique with single cusps to erect with five cusps (SharkTrust 2010). *S. canicula* is a demersal scavenger that shows a preference for crustaceans in its diet, although it often relies on fisheries discards as a source of food (Olaso et al. 2002) as well as hunting for small demersal fish species (Kay and Dipper 2009). It also tends to show a preference for easily accessible prey such as small benthic invertebrates, particularly following a period of disturbance such as trawling (Kaiser and Spencer 1994). One *S. canicula* gut was analysed for this study, which was taken from a juvenile that was found to be dead upon retrieval of the trawl (**Table 5.2**). A limited range of prey (2 taxa) were found in the single *S. canicula* gut analysed. The majority of the gut biomass was made up by nereid remains which was the most important prey taxon in the diet (70.88 %IRI) (**Table 5.17**). The rest of the prey in the *S. canicula* gut were identified as decapod remains (29.12 %IRI). The diet observed here is consistent with published records of *S. canicula* diet (Kaiser and Spencer 1994; Olaso et al. 2002) and do not indicate any particular reliance on *S. spinulosa* reefs for food.

Table 5.17 The relative importance of all prey taxa of juvenile *Scyliorhinus canicula* (n=1) in terms of abundance (%N), biomass (%W), frequency of occurrence (%O), index of relative importance (IRI) and overall importance (%IRI). Unidentifiable gut content and parasites were excluded from this analysis.

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
Nereididae	50.00	91.76	100	14176	70.88
DECAPODA	50.00	8.24	100	5824	29.12

***Platyichthys flesus* - Flounder**

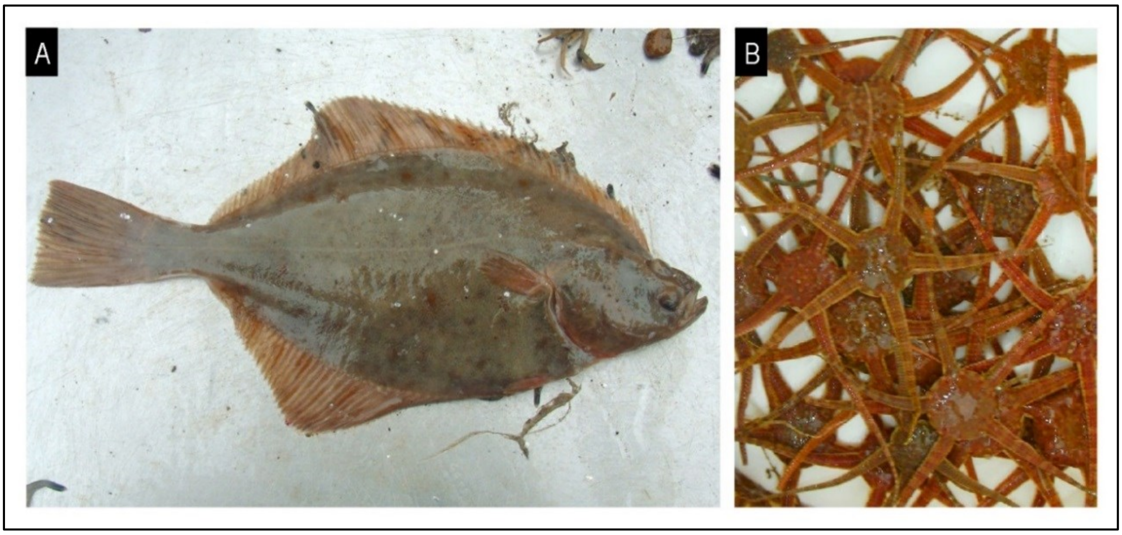


Figure 5.17 Photographs of the Flounder, *Platichthys flesus* (A) and the single prey item identified in the stomach contents of 1 specimen collected in association with Sabellaria spinulosa reefs at the East Coast REC study site: B) the brittle star, *Ophiura albida*.

The flounder, *Platichthys flesus,* (**Figure 5.17**) is an opportunistic feeder that preferentially feeds on the most dominant fauna, ranging from polychaetes and oligochaetes to crustaceans, echinoderms and small molluscs (Maes et al. 2003; Andersen et al. 2005; Dolbeth et al. 2008; Teixeira et al. 2010). Andersen et al. (2005) and Dolbeth et al. (2008) found that juvenile flounder feed preferentially on *Corophium* spp. where they are abundant. Ontogenetic dietary shifts have also been noted in *P. flesus* with a progression in their target prey reflecting their growing body size (Andersen et al. 2005). As only a single gut content was analysed (**Table 5.2**) it is impossible to draw any conclusions on the dietary preferences of this species in the East Coast REC study area, but this result does indicate that high abundances of *O. albida* may be associated with *S. spinulosa* reefs.

Table 5.18 The relative importance of all prey taxa of adult *Platichthys flesus* (n=1) in terms of abundance (%*N*), biomass (%*W*), frequency of occurrence (%*O),* index of relative importance (IRI) and overall importance (%*IRI*). Unidentifiable gut content and parasites were excluded from this analysis.

Juveniles

Prey Taxa	% N	% W	% O	IRI	%IRI
Ophiura albida	100	100	100	20000	100

Summary of the Diet of Demersal Fish Associated with *Sabellaria spinulosa* Reefs

There is a high degree of variability between the prey choices made by the 16 fish species collected from *Sabellaria spinulosa* reefs in the East Coast REC study area as summarised in **Table 5.19**. Despite this variability, there are some clear indications that the presence of *S. spinulosa* reefs has some influence on the prey available to these fish species. Of the 16 species included in this study, only three showed signs of a possible shift in feeding behaviour that could be related to the presence of *S. spinulosa* reefs (Table 5.19). The Dover sole, *Solea solea*, is known to feed preferentially on infaunal polychaetes such as the nereid polychaetes or rag worms and molluscs and its mouth is well adapted for sucking-up and grasping this type of prey (Wootton 1990; Gerking 1994; Cabral 2000; Amezcua et al. 2003). In contrast, the Dover sole examined in this study were feeding on more epifaunal species, including *S. spinulosa*, which was the most important prey item for the juvenile fish. Trumpet worms, belonging to the family Pectinariidae were the most important prey for the adult Dover sole but sea anemones were also found to be an important prey item. This indicates a shift in the feeding behaviour of Dover sole towards more epifaunal species, especially in the juveniles, which may have been caused by the presence of *S. spinulosa* reefs (Gerking 1994). The sea scorpions, *Tauralus bubalis*, included in this study were all adults and they also showed a marked difference in their diet compared with records in DAPSTOM, switching from a predominantly piscivorous diet to one that is dominated by crustaceans (**Table 5.19**). *T. bubalis* has not however, been the subject of any formal feeding studies and there were relatively few records in DAPSTOM so this may simply be an indication that this species is a generalist feeder, taking advantage of whatever prey items are most abundant. The final species which exhibited a marked difference in its diet compared with published records was the poor cod, *Trispoterus minutus*, which again were all adults. Poor cod are known to exhibit dietary partitioning based on size, with juveniles feeding primarily on small crustaceans whilst the adults feed on larger crustaceans and fish (Armstrong 1982; Morte et al. 2001). Here the adults were found to have a diet dominated by Mysid shrimp which would more typically be associated with juveniles of the same species. Mysid shrimp were not recorded in the trawl or grab samples taken serendipitously from the reefs in this area as they are too small to be retained in the trawls and would move out of the way of a grab (SanVicente and Sorbe 1995; Rappe et al. 2011)., but very high abundances of mysids were observed in seabed footage taken of the reef (Limpenny et al. 2011; Pearce et al. 2011b). It is possible therefore that this species is utilising a prey item that are available in high abundances in the reef habitat, although the small sample size (n=3) and lack of equivalent samples from adjacent sedimentary habitats means it is impossible to make any firm conclusions.

Possible changes in feeding behaviour which could be related to the presence of the *S. spinulosa* reef were only identified in three species. However, a further 5 of the 24 predator groups studied were feeding on *S. spinulosa* itself including juvenile plaice, dab and Dover sole (**Table 5.19**). Holt et al. (1998) postulated that flatfish could easily obtain *S. spinulosa* by crunching up their tubes and the results here support this assertion, although direct observations would be required to determine the mechanism through which they are obtaining this prey. *S. spinulosa* also formed a key component in the diet of *P. gunnellus* and *C. lyra*, both of which are important prey items in the diet of higher predators including other fish, seabirds and otters (Watt 1995; Greenstreet et al. 1998; Kingston et al. 1999; Carss and Elston 2003; Lilliendahl and Solmundsson 2006), providing evidence that this habitat may play an important role in supporting marine food webs.

Furthermore, with only a few exceptions, the demersal fish included in this study were found to be feeding on fauna that have been recorded in very high abundances on the reefs, including the porcelain crab *P. longicornis* the amphipods *Gamarellus homari, Abuldomelita obtusata* and *Atylus swammerdamei* and mysid shrimps (Limpenny et al. 2011; Pearce et al. 2011b). We can conclude then, that fish are utilising the *S. spinulosa* reefs in this area for food and that the reefs play a part in supporting higher trophic levels here. Unfortunately, due to the limitations in the sampling employed, it is not possible to assess the relative importance of this habitat for fish feeding compared to nearby sedimentary habitats.

Table 5.19 Comparison between the three most significant prey taxa (% IRI) in the diets of the demersal fish sampled from *Sabellaria spinulosa* reefs in the East Coast REC study area, and those identified from published records and dietary records held in the Integrated Database and Portal for Fish Stomach Records (DAPSTOM) (Pinnegar 2009). Initial observations regarding possible changes to the feeding behaviour of the fish and / or the composition of their diet that could be attributable to the presence of *S. spinulosa* reefs have also been made. *See earlier sections of this report for details of the literature consulted in this review.

Scientific Name & Developmental Stage		**n**	**Most Important Prey Taxa** (%*IRI* This Study)			**Most Important Prey Taxa** (Published Records / DAPSTOM)*			**Feeding Behaviour**	**Diet**
			1	**2**	**3**	**1**	**2**	**3**		
Pholis gunnellus	Adult	44	*Pisidia longicornis*	*Sabellaria spinulosa*	AMPHIPODA	AMPHIPODA	ISOPODA	"Benthic Invertebrates"	No change	Feeding on reef fauna inc *S. spinulosa*
	Juvenile	2	*Abludomelita obtusata*	Podoceridae	AMPHIPODA					
Solea solea	Adult	4	*Lagis koreni*	Pectinariidae	ACTINIARIA	Nereidae	POLYCHAETA	MOLLUSCA	Shift from infaunal to epifaunal species	Juveniles feeding on *S. spinulosa*
	Juvenile	41	*Sabellaria spinulosa*	POLYCHAETA	Pectinariidae					
Limanda limanda	Adult	2	*Ophiura ophiura*	*Crangon crangon*	*Pisidia longicornis*	MOLLUSCA	POLYCHAETA	ECHINODERMATA	No change	Feeding on reef fauna inc *S. spinulosa*
	Juvenile	43	*Sabellaria spinulosa*	ACTINIARIA	AMPHIPODA					
Ciliata septentrionalis	Adult	39	CRUSTACEA	DECAPODA	*Pisidia longicornis*	*Galathea*	*Pisidia*	MYSIDACEA	No change	Feeding on reef fauna
	Juvenile	1	AMPHIPODA	CRUSTACEA	POLYCHAETA					
Agonus cataphractus	Adult	13	*Pisidia longicornis*	CRUSTACEA	*Crangon almanni*	CRUSTACEA	DECAPODA	AMPHIPODA	No change	Feeding on reef fauna
	Juvenile	15	*Pisidia longicornis*	DECAPODA	AMPHIPODA					
Callionymus lyra	Adult	6	OPHIUROIDEA	AMPHIPODA	Nereidae	POLYCHAETA	ECHINODERMATA	MOLLUSCA	No change	Feeding on reef fauna inc *S. spinulosa*
	Juvenile	18	*Sabellaria spinulosa*	AMPHIPODA	*Pisidia longicornis*					
Echiichthys vipera	Adult	9	*Gammarellus homari*	AMPHIPODA	MYSIDACEA	CRUSTACEA	MYSIDACEA	AMPHIPODA	No change	Feeding on reef fauna
	Juvenile	11	*Schistomysis spiritus*	MYSIDACEA	*Atylus swammerdamei*					
Myoxocephalus scorpius	Juvenile	11	CRUSTACEA	*Pisidia longicornis*	DECAPODA	AMPHIPODA	ISOPODA	DECAPODA	No change	Feeding on reef fauna
Merlangius merlangus	Adult	1	MYSIDACEA	~	~	OSTEICHTHYES			No change	Feeding on reef fauna
	Juvenile	8	AMPHIPODA	OSTEICHTHYES	*Atylus swammerdamei*	COPEPODA	MYSIDACEA	CRUSTACEA		
Taurulus bubalis	Adult	5	*Pisidia longicornis*	Paguridae	DECAPODA	OSTEICHTHYES	MOLLUSCA		Shift to crustaceans	Feeding on reef fauna
Hyperoplus lanceolatus	Adult	2	COPEPODA	Nereidae	CRUSTACEA	OSTEICHTHYES	"Benthic Invertebrates"		No change	~
	Juvenile	2	COPEPODA	~	~	COPEPODA				
Trisopterus minutus	Adult	3	*Schistomysis spiritus*	CRUSTACEA	MYSIDACEA	DECAPODA	OSTEICHTHYES	POLYCHAETA	Shift to small crustaceans	Possibly feeding in reef fauna
Trisopterus luscus	Juvenile	2	*Schistomysis spiritus*	MYSIDACEA	AMPHIPODA	COPEPODA	MYSIDACEA	*Crangon crangon*	No change	Possibly feeding in reef fauna
Pleuronectes platessa	Juvenile	2	*Sabellaria spinulosa*	*Ophelia*	MYSIDACEA	MOLLUSCA	POLYCHAETA		No change	Feeding on reef fauna inc *S. spinulosa*
Scyliorhinus canicula	Juvenile	1	Nereidae	DECAPODA	~	DECAPODA	OSTEICHTHYES		No change	~
Platichthys flesus	Adult	1	*Ophiura albida*	~	~	POLYCHAETA	OLIGOCHAETA	CRUSTACEA	No change	Possibly feeding in reef fauna

5.3.2 Dietary Trends in Fish Associated with Sabellaria spinulosa reefs

Multivariate analysis of the gut content data revealed four statistically significant feeding groups, using a SIMPROF test set at the 10% significance level, ranging in size from 2 to 5 predator groups (**Figure 5.18**). A SIMPER analysis revealed the prey taxa that contributed to the similarity within each of the feeding groups as well as the dissimilarity between them (as summarised in **Table 5.19**). The four feeding groups are represented by different colours in the group sorting dendrogram (**Figure 5.18**) and have been named according to their equivalent feeding mode functional group (FMFG) proposed by (Elliott et al. 2007) and the dominant prey species in the corresponding nMDS plot (**Figure 5.19**). All of the fish included in this analysis were identified as being zoobenthivores (ZB), that is fish feeding primarily on invertebrates associated with the substratum, and the vast majority of those were identified as feeding mostly on epifaunal animals (ZB-E), although one group was found to be feeding mostly on the hyperbenthos (ZB-H), in this case Mysid shrimp (Elliott et al. 2007).

Adult Dover sole, *Solea solea* (SOL (A)), and sea scorpion, *Tauralus bubalis* (TAU (A)), had quite different diets from all of the other fish included in the study and hence did not fall into any of the four feeding groups or guilds. Adult Dover sole were feeding on *S. spinulosa* like the juveniles of this species, but in contrast to the juveniles, trumpet worms (Pectinariidae) were their most important prey. The porcelain crab, *Pisidia longicornis*, was found to be the main prey of adult *T. bubalis*, as it was for many other predator groups included in this study. *P. longicornis* was however, more dominant in the diet of *T. bubalis* and they were also found to feed on hermit crabs which were largely absent from the diet other fish included in this analysis.

The predator groups belonging to the “ZB-H Mysid Feeders” guild were, as the name suggests, feeding primarily on mysid shrimps which are known to be an important food resource for demersal fish (Hostens and Mees 1999). The majority of the fish belonging to this guild are small gadoids which are known to have considerable overlap in their diets (Armstrong 1982; Hamerlynck and Hostens 1993; Greenstreet et al. 1998; Hostens and Mees 1999). An interesting addition to this widely recognised feeding group is the lesser weever, whose diet has also been reported to contain mysids and amphipods but has not previously been linked with gadoids (Vasconcelos et al. 2004).

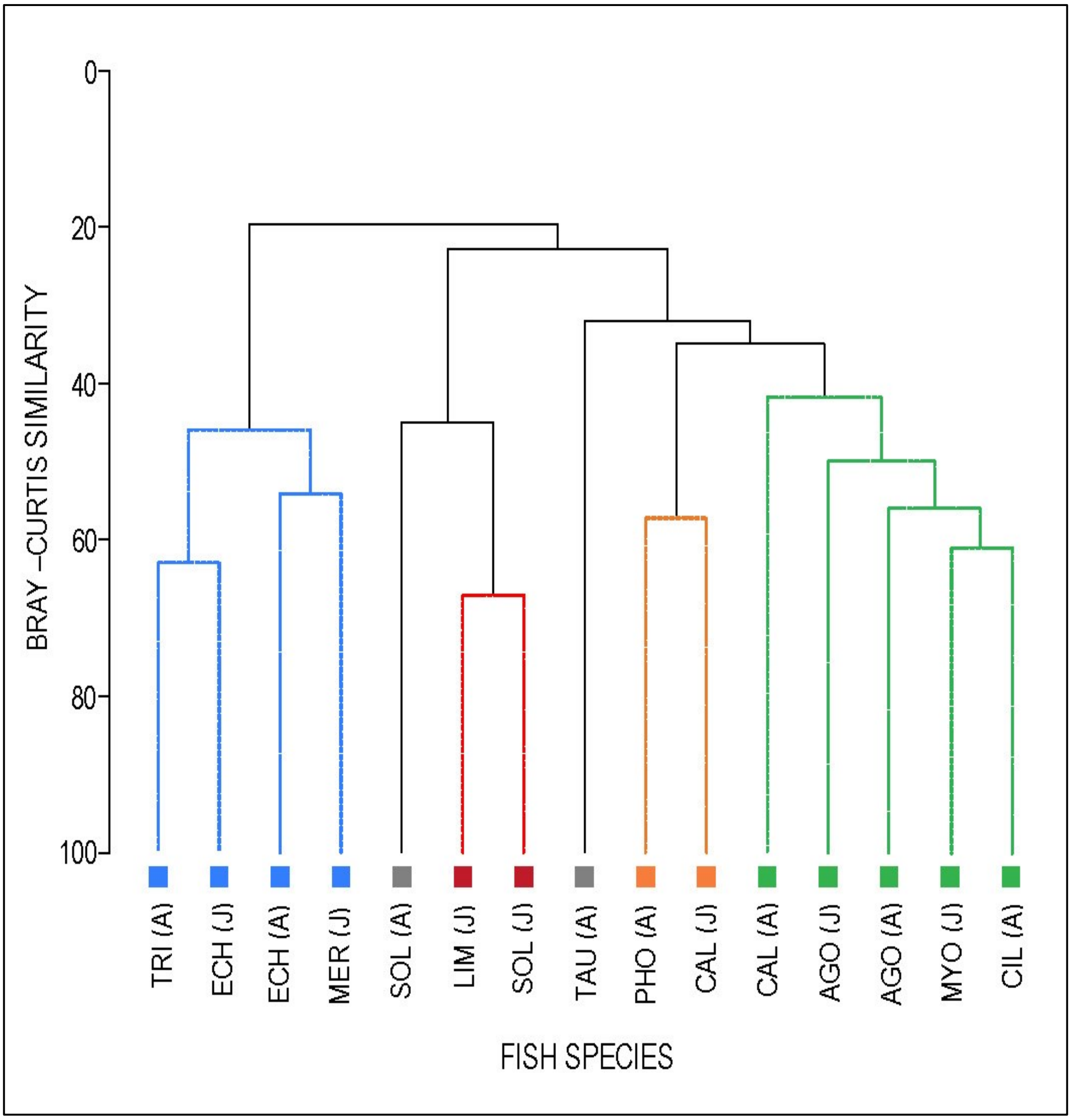


Figure 5.18. Group average sorting dendrogram based on a Bray-Curtis similarity matrix of standardised gut content (abundance) data averaged by fish species *Pholis gunnellus* (PHO), *Solea solea* (SOL), *Limanda limanda* (LIM), *Ciliata septentrionalis* (CIL), *Agonus cataphractus* (AGO), *Callionymus lyra* (CAL), *Echiichthys vipera* (ECH), *Myoxocephalus scorpius* (MYO), *Merlangius merlangus* (MER), *Tauralus bubalis* (TAU), *Hyperoplus lanceolatus* (HYP), *Trisopterus minutus* (TRM), *Trisopterus luscus* (TRL) and *Pleuronectes platessa* (PLE) and their developmental stage, adult (A) and juveniles (J). Overlaid on this cluster are the four statistically significant groups identified using a SIMPROF test (5%). Flounder and dogfish were removed from the analysis due to the small sample size (n=1). Unidentifiable gut content and parasites were also excluded from the analysis

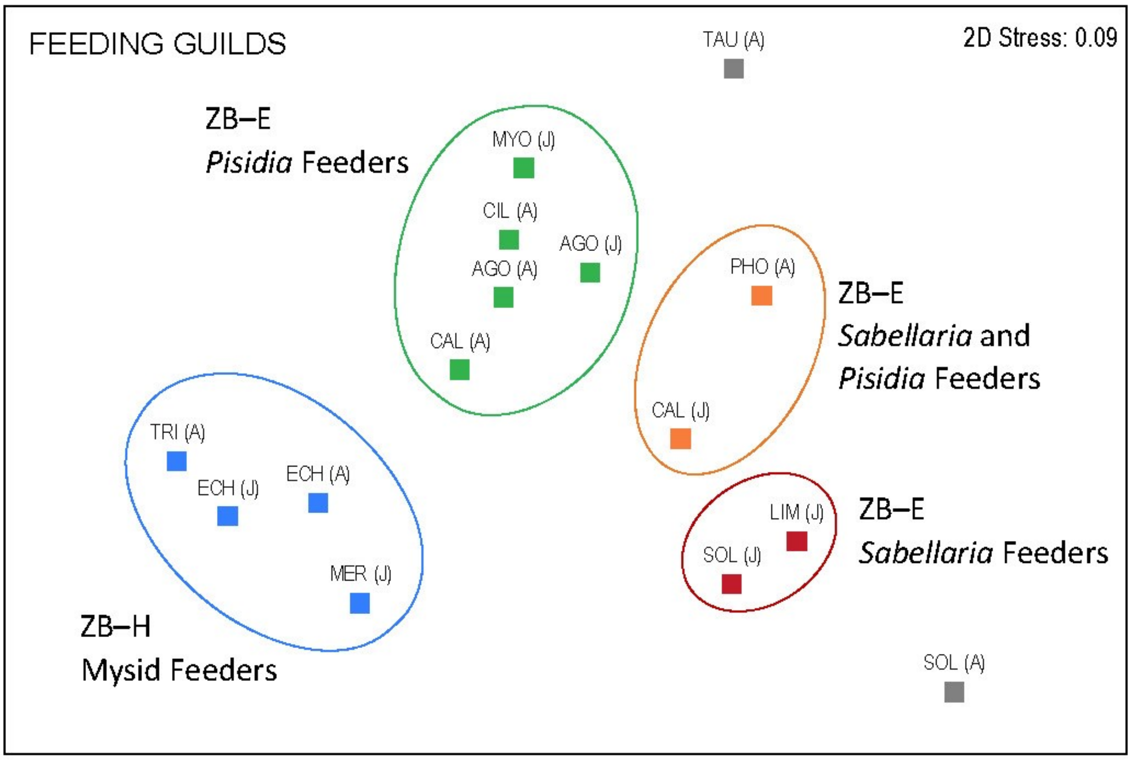


Figure 5.19. Two-dimensional MDS ordination based on a Bray-Curtis similarity matrix of standardised gut content (abundance) data averaged by predator group (fish species and development stage; see legend for **Figure 5.18** for codes). Overlaid on this plot are the feeding groups identified using a SIMPROF test (5%). These groups have been named according to their equivalent feeding mode functional group (FMFG) proposed by (Elliott et al. 2007) where ZB-H = Zoobenthivore-hyperbenthos and ZB-E = Zoobenthivore-epifauna, and the dominant prey species. Fish groups with ≤2 individuals were excluded in this analysis (**Table 5.2**). Unidentifiable gut content and parasites were also excluded from this analysis.

Some mysid species, including the two species identified in stomach contents in this study, *Schistomysis spiritus* and *Gastrosccus spinifer,* live all or part of their lives associated with the water layer adjacent to the seafloor, the suprabenthos or hyperbenthos (Williams and Collins 1984; SanVicente and Sorbe 1995; Cunha et al. 1997; Dewicke et al. 2003; Rappe et al. 2011), whilst others are wholly pelagic (Viherluoto and Viitasalo 2001). Since many of the mysid shrimp consumed could not be identified to species level it is impossible to determine whether or not they were all associated with the *S. spinulosa* reefs. However, as many of the fish belonging to the “ZB-H Mysid Feeders” guild were also feeding on benthic species associated with the reefs, it seems likely that the mysids are also associated with the reef in some way.

High densities of mysid shrimp were observed in video footage collected from the reefs providing further evidence of this association (Limpenny et al. 2011; Pearce et al. 2011b).

Table 5.20 Summary of the average abundance of prey taxa that contribute to ≥2% of the dissimilarity between the diets of demersal fish belonging to the feeding guilds identified by multivariate analysis of the stomach contents of demersal fish collected from *Sabellaria spinulosa* reefs in the East Coast REC study site (**Figure 5.18** and **Figure 5.19**). The predator groups (defined by fish species and development stage) belonging to each guild (see legend for **Figure 5.18** for codes) and the average similarity is also shown along with the average similarity within each guild. The feeding guilds have been named in accordance with the "Feeding Mode Functional Groups" proposed by (Elliott et al. 2007) where ZB-H = Zoobenthivore-hyperbenthos and ZB-E = Zoobenthivore-epifauna.

Feeding Guild	**ZB-H** **Mysid Feeders**	**ZB-E** ***Pisidia* Feeders**	**ZB-E** ***Sabellaria* & *Pisidia* Feeders**	**ZB-E** ***Sabellaria* Feeders**
Average Similarity	**50.12**	**48.98**	**57.22**	**67.09**
Predator Groups	**TRI (A)** **ECH (J)** **ECH (A)** **MER (J)**	**CAL (A)** **AGO (J)** **AGO (A)** **CIL (A)** **MYO (J)**	**PHO (A)** **CAL (J)**	**LIM (J)** **SOL (J)**
Prey Taxa				
Sabellaria spinulosa	0.39	2.81	19.95	43.93
Pisidia longicornis	0	14.36	25.87	2.67
CRUSTACEA	16.49	17.96	4.2	3.47
AMPHIPODA	10.29	6.8	10.97	6.13
DECAPODA	1.98	11.19	11.19	2.39
POLYCHAETA	1.4	9.43	1.37	9.28
Schistomysis spiritus	19.96	0.14	0	0.44
MYSIDACEA	17.18	0.41	0	0.83
Atylus swammerdamei	7.37	2.11	2.88	2.06
Gammarellus homari	5.82	1.03	1.44	0.33
ACTINIARIA	0	0	0	8.18
Podoceridae	0.41	1.82	4.93	0
Crangon crangon	4.17	1.79	0	0.48
Pectinariidae	0	0	1.05	4.25
Galathea intermedia	0	3.71	0.42	0.16
Crangon allmanni	0.31	2.75	0.77	0.3
COPEPODA	0	0	3.58	0
PELECYPODA	0	0	2.69	0.48

Fish from the remaining three groups fed primarily on benthic prey known to be associated with the *Sabellaria spinulosa* reefs (**Chapter 4**) in the East Coast REC study area. They can be considered as three different feeding guilds based on their respective dominant prey taxa. Juvenile Dover sole and dab form a feeding guild whose diet is dominated by *S. spinulosa* (ZB-E *Sabellaria* Feeders). Adult butterfish, *P. gunnellus* and juvenile dragonet, *C. lyra* form another feeding guild whose diet is dominated by *S. spinulosa* and *P. longicornis* in roughly equal proportions (ZB-E *Sabellaria* and *Pisidia* Feeders). The remaining small demersal fish form a feeding guild whose diet is dominated by *P. longicornis* (ZB-E *Pisidia* Feeders).

5.4 Conclusions

The diets of fish sampled from *S. spinulosa* reefs in the East Coast REC study area are broadly comparable to published records, indicating that the presence of the reef is not radically altering fish feeding behaviour. Exceptions to this included, Dover sole which appeared to shift its feeding behaviour to feed on more epifaunal species including *S. spinulosa* and sea anemones (Actiniaria). It is not clear however, whether this shift has been caused by the increased abundance of these prey items on the reef or the fact that the reef has to some extent excluded the sandy substrates in which it would normally hunt for its prey (Amezcua et al. 2003). The adult poor cod included in this study also appear to show a shift in their feeding behaviour, with a diet more typically associated with juveniles of this species (Armstrong 1982). The switch from a piscivorous diet to one dominated by small mysid shrimp, may reflect the high abundances of mysid shrimp seen in association with the reefs on video footage (Limpenny et al. 2011; Pearce et al. 2011b) or it could reflect a decline in its normal target prey species. A similar shift in the feeding behaviour of the sea scorpion, *Tauralus bubalis*, was noted although this species has not been the subject of any formal dietary assessments and there were only a very small number of records in DAPSTOM. This species was nevertheless found to shift from a piscivorous diet to one dominated by crustaceans. Crustaceans are known to be an important component in the diet of demersal fish species (Elliott et al. 2002) and given that there is now evidence that this habitat supports an increased abundance of crustacean, it does seem likely that it will play some role in supporting marine food webs.

Despite the similarities observed between published records and the diets recorded in this study, there were notable differences which suggest that most of the fish species included here are feeding on the *S. spinulosa* reefs from which they were sampled. Fish that were feeding directly on the benthos were feeding on either *S. spinulosa* itself or fauna that is typically present in high abundances on *S. spinulosa* reefs (**Chapter 4**), including *Pisidia longicornis* and a variety of amphipods and Mysid shrimp. *Sabellaria spinulosa* had not previously been reported as being an important prey item in the diet of any of the fish included in this study, although Holt et al. (1998) has previously suggested that flatfish were likely to feed on *S. spinulosa* and a small number of records held in the DAPSTOM database (Pinnegar 2009) indicate that *S. spinulosa* is eaten sporadically by dab, *Limanda limanda*.

The fish associated with the reefs form four feeding guilds: ZB-H Mysid Feeders, ZB-E *Pisidia* Feeders, ZB-E *Sabellaria* and *Pisidia* Feeders and ZB-E *Sabellaria* Feeders. Of all of the feeding guilds identified, ZB-E *Sabellaria* Feeders and ZB-E *Sabellaria* and *Pisidia* Feeders are the only ones that can be unequivocally linked to the reef habitat. *S. spinulosa* was identified as the main prey item in the diets of juvenile Dover sole, plaice, dab and dragonet as well being the second most important prey item for adult butterfish. That *S. spinulosa* was found to be such an important prey item in the diet of so many juvenile fish, and a greater proportion of juveniles were sampled from this habitat than adults (1.2:1) especially within the gadoids and flatfish species (8.8:1) could indicate that this habitat also provides and important nursery ground for some fish species, an aspect of *S. spinulosa* reef ecology that has not yet been considered. *S. spinulosa* reefs are inherently patchy structures and the gaps within the reef may provide important refugia for juvenile fish to escape predation, as is the case in other biogenic habitats (Borg et al. 2006; Bouma et al. 2009; Rabaut et al. 2010)

The remaining two benthic feeding guilds seem to be predating selectively on fauna that are associated with the reefs in high abundance, including the long clawed porcelain crab, *Pisidia longicornis* and mysid shrimp. However, these species also occur in sedimentary habitats, albeit in smaller numbers (**Chapter 4**) and hence more work would be required to investigate this trophic association more fully. It is assumed that the foraging range of the fish sampled here is less than the area of the reef habitats from which they were sampled (7.75 km^2 – 49.87 km^2). However, as this is not known for most of the species included in this study it is possible that these fish are feeding on adjacent sedimentary habitats as well as, or instead of, on the reefs themselves.

The widely recognised gadoid feeding guild, including whiting, *Merlangius merlangus* and bib, *Trispoterus luscus* (Armstrong 1982; Hamerlynck and Hostens 1993; Greenstreet et al. 1998; Hostens and Mees 1999) were found to have considerable dietary overlap with the lesser weever, *Echiichthys vipera*, and together formed the ZB-H Mysid Feeder guild. Whilst mysids have previously been recorded as an important prey item for the species included in this guild (Armstrong 1982; Hostens and Mees 1999; Vasconcelos et al. 2004), this is the first time that the dietary overlap between gadoids and the lesser weever has been reported. This could indicate that previous studies investigating the dietary partitioning among gadoids have underestimated the competitive pressures exerted on this predator group.

5.5 Limitations

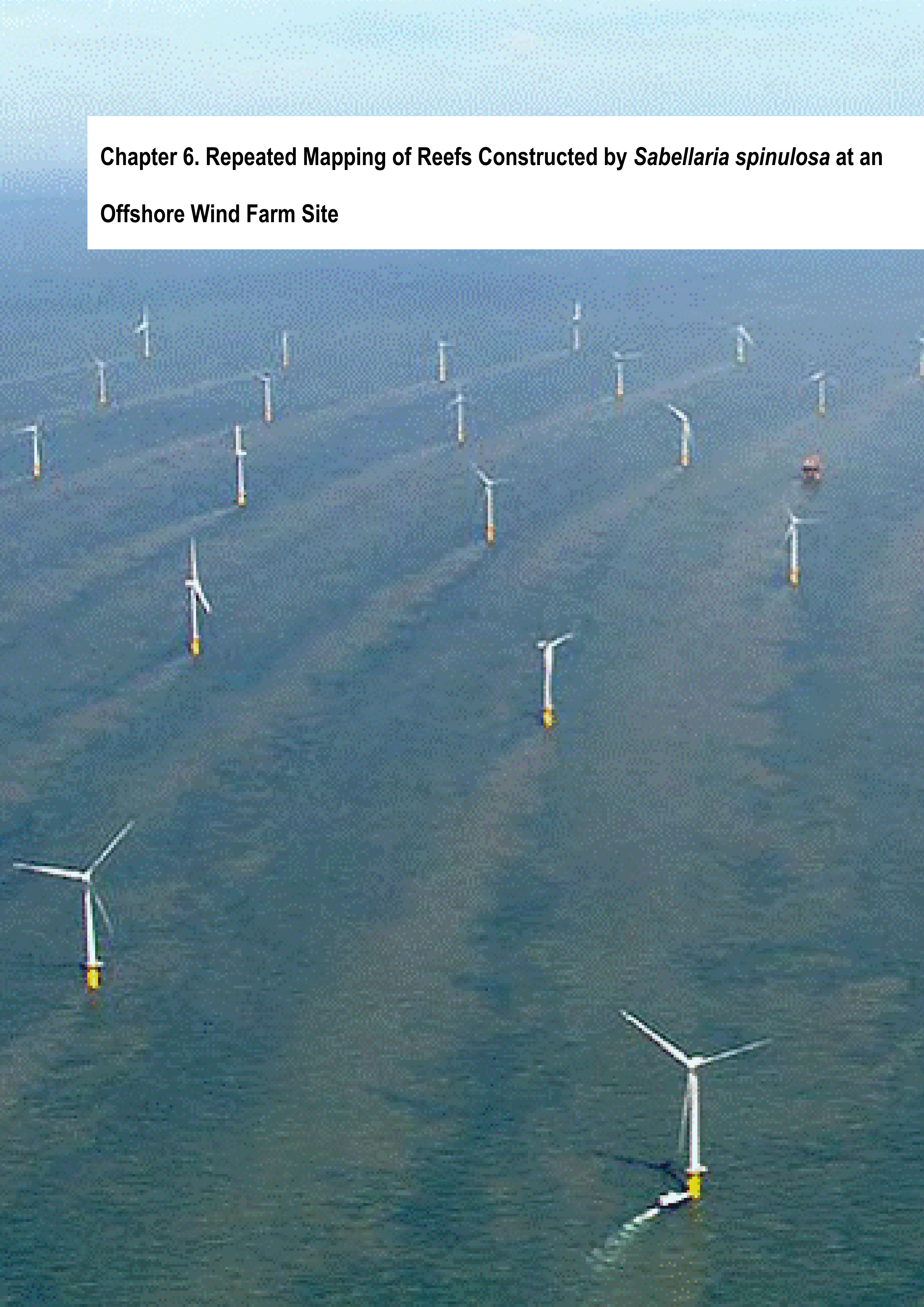
A number of limitations have been identified within this study, the most notable being the absence of structured sampling to include individuals from on and off the reef habitats. This was not possible due to the serendipitous nature in which these samples were obtained, and the limited time and sample processing materials available for this additional and unplanned component of the survey cruise. Sampling fish on and off the reefs in the same broad area would have facilitated an assessment of the degree to which the presence of the reef was influencing both the diet and the feeding behaviour of the fish included in this study. Concurrent sampling of prey populations would also have facilitated and investigation into the degree of selectivity in the feeding behaviour of the fish studied (Hinz et al. 2005).

The low numbers of fish specimens examined, has limited both the analyses that could be undertaken and the confidence or statistical power of the conclusions made. For example niche breadth (H’) was found to be positively correlated with the number of specimens examined in the each group, casting doubt on its utility in this context. As *S. spinulosa* reefs are listed under the Habitats Directive (EC 2013) and the OSPAR list of threatened and endangered habitats (OSPAR 2008), direct sampling of this habitat is rarely permitted. It might be possible to set traps for fish to sample this component of the marine food web more comprehensively, but as such devices usually rely on food bait this is not considered to be the most appropriate sampling method for studies relying on gut content analysis. An alternative may be to request that fish are retained from any incidental sampling of this habitat to expand on the analyses presented here.

Ontogenetic shifts in diet are commonplace in marine fish and are a considerable source of variability in both feeding behaviour and prey choice. Species were separated based on their developmental stage (based on length: **Table 5.1**), which appears to have been successful as dietary differences were detectable at this level for the majority of species studied. However, had a greater number of fish been available for inclusion in this study it would have been preferable to investigate ontogenetic shifts for each fish population individually, as some species may have more than one shift in their diet. Detailed population level investigations would also mean that regional differences in the size structure of fish populations would be identified.

Another limitation of this, and any, study using stomach content analysis is the variability in evacuation or digestion rates that exists between different prey types (Andersen and Beyer 2008; Couturier et al. 2013) and between different predator species. Although gastric evacuation models have been proposed for some well-studied groups such as the gadoids (Andersen 2001) the evacuation rates have not previously been studied for many of the species included in this investigation, and hence no attempt was made to account for, or quantify this source of variation. A great deal more work on the diets of small demersal fish, and on the digestion of individual species would be required before digestion rates could be incorporated in studies of this nature. There are recognised differences between the evacuation rates of soft and hard bodied prey (Couturier et al. 2013) which could mean that the importance of crustacean prey is overestimated. The fact that these analyses were able to detect diets dominated by soft bodied species and mixed diets as well as those dominated by hard bodied species must, however, give some confidence that dietary preferences are being accurately detected.

Chapter 6. Repeated Mapping of Reefs Constructed by *Sabellaria spinulosa* at an Offshore Wind Farm Site



6.1 Introduction

The global environmental benefits of offshore wind energy developments are undisputed and there is considerable political support for the continued expansion of this industry (Brennand 2004; Portman et al. 2009; Saidur et al. 2010; Baltas and Dervos 2012). As in any industry however, there are environmental impacts associated with construction, operation and decommissioning activities and it is vital that these are given due consideration. The UK currently has the largest installed offshore wind capacity in the world, exceeding 3GW (BVG 2013). Predicted expansions in the industry could see this figure rise to 18 GW by 2020. There has been a greater than tenfold increase in the generation capacity of wind turbines since the first wind farm was installed in UK waters, although this has not resulted in an equivalent reduction in the overall size of each development. The footprint of individual wind farms has steadily increased in-line with the UK governments renewable energy targets (Brennand 2004). Under Round 1 of the UK's offshore wind farm development scheme, administered in December 2000, sites ranged from 4 to 45 km^2 (mean 13 km^2) (4COffshore 2013). Under Round 2 of the scheme, development sites ranged in size from 8 to 230 km^2 (mean 70 km^2) (4COffshore 2013). Many of the Round 1 and Round 2 sites were subsequently extended and nine significantly larger zones were designated for offshore wind development under Round 3 in January 2010. The Round 3 zones range in size from 162 km^2 (Rampion Offshore Wind Farm) to 8,660 km^2 (Dogger Bank) (4COffshore 2013). The ambition is that the larger Round 3 zones will ultimately house multiple adjacent wind farms that will collectively produce a total output of 33 GW. The rate at which the offshore wind industry is developing and the fact that these developments are occurring against a backdrop of unprecedented levels of anthropogenic disturbance (Blaber et al. 2000; RCEP 2004; Kaiser et al. 2006; Cardoso et al. 2008; Tappin et al. 2010; Merchant et al. 2012) makes environmental consideration all the more important.

In a widely cited review of the potential impacts of offshore renewable energy developments Gill (2005) identified numerous sources of likely environmental damage. Abbasi and Abbasi (2000) concluded that the adverse environmental impacts associated with renewable energy sources could be as strongly negative as the impacts of conventional energy sources. In contrast, there is a growing body of thought that offshore renewable energy developments may enhance the marine environment by creating artificial reef habitats, by acting as aggregation devices for fish and by forming *de-facto* marine reserves by excluding other sea users (Wilhelmsson et al. 2006; Wilson et al. 2007; Wilhelmsson and Malm 2008; Inger et al. 2009; Wilson and Elliott 2009; Reubens et al. 2011; Reubens et al. 2013a; Reubens et al. 2013b; Reubens et al. 2013c; Ashley et al. 2014). This is of course dependent on the environment being given careful consideration during the planning and design phases and would only apply where developments occur in non-pristine environments.

Knowledge of the distribution, quality and quantity of habitats and species, is fundamental to our ability to protect them (Jackson et al. 2001). Historically, distribution records were based entirely on point observations and samples but this changed with the wide acceptance of remote sensing techniques in the early 1990s. Remote sensing techniques, most notably sidescan sonar and multibeam echo sounder (MBES) systems are now considered the tool of choice when mapping large areas of the seabed (Coggan et al. 2007). These survey tools are able to ensonify large areas of the seabed with 100% coverage at a resolution finer than 1m^2 (Anderson et al. 2008a). Sidescan sonar and MBES data can be used to define roughness characteristics, acoustic properties and morphological features of the seabed which in turn can be used to map habitat boundaries (Brown and Blondel 2009). In recent years this mapping process has been taken a step further with the incorporation of biological ground-truthing. Acoustic signatures have been found to behave as reliable surrogates of biotopes, and with sufficient ground-truthing can be used to create full coverage biotope maps with moderate to high levels of confidence (Brown and Collier 2008; Ierodiaconou et al. 2011; Micallef et al. 2012). A number of studies have demonstrated the utility of very-high resolution acoustic data in mapping discrete biological features such as the reefs formed by the tube-worm *Lanice conchilega* (Degraer et al. 2008), the horse mussel *Modiolus modiolus* (Wildish et al. 1998; Lindenbaum et al. 2008) and seagrass beds (Ardizzone et al. 2006).

Aggregations of the tubiculous polychaete *S. spinulosa* were identified within the Thanet offshore wind farm site during baseline characterisation surveys in 2005 (MESL 2005). Where this species forms reef structures, it is considered to be a conservation priority both at a national and European level. *S. spinulosa* reefs are included in the Habitats Directive definition of reef habitats 1070 and may also be afforded protection as features of broader physiographic habitats listed under the directive such as Estuaries (EC 2013). *S. spinulosa* reefs are also listed in the OSPAR list of threatened and / or declining habitats (OSPAR 2008) and are identified as Habitats of Principal Importance under Section 42 of the English

Natural Environment and Rural Communities (NERC) Act 2006. Despite being listed as a habitat of significant conservation importance the definition of what constitutes an *S. spinulosa* reef remains a topic of much discussion (Hendrick and Foster-Smith 2006; Gubbay 2007). The Habitats Directive defines reefs as concretions which arise from the sea floor (EC 2013) whilst the OSPAR definition is based on percent cover (30% on mixed substratum, 50% on rock) but also notes that the habitat should be thick and persistent and support an epibiota that is distinct from surrounding substrata (OSPAR 2008). Gubbay (2007) and Hendrick and Foster-Smith (2006) noted that extent, elevation and patchiness are important attributes for defining an *S. spinulosa* reef and both advocate the use of a sliding scale of “reefiness”. A potential relationship between an irregular acoustic signature and the presence of *S. spinulosa* aggregations that are likely to qualify as reefs of conservation significance based on the aforementioned definitions was noted in Chapter 5. The aim of this study is to test the relationship between the textured signature observed in acoustic data and the presence of *S. spinulosa* reefs that may qualify for statutory protection.

Although the *S. spinulosa* aggregations identified at the site were not protected by any formal conservation designations, the wind farm developer and the UK statutory nature conservation bodies (Natural England and the Joint Nature Conservation Committee (JNCC)) decided at an early stage that it would be favourable to protect the best examples of this habitat during the construction phase with a view to the wind farm potentially acting as a reserve for this habitat in years to come. The work presented here is one of the first examples of an integrated environmental assessment, where conservation agencies and marine scientists have actively worked with the developer to facilitate an environmentally responsible construction process. It presents the first attempt to map *S. spinulosa* reef extent and distribution over time in relation to a new offshore wind farm development, representing an important step forward in our ability to map, monitor and manage sensitive marine habitats in the face of increasing anthropogenic activity.

In order to evaluate the feasibility of using remote sensing technology to delineate *S. spinulosa* reefs and to explore the interaction between the reefs and the construction of an offshore wind farm the following hypotheses have been tested:

Hypothesis E

H_{0E}: Substrates identified as being possible *S. spinulosa* reef using high resolution sidescan sonar are no more likely to contain *S. spinulosa* than areas not identified as being possible reef.

H_{1E}. *Sabellaria spinulosa* are present in significantly higher densities and cover a greater proportion of the substrate in areas identified as possible reef using high resolution sidescan sonar.

Hypothesis F

H_{0F}: *Sabellaria spinulosa* reefs are unchanged in terms of their extent and quality (worm density, % cover or the diversity of associated macrofauna) following the construction of an offshore windfarm.

H_{1F}. There is a reduction in *S. spinulosa* reefs in terms of either their extent or quality (worm density, % cover or the diversity of associated macrofauna) associated with the construction of an offshore windfarm.

H_{2F}. There is an enhancement in *S. spinulosa* reefs in terms of either their extent or quality (worm density, % cover or the diversity of associated macrofauna) associated with the construction of an offshore windfarm.

6.2 Methodology

High resolution acoustic data and seabed images were collected from across the Thanet Offshore Windfarm site, in the southern North Sea, in 2005, 2007 and 2012, corresponding to a baseline, pre-construction baseline and post-construction survey as detailed in **Chapter 2**.

6.2.1 Seabed Image Analysis

Tube counts

Estimates of S. spinulosa density were determined using the open source image processing software, Image J® (Schindelin et al. 2012). The number of tube openings were used as a proxy for the density of live S. spinulosa as animals were completely retracted in the majority of photographs obtained. Image J® standard methods for particle counting were adapted for S. spinulosa density estimations. The process involved image smoothing and sharpening and overlaying a reference grid. Tube openings were counted using the Image J® cell-counting utility. Counts for each image were repeated 3 times and the mean calculated. As this method relies on high quality images with low background noise, images collected in 2005 could not be analysed using this method and 50 of the 268 images collected in 2007 and 2012 also had to be excluded from the analysis due to high levels of background noise, poor focus and / or high turbidity levels.

Percent Cover Calculations

The total percent cover of S. spinulosa structures, including dead and broken tubes, was estimated for each image collected in the 2007 and 2012 surveys. Working on the assumption that any structures that were intact and growing vertically were living, the percent cover of live S. spinulosa structures was also estimated. A grid was overlaid on each image in Photoshop, and a series of reference images were produced to aid the consistency of estimations.

Macrofaunal abundance

All macrofauna visible in the seabed images were identified to the highest possible taxonomic resolution (species level where possible) and their abundance recorded. Colonial species that cannot be accurately enumerated were recorded as present or absent (1 or 0 respectively). The World Register of Marine

Species (WoRMs; http://www.marinespecies.org/) was used to ensure consistency in the species nomenclature.

6.2.2 Habitat Mapping

The acoustic data were interpreted to provide estimates of the distribution and extent of *S. spinulosa* reefs within the Thanet offshore wind farm site using the presence of an irregular surface texture noted at the Hastings Shingle Bank Site in **Chapter 5** (**Figure 6.1**). The side-scan sonar data formed the primary data source for mapping the extent and distribution of *S. spinulosa* reefs, although digital elevation models (DEMs) produced from the MBES data, and the associated backscatter data, were used to further aid the delineation of reef boundaries. Since the irregular texturing produced by *S. spinulosa* habitats cannot definitively be distinguished from other biogenic structures, ground-truthing data were used to verify the species responsible for the putative reefs. For example, during the 2007 surveys an area initially identified as potential *S. spinulosa* reef was subsequently identified as a mussel bed formed by the blue mussel, *Mytilus edulis*. This habitat only occupied a small area, was only captured at one ground-truthing station, and has been excluded from the current study.

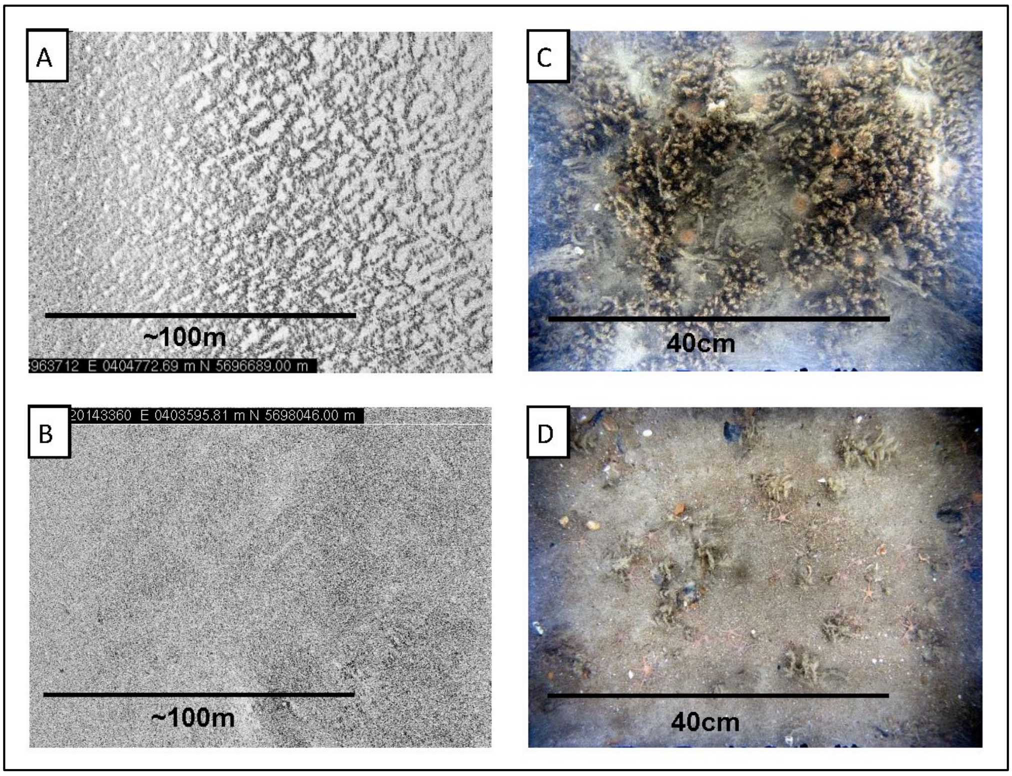


Figure 6.1 High resolution (410 kHz) sidescan sonar snapshot images (EdgeTech 4200FS) of A) *Sabellaria spinulosa* reef; B) Flat sedimentary habitats within the Thanet offshore wind farm site in 2012; C) seabed image taken at the same location as A; D) seabed image taken at the same location as B.

6.2.3 Verification of acoustic reef classification

The detection of *S. spinulosa* reefs using acoustic data was verified using quantitative measures of *S. spinulosa* tube density and % cover of *S. spinulosa* structures derived from seabed images. For each measure, values within stations were averaged, and then pairwise differences between stations were calculated using Euclidean distance. A permutational dispersion test (Anderson 2006) revealed that the variance in density was significantly different between the two habitat classes and hence the density data was Log(x+1) transformed, before being averaged. The resulting resemblance matrices were analysed using a 2-way permutation-based analysis of variance (PERMANOVA; Anderson 2001b; Anderson 2001a; McArdle and Anderson 2001) to determine the significance of differences between acoustically-derived habitat classes (*S. spinulosa* reef and sediment) and years (2007 and 2012). This procedure is formally equivalent to standard Analysis of Variance, but the flexibility and robustness of the permutation approach avoids the necessity for variables to fulfil standard normality assumptions.

6.2.4 Impact Assessment

The impact of the wind farm development on the *S. spinulosa* reefs and adjacent sedimentary habitats was investigated by calculating the relative extent of reefs recorded in the acoustic data in 2005, 2007 and 2012, and by examining the associated macrofaunal communities. Quantitative macrofaunal abundance data extracted from the seabed images collected in 2007 and 2012 were used to calculate a range of univariate measures of community structure. These were: S, number of taxa; N, number of individuals; H', Shannon's diversity and J, Pielou's J', an evenness measure. *S. spinulosa* was removed from the data before measures were calculated since the aim was to test for differences in the macrofauna associated with the reef rather than in the reef builder itself. Sample values were averaged within sampling stations, pairwise differences calculated between stations, and the resulting resemblance matrix analysed using 2-way PERMANOVA. A permutational dispersion test (PERMDISP; Anderson 2006) revealed that the variance in S was significantly different between the two habitat classes and hence a Log (x+1) transformation was applied before the number of species (S) was averaged by station.

Differences in the faunal composition between 2007 and 2012 and between the different acoustic habitat classes were also investigated using a 2-way PERMANOVA carried out on a Bray-Curtis similarity matrix calculated using untransformed, station-averaged macrofaunal abundance data. Finally, a one-way SIMPER analysis was carried out on the same data, using a combined factor of habitat class and year, to ascertain which taxa were responsible for the observed differences (Clarke and Warwick 2001; Clarke and Gorley 2006; Clarke et al. 2006).

6.3 Results

6.3.1 Verification of Acoustic Reef Classification

***Sabellaria spinulosa* Density**

The density of *S. spinulosa* tubes recorded in seabed images was higher in areas identified as *S. spinulosa* reef than in adjacent sedimentary habitats (**Figure 6.2a**). The range of *S. spinulosa* densities was notably higher in 2012, both within and outside areas that were identified as reef, and much higher densities of *S. spinulosa* were recorded in adjacent sediments in 2012. This suggests that the reef habitats became patchier over this time period, and the increase in *S. spinulosa* density in adjacent sediments could be a precursor to future reef development. Although differences in *S. spinulosa* densities on and off acoustically defined reef habitats were significant, whilst differences between years were not (**Table 6.1**), there is a decrease in the median density of *S. spinulosa* within reefs between 2007 and 2012, driven by a small number of stations sampled in 2007 with densities of > 6,000 individuals per image. The tubes identified in these images were very small (< 0.5mm in diameter) indicating that this was a new settlement. Tube openings with this diameter were not recorded at any other stations or in any other year.

Percent cover of *Sabellaria spinulosa* structures

The total % cover of *S. spinulosa*, including dead and broken structures, and the % living *S. spinulosa* structures, were found to differ significantly on and off acoustically-defined areas of reef (**Table 6.1**). A marginally significant difference was also detected in the total % cover between years. The relationship between the acoustic reef classification and the % living *S. spinulosa* (**Figure 6.2b**) is similar to that observed with tube density (**Figure 6.2a**). The relationship between the acoustic reef classification and the total % cover of *S. spinulosa* (**Figure 6.2c**), which includes dead and broken up structures, followed the same general trend but there was a larger overlap between classes.

Table 6.1 Summary of a series of Permutational Multivariate Analysis of Variance (PERMANOVA) tests carried out on Log (x+1) transformed, station averaged *Sabellaria spinulosa* tube density and station averaged live and total *S. spinulosa* cover (%) derived from seabed images collected across the Thanet wind farm site in 2007 and 2012 in acoustically defined *S. spinulosa* reefs and adjacent sedimentary habitats. A 2-factor crossed design was tested using Type I (sequential) sums of squares with permutations under a reduced model. The test results for interactions between habitat class and year (Habitat X Year) are also provided. The Pseudo-F (F) test statistic is provided alongside the probability (P) of obtaining that test statistic, generated using permutations. Significant results (P ≤0.05) are highlighted in bold font.

	Acoustic Habitat Class		**Year**		**Habitat Class x Year**	
	F	**p**	**F**	**p**	**F**	**p**
S. spinulosa tube density (Log (x+1))	**35.73**	**0.001**	0.05	0.827	0.48	0.477
Live *S. spinulosa* cover (%)	**27.76**	**0.001**	0.66	0.43	1.22	0.265
Total *S. spinulosa* cover (%) (including dead and broken up structures)	**12.30**	**0.002**	4.45	0.045*	0.0001	0.987

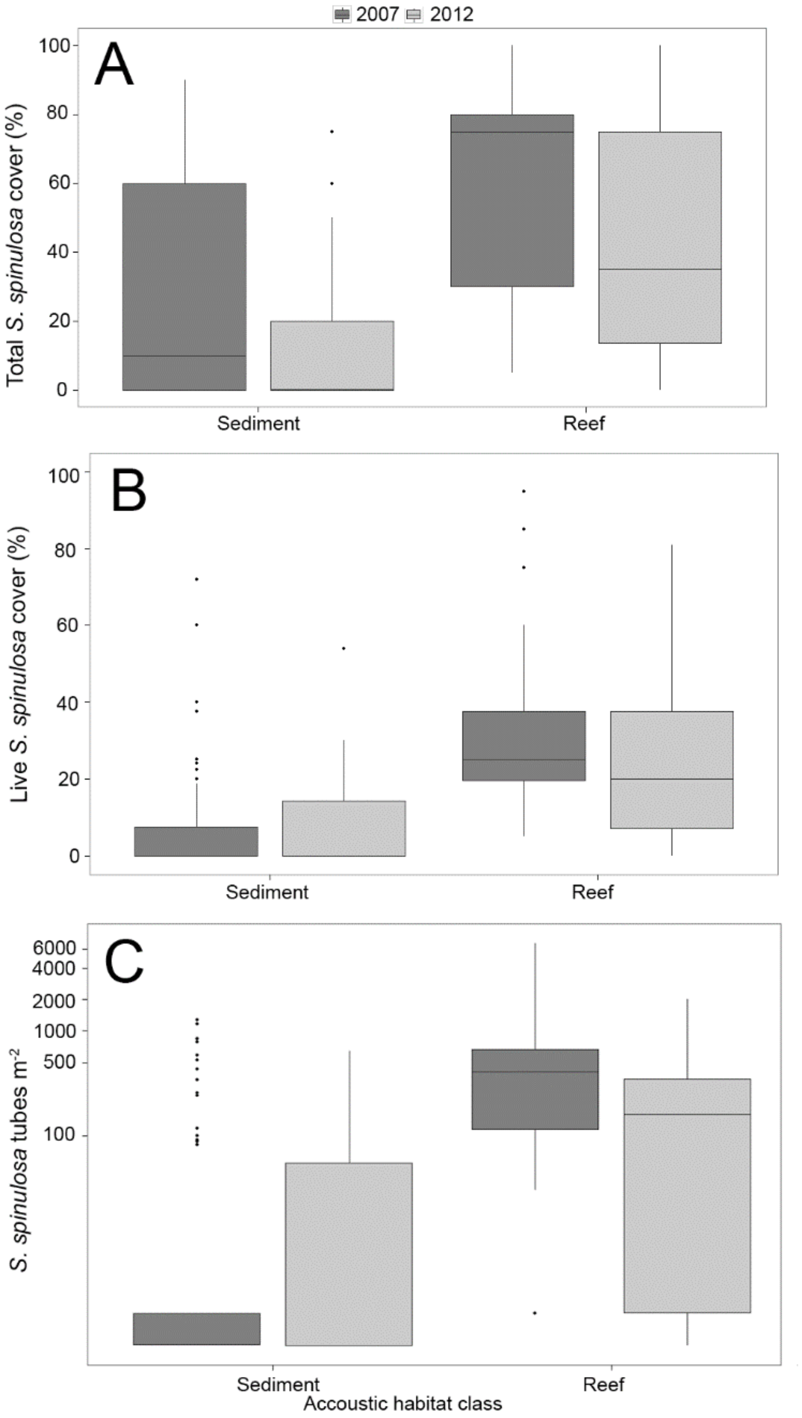


Figure 6.2 Box plots showing A) % cover of living *Sabellaria spinulosa* structures B) total % cover and C) the density of *S. spinulosa* tube openings, recorded in seabed images taken within acoustically defined *S. spinulosa* reefs and adjacent sedimentary habitats in 2007 and 2012 within the Thanet offshore wind farm site (**Figure 2.8**). Each of the boxes represents the interquartile range of densities recorded whilst the central line represents the median value. The upper and lower limits of the density records (Median ± 1.5 x IQR) define the limits of the whiskers and any outlying values (< or > Median ± 1.5 x IQR) are represented by a dot.

6.3.2. Impact of the wind farm development on benthic habitats

***Sabellaria spinulosa* reef extent**

Acoustically-derived maps of the extent and distribution of *S. spinulosa* reefs in 2005, 2007 and 2012 (**Figure 6.3**) show that although there were differences in the areas surveyed between 2005 and 2012 there was a considerable level of change in the distribution and extent of *S. spinulosa* reefs during this time (**Figure 6.3**; **Table 6.2**). Between the baseline characterisation survey undertaken in 2005 and the pre-construction survey carried out in 2007 there was a marked decrease in the extent of *S. spinulosa* reef in the southern sector of the development site. However, a new area of reef was detected in the north of the site which was of roughly equivalent extent. As this area was not covered by the 2005 high resolution acoustic survey it is impossible to know whether or not the reef was present at that time. An increase in reef extent was recorded between the 2007 pre-construction survey and the 2012 post-construction survey, both in the southern sector and across the site as a whole. The *S. spinulosa* reefs in the southern sector increased in extent by 0.42km^2 during this time and the across the site as a whole there was an increase of 0.32km^2.

Table 6.2 Summary of the extent (km^2) of *Sabellaria spinulosa* reef identified within the Thanet offshore wind farm site using high resolution sidescan sonar data (see also **Figure 2.8**). Note that only the southern sector of the site was surveyed using high resolution sidescan sonar in 2005.

	Southern Sector			**Whole Site**	
	2005	**2007**	**2012**	**2007**	**2012**
Sabellaria spinulosa Reef (km^2)	2.57	0.48	0.90	2.59	2.91

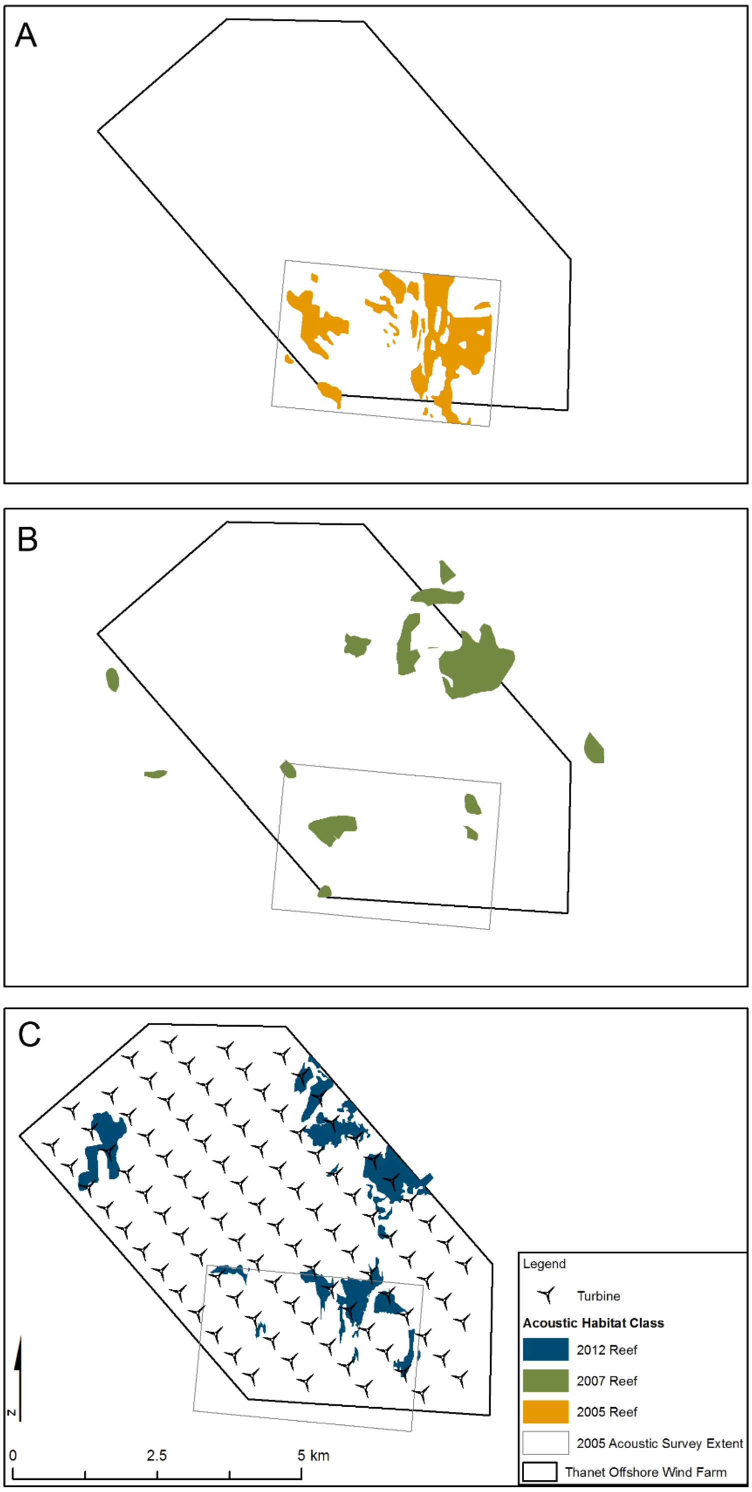


Figure 6.3 Charts showing the distribution and extent of *Sabellaria spinulosa* reefs identified within the Thanet Offshore Wind Farm site in 2005 (A), 2007 (B) and 2012 (C) using high resolution sidescan sonar and multibeam echo sounder data (MESL 2005; Gardline 2007; MESL 2007b; Gardline 2012; MESL 2012). Also shown are the extent of the reduced 2005 acoustic survey and the turbines installed at the site in 2011.

Macrofaunal Diversity

In both 2007 and 2012 numbers of species (S) and Shannon Weiner's diversity (H') were significantly higher in seabed images taken from within acoustically defined areas of *S. spinulosa* reef than in samples taken from areas identified as being sedimentary habitats (**Table 6.3**; **Table 6.4**). These two indices also increased between 2007 and 2012. Differences in the numbers of individuals (N) and Pielou's evenness (J'), a measure of the equitability of species abundance, between samples taken on and off acoustically defined areas of reef were not significant (**Table 6.4**).

Table 6.3 Mean values of macrofaunal diversity indices (S= No. Species, N=No. Individuals, H' = Shannon's diversity and J' = Pielou's evenness) calculated from macrofaunal abundance data obtained from seabed images collected in each of the acoustically defined habitat classes (*Sabellaria spinulosa* reef and sedimentary habitats). *S. spinulosa* abundances were excluded from this analysis.

		S		**N**		**H'**		**J'**	
		2007	**2012**	**2007**	**2012**	**2007**	**2012**	**2007**	**2012**
Mean	*S. spinulosa Reef*	3.00	4.74	14.85	15.20	0.69	1.05	0.68	0.74
	Sediment	1.70	3.77	5.90	20.42	0.41	0.81	0.75	0.61

Table 6.4 Summary of a series of Permutational Multivariate Analysis of Variance (PERMANOVA) tests carried out on station averaged diversity indices calculated for macrofaunal abundance data from seabed images collected across the Thanet wind farm site in 2007 and 2012 in acoustically defined habitat classes (Sabellaria spinulosa reef and sedimentary habitats). A 2-factor crossed design was tested using Type I (sequential) sums of squares with permutations under a reduced model. The test results for interactions between habitat class and year (Habitat X Year) are also provided. The Pseudo-F (F) test statistic is provided alongside the probability (P) of obtaining that test statistic, generated using permutations. Significant results (P≤0.05) are highlighted by bold font.

	Acoustic Habitat Class		**Year**		**Habitat Class x Year**	
	F	p	F	p	F	p
S	**24.53**	**0.001**	**22.67**	**0.001**	0.13	0.714
N	1.63	0.216	**4.75**	**0.032**	3.37	0.062
H'	**17.79**	**0.003**	**13.4**	**0.004**	0.03	0.851
J'	0.51	0.469	0.89	0.362	2.87	0.091

Community Composition

To determine whether observed differences in diversity reflected differences in community composition, the Bray-Curtis resemblance matrix derived from macrofaunal abundance data was analysed using permutational analysis of variance (**Table 6.5**). There were statistically significant differences between the macrofaunal communities associated with each acoustic habitat class, and between 2007 and 2012. SIMPER analysis (**Table 6.6**) showed that the relative abundance of fauna present was driving the differences between the acoustically defined habitat classes and between 2007 and 2012. Whilst differences in the abundance of individual taxa recorded in each habitat and year class exist, the taxa present remain broadly comparable across all classes.

Table 6.5 Summary of a Permutational Multivariate Analysis of Variance (PERMANOVA) test carried out on station averaged macrofaunal abundance data from seabed images collected across the Thanet wind farm site in 2007 and 2012 within and outside acoustically defined areas of *S. spinulosa* reef. A 2-factor crossed design was tested using Type I (sequential) sums of squares with permutations under a reduced model. The test result for the interaction between habitat class and year (Habitat X Year) is also provided. The Pseudo-F (F) test statistic is provided alongside the probability (P) of obtaining that test statistic, generated using permutations. Also shown are the degrees of freedom (df), sums of squares (SS) and mean squares (MS). Significant results (P ≤0.05) are highlighted by bold font.

Source	df	SS	MS	Pseudo-F	P
Acoustic Habitat Class	1	7751	7752	**2.66**	**0.011**
Year	1	14531	14531	**4.98**	**0.001**
Habitat Class x Year	1	5334	5334	1.83	0.062
Residual	62	180800	2916		
Total	65	2084200			

A number of attached epifaunal taxa including anemones belonging to the genus *Sagartia*, and hydroids belonging to the genera *Obelia* and *Halecium* were more abundant in samples taken from *S. spinulosa* reefs than in samples taken in sedimentary habitats. These taxa were also more abundant in 2012 than in 2007. Colonial animals such as the hydroids were only recorded as being present (1) or absent (0), so the differences observed in these taxa are likely to be more ecologically significant than the numbers presented in **Table 6.6** suggest. Some mobile species, such as the brittle star *Ophiura albida*, the pink shrimp *Pandalus montagui* and the hermit crab *Pagurus berhardus*, also increased in abundance between sediment habitats and reefs, and between 2007 and 2012. In contrast, the queen scallop, *Aequipecten opercularis,* was all but absent from the *S. spinulosa* reef habitat in 2012 despite being present in high numbers in 2007.

Table 6.6 The average abundance (n) of the taxa that collectively contribute to 90% of the dissimilarity between the different acoustic habitat classes and the different years. Determined through a SIMPER analysis on untransformed, station averaged macrofaunal abundance recorded from seabed images. Note *S. spinulosa* itself was excluded from this analysis.

Taxa	**Sediment**		**Reef**	
	2007	**2012**	**2007**	**2012**
Ophiura albida	3.19	8.18	2.67	5.97
Sagartia spp.	1.05	1.43	2.81	3.84
Aequipecten opercularis	0.13	0.08	6.56	0.43
Pagurus bernhardus	0.08	0.58	0.26	0.79
Pandalus montagui	0	0.18	0.15	0.75
Sagartiogeton laceratus	0.15	7.67	0.59	0.1
Obelia spp.	0	0.32	0.04	0.57
Asterias rubens	0.19	0.17	0.33	0.34
Pisidia longicornis	0.03	0.02	0.52	0.32
Halecium spp.	0.03	0.3	0.04	0.36
Pomatoceros spp.	1.13	0.2	0.19	0.11
Hydrallmania falcata	0	0.25	0	0.04

The common starfish, *Asterias rubens*, and the long clawed porcelain crab, *Pisidia longicornis*, were both more abundant on the *S. spinulosa* reefs than in adjacent sedimentary habitats but their abundance showed little change between 2007 and 2012. This indicates that the presence of reef has a greater influence on the distribution of these species than other elements of the environment that changed between 2007 and 2012. Conversely, a dramatic increase in the abundance of the anemone *Sagartiogeton laceratus* was observed between 2007 and 2012 in sedimentary habitats, indicating that this species may be responding positively to changes in environmental conditions that occurred during this time.

6.4 Discussion

6.4.1 Mapping Sabellaria spinulosa habitats using high resolution acoustic data

Sidescan sonar technology has been shown to be effective in the detection of small-scale seabed features such as seagrass beds, horse mussel beds and *Lanice conchilega* beds through the discrimination of textural differences on the seafloor (Wildish et al. 1998; Ardizzone et al. 2006; Degraer et al. 2008; Lindenbaum et al. 2008). This study demonstrates that this technology can also be used to reliably detect *S. spinulosa* reefs. In addition, high resolution multibeam backscatter and bathymetry data were used to supplement the sidescan sonar data interpretation and these methods were also found to be successful in distinguishing the textural differences between *S. spinulosa* reefs and surrounding sediments. All of these detection methods rely on textural differences, and hence there will be instances where, for example, *S. spinulosa* reefs occur on rough ground, it is harder and perhaps impossible to differentiate between a reef and the surrounding substratum. Other reef habitats such as horse mussel beds and stony reefs can also return an irregular signature and therefore some ground truthing will be necessary to confirm the presence of *S. spinu*losa reef, until such a time that the differences between the acoustic signatures of these habitats are better understood and quantified (Limpenny et al. 2010).

S. spinulosa aggregations are visible in both high resolution sidescan sonar and backscatter derived from MBES data as an irregular texturing of the seafloor. The precise physical qualities of *S. spinulosa* reefs that generate the irregular acoustic signature is not yet fully understood, but it seems likely that it is a combination of both physical and biological factors. The high rigidity of the tube structures would result in areas of high reflectivity in the acoustic data, as has been observed in other polychaete reefs (Degraer et al. 2008). Conversely the high volume of biological material associated with *S. spinulosa* reefs, both in terms of the reef-building organisms themselves and the associated fauna, would result in low reflectivity in the acoustic data, as observed in the acoustic signature of seagrass beds (Ardizzone et al. 2006). This combination of high- and low-reflectivity attributes of the reefs is likely to be, at least partially, responsible for the irregular texturing observed in the acoustic signature which is characteristic of these habitats.

Significant differences in tube density and percentage cover (living and total) between samples taken on and off the reefs identified in acoustic data, supports this hypothesis. Furthermore, as differences in percentage live cover and tube density between samples collected from the *S. spinulosa* reefs and from adjacent sediments were more pronounced than differences in total cover, which includes broken structures, it seems likely that healthier reefs, containing high densities of living worms, will be more detectable using these acoustic techniques. Tube densities and percent living cover will be highly correlated with each other as only erect tubes can be counted reliably using automated image counting techniques, and these are likely to be alive. Both tube density and percent living cover are also likely to be correlated with the biomass of *S. spinulosa*, which may explain the stronger relationship with the acoustic signatures. However, it is also possible that aspects of the non-living *S. spinulosa* cover such as tube degradation or horizontal positioning could be responsible for the weaker relationship observed with the acoustic signatures.

Fine sediment, known to collect in the gaps in Sabellariid reef structures (Kirtley and Tanner 1968; Cunningham et al. 1994; Pandolfi et al. 1998) may also contribute to the variable reflectivity observed in the acoustic signature but this aspect was not measured during the current study. Well-developed *S. spinulosa* aggregations, in terms of size and elevation, are visible not only in the MBES backscatter data but also in the digital elevation model (DEM), indicating that a component of the irregular signature observed may be caused by variations in the height of these structures as well as by differences in reflectivity.

6.4.2 New insights into the impacts of offshore wind farm developments

In addition to demonstrating the ability of high resolution acoustic data to detect and delimit *S. spinulosa* reefs, this study provides new insights into the response of these and adjacent sedimentary habitats to an offshore wind farm development. Offshore wind farms have previously been reported to increase biomass by acting as an artificial reef (Wilhelmsson et al. 2006; Wilson and Elliott 2009; Krone et al. 2013) and by acting as fish aggregation devices (Reubens et al. 2011; Reubens et al. 2013a; Reubens et al. 2013c). It has also been postulated by some authors that these developments could act as *de-facto* marine reserves (Inger et al. 2009; Ashley et al. 2014). This study provides some evidence for the latter. *S. spinulosa* reef habitats were found to have increased in extent by 0.32km^2 18 months after construction at the site had been completed. The absence of any significant *S. spinulosa* reef losses during and after construction indicates that the micro-siting of turbines was effective at this site, and that these habitats have not been negatively impacted by the development.

A decrease in reef extent (2.09km^2) was observed in the southern sector of the development site, between the 2005 baseline survey and the 2007 pre-construction survey. The reduction in reef extent in the absence of any construction activities associated with the wind farm development is indicative of a habitat with a high level of natural variability. However, these changes in extent may be attributable to other anthropogenic pressures acting on this area, such as commercial fishing. Commercial fishing, and towed bottom gear in particular, is widely accepted as having detrimental impacts on the benthos (Kaiser et al. 2006; Cook et al. 2013) and scars which are very likely to have been caused by paired beam trawlers were noted in the high resolution acoustic data collected across this site in 2005 and 2007 (MESL 2005; MESL 2007b). It is therefore impossible to separate the natural variation in reef extent and distribution from the physical impact of fishing activities that occurred in this area between 2005 and 2007. Future monitoring surveys of the Thanet wind farm site may provide important information to help tease apart these aspects of reef ecology.

The diversity of macrofauna supported by both *S. spinulosa* reefs and adjacent sedimentary habitats was significantly higher in 2012 (post-construction) than in 2007 (pre-construction). In the absence of any non-impacted reference sites it is impossible to attribute the enhancements observed to the presence of the wind farm unequivocally. However, this area was known to be targeted by commercial beam trawlers prior to the construction of the wind farm and it is likely that this source of anthropogenic disturbance has been reduced. Although there are no legislative barriers to commercial fishing in the Thanet offshore wind farm site, the presence of the turbines makes towing a beam trawl through the site both dangerous and undesirable. It is possible therefore that a reduction in these activities may be responsible for the increase in macrofaunal diversity and increase in abundance of epifauna associated with *S. spinulosa* reefs in this area.

6.4.3 The importance of repeat mapping in support of offshore wind farm developments

This study demonstrates the application of seabed mapping using acoustics for environmental impact assessment, and also demonstrates the importance of these technologies to an emerging offshore industry. The Thanet offshore wind farm development exemplifies pro-active environmental consideration through the life of the development. Conservation agencies and environmental consultants were actively involved in the environmental impact assessment from an early stage, and this has facilitated the protection of an important benthic habitat during construction through influencing the placement of turbines and cables. Early indications are that this wind farm is now acting as a *de-facto* marine reserve for this habitat, providing a unique opportunity for scientists and conservation agencies to track the development of *S. spinulosa* reefs over time. There are few (if any) examples of pristine *S. spinulosa* reefs in the UK, that is, reefs that are not being modified by anthropogenic activities, and it is possible that in years to come the reefs at this site may recover to a pristine or near pristine state, providing a unique opportunity to study the natural variability of this habitat in the absence of fishing.

Repeated baseline surveys are rare in environmental impact assessment work, but this paper goes some way towards demonstrating their potential importance to both the developer and to science in general. It has been widely postulated that *S. spinulosa* aggregations are ephemeral in nature (Holt et al. 1998; Hendrick and Foster-Smith 2006) but there have been no studies to date that demonstrate this unequivocally. The 2005 and 2007 surveys undertaken at this site are one of the first records of this habitat having moved and changed in extent, although the cause of this change may be, at least partly, attributable to commercial fishing activities. The change in *S. spinulosa* distribution and extent between the baseline survey and the pre-construction survey also has important implications for the developer. Had the pre-construction survey not been carried out, micro-siting of the turbines would have been somewhat fruitless as the reefs identified in 2005 were no longer present in 2007 and new reefs had been detected elsewhere in the site. Perhaps more critically, the two baseline surveys allow the effects of the development to be put into the context of the natural background variability of this habitat. Decreases in the extent of *S. spinulosa* reefs were noted between the first and second baseline survey. Had this not been recorded these losses could have been attributed wrongly to the construction of the wind farm, and increases in the extent of *S. spinulosa* reefs following the construction of the wind farm would also have gone undetected. Ideally, repeat baselines would be undertaken for many more than two years, in order to capture the true temporal variability of the system being studied and to allow for robust Before-After-Control-Impact (BACI) type assessments to be made. The costs associated with survey work in the marine environment, and the timescales of most developments will however, prohibit such an approach in most cases.

6.4.4 Limitations

The data presented here were collected as part of the licensing procedures for wind farm developments in the UK, and were therefore subject to stringent budgetary and timing constraints. The surveys were designed to meet regulatory requirements, which are a compromise between “best science” and the financial burden placed on the developer. This inevitably means that there are imperfections in the survey design. In this case the most notable gap in the survey design is the lack of any reference areas outside the boundary of the wind farm. Had reference sites been placed in suitable areas outside the wind farm boundary a better understanding of the natural temporal and spatial variability in reef extent and quality could have been gained and it would have been possible to place the findings reported here, in a more robust context of background variation. The inclusion of some control areas would have facilitated the application of a BACI Paired-Series (BACIPS) survey design which ultimately would have meant that the amount of change attributable to the construction of the wind farm could have been estimated (Osenberg et al. 2006).

The acoustic data collected as part of this study was acquired by two different contractors, using different equipment. Even in the two years where the data were collected by the same contractor using the same equipment (2007 and 2012) the interpretation was undertaken by different individuals. The use of different equipment and different personnel introduces a number of sources of potential error. Time-series data are a very valuable commodity in the marine environment (Frost et al. 2006) unfortunately, where data are collected as part of a licensing and/or monitoring requirement the error levels associated with requirements to reduce costs and deliver outputs within short timescales may significantly reduce their scientific value. Efforts to standardise the way that acoustic data are collected across Europe will help to reduce levels of error and subjective differences in interpretation between contractors and scientists (Coggan et al. 2007). There is also a considerable amount of research currently underway to develop mechanisms of automated acoustic data classification which may ultimately remove the subjectivity of manual interpretation and allow for much more homogeneous time-series assessments (Brown and Collier 2008; McGonigle et al. 2009; Brown et al. 2011).

It was not possible to use the seabed images collected in 2005 because of the poor image quality, caused in part by the very high levels of turbidity experienced at this site. As photographic technology advances it is likely that our ability to monitor the environment remotely will also advance. However, there are limitations to this sampling technique which will not change. For example, it is not possible to identify all taxa to species level from seabed images alone. Many species, including colonial hydroids, can only be identified reliably to the species level using a stereo-microscope because important morphological differences are not visible to the human eye. Other taxa, such as tubiculous polychaetes, cannot be identified to the species level because the animals themselves are concealed within their tubes. In this study the identification of sea anemones was particularly problematic. *Sagartia* spp. could not be identified to species as this requires detailed examination their anatomy (e.g. tentacle positioning) as well as knowledge of the substratum upon which they are attached. The latter could not be determined reliably from all images because of the high level of habitat heterogeneity. Both *S. elegans* and *S. troglodytes* were present across the site but could not be separated consistently. In many instances the loss of species-specific information will not be significant but in this instance it is likely that failure to detect differences in the relative abundance of these two species may have masked important information about the environmental changes that occurred between 2007 and 2012.

Seabed imagery is also limited to the assessment of epifaunal taxa, as most infauna will not be visible from the surface of any given substratum. Grab sampling would have facilitated a more complete assessment of the faunal assemblages in the area, and the potential impacts of the wind farm development. Statutory advice is to avoid direct (destructive) sampling of *S. spinulosa* habitats as this is thought to be more damaging than using remote sampling systems. However, there is no evidence to support this assertion as most drop-camera systems come into direct contact with the seabed and it is likely that they also cause some damage to the habitat. A mini Hamon grab, as would typically be used to sample the benthos offshore (Ware et al. 2011) removes an area of 0.1m^2 which would equate to $2 \text{ X } 10^{-4}$ % of the smallest (0.48 km^2) area of reef identified at this site, in 2007 (**Table 6.2**) representing an incredibly small loss of habitat. Furthermore, evidence collected from an aggregate extraction site in the English Channel (Pearce et al. 2007) indicates that these habitats are able to recover from physical disturbance in a very short period of time. A limited amount of direct sampling would therefore be unlikely to cause long-lasting damage to the habitat, and the contributions this could make to its future management are thought to outweigh the risks.

Evidence presented here indicates that offshore wind farms may have positive impacts on benthic communities, possibly through the exclusion of other more damaging activities such as fishing. However, this study only considers one site, and only one post-construction survey has been undertaken to date. The effects of the Thanet offshore wind farm on associated benthic assemblages may not yet have been fully realised, and we cannot yet be confident that the apparent enhancements in *S. spinulosa* reef habitat extent and diversity are attributable to the development. The impacts of offshore developments may also be very site specific, so caution should be exercised when extrapolating the results presented here to other wind farm sites.

6.5 Conclusions

High resolution acoustic data have been shown to successfully discriminate *S. spinulosa* reefs from surrounding sedimentary habitats. Significant differences in the density of *S. spinulosa* tubes, and both living and total percent cover of *S .spinulosa* structures, were observed between reef and non-reef habitats delineated using high-resolution acoustic imaging, validating the use of this survey technique in environmental assessment work.

The extent of *S. spinulosa* reefs identified within the Thanet offshore wind farm site increased between the pre-construction survey in 2007 and the post-construction survey in 2012, indicating that the wind farm may be providing some protection to this habitat. The diversity of macrofauna associated with the *S. spinulosa* reefs at the site was greater than that observed in adjacent sedimentary habitats, suggesting that increasing the extent of this habitat will have a positive impact on the benthic biodiversity at this site. An increase in the diversity of macrofauna associated with both the *S. spinulosa* reefs and the sedimentary habitats at this site between 2007 and 2012 provides evidence that the wind farm is acting as a *de-facto* marine reserve, by reducing other pressures.

Chapter 7. General Discussion

7.1 Summary of Findings

Reef habitats built by the tubiculous polychaete *Sabellaria spinulosa* have been identified as a habitat with significant conservation importance, based on their historic decline across Europe and the assumption that, like many other biogenic reef systems, *S. spinulosa* reefs enhance biodiversity. *S. spinulosa* reefs are listed in Annex I of the European Habitats Directive, the OSPAR list of threatened and declining species and habitats, and are included in national conservation legislation. However, despite the high conservation status of this habitat, very little work had been undertaken, prior to this study, to explore the role that *S. spinulosa* reefs play in marine ecosystems or their sensitivity to anthropogenic disturbance. Although it was not possible to address all of the known information gaps that exist relating to the ecology of *S. spinulosa* reefs, the following four broad aims were identified as the key first steps to providing a scientific grounding for the management and conservation of this habitat:

1. Investigate the reproductive mode and life cycle of *Sabellaria spinulosa*
2. Establish the degree to which *Sabellaria spinulosa* reefs influence the composition and nature of the macrobenthos
3. Determine whether or not demersal fish feed on *S. spinulosa* reefs and investigate the commonalities between the diets and feeding behaviours of fish species associated with the reefs
4. Evaluate the feasibility of using remote sensing technology to delineate *S. spinulosa* reefs and explore the interaction between the reefs and the construction of an offshore wind farm.

Elucidating the reproductive cycle of *S. spinulosa* was not initially identified as a primary aim of this thesis. However, given the paucity of our knowledge in this area and the implications for the management of *S. spinulosa* reefs, additional sampling and analyses were undertaken in a serendipitous manner allowing for a preliminary investigation into the reproductive cycle. Observations made here of the reproductive ecology and population dynamics of the reef building organism indicate that *S. spinulosa* have a high reproductive output and fast early growth rates which are traits typical of *r*-strategists. This means that *S. spinulosa* have a high capacity to adapt to changes in the environment and to recover from adverse impacts. However, since many of the life-history traits of *S. spinulosa* including mortality and recruitment rates are not yet known, this species should not be considered as wholly opportunistic. It should also be noted that these traits belong to the species and not necessarily the reef habitats that it creates. It is not yet known how long it takes for stable *S. spinulosa* reefs to develop, although some of the evidence presented here suggests that reefs can develop in a matter of months in some areas.

In contrast to the congener *S. alveolata*, female *S. spinulosa* were found to contain eggs in all stages of development, throughout the year. Ripe males were also present throughout most of the year. The availability of larvae in the water column and the reproductive state of individuals studied indicate that this species is able to reproduce throughout much of the year and that it either has a protracted spawning period or several shorter ones. This species was found to have a main spawning event between December and February which has important implication from a management and monitoring perspective. It is normally recommended that benthic monitoring is carried out between April and September, after major settlement events, to ensure that impacts on recruitment are detected (JNCC 2004). However, given that *S. spinulosa* may have its main spawning event as late as February a survey in April could feasibly precede or coincide with the main settlement event. Surveys of this habitat should therefore be undertaken between June and September to allow time for the new settlement to grow to a size that would be retained in a grab sample (>1 mm) or be visible in seabed images. Where this is not possible the timing of the main settlement can at least be taken into account when interpreting the results of the survey. From a management perspective, this information can also be used to inform the timing of activities (e.g. construction or cable burial) that could impact on settlement such that the main settlement is protected.

Further evidence of the resilience of *S. spinulosa* reefs was obtained through a time-series study at the Thanet Offshore Windfarm development site. Surveys of the reef extent immediately before, and approximately 18 months after, construction of the windfarm revealed that the extent of *S. spinulosa* reef increased after construction, despite extensive cable laying and turbine piling activities. The densest area of reef was avoided during construction which appears to have ensured an adequate supply of larvae to facilitate re-colonisation after works on the site had been completed. However, it is not possible to rule out *S. spinulosa* reefs outside the site surveyed as the source of new recruitments as the hydrodynamics of the area have not been studied in detail. *S. spinulosa* reefs in the Thanet site were found to have reduced in their extent between the two baseline surveys, prior to any construction work related to the windfarm. Although the source of this decline is unclear the area was targeted by commercial fisheries (local fishermen, personal comms) and apparent trawl damage was evident in the side-scan sonar data collected from this site (**Figure 7.1**). It is unclear whether or not commercial fishing activities will be reduced by the presence of the windfarm in the longer term, but the enhancement observed at this site does provide strong evidence that the extent of reefs in this area was being limited by these activities. That the reefs continue to exist in this area, albeit as widely dispersed patches, despite ongoing fishing pressures is however, considered to provide further evidence of their ability to recover quickly from physical impacts. Although it seems unlikely that the *S. spinulosa* reefs have reached a stable / climax community under the ongoing pressure of bottom trawling.

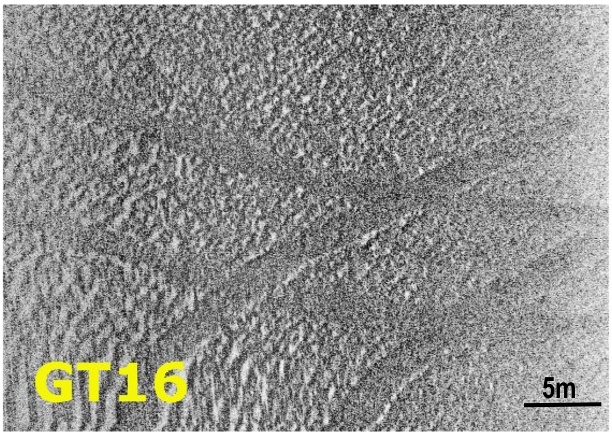


Figure 7.1 Sidescan sonar image showing parallel linear depressions in an area of *Sabellaria spinulosa* reef at the Thanet offshore windfarm site in 2005, thought to be the scars of a twin beam trawl.

It has been widely postulated across the grey literature that *S. spinulosa* reefs enhance biodiversity and provide a habitat for species that would not otherwise exist in the area (Jones 1998; Foster-Smith and White 2001; Foster-Smith and Hendrick 2003; UKBAP 2007b; BRIG 2008). Detailed investigations into the macrofauna associated with *S. spinulosa* reefs in the eastern English Channel presented in this study found little evidence to support these assumptions. *S. spinulosa* reefs were found to support a higher density of species found more sporadically in the surrounding sedimentary deposits, most notably, the long clawed porcelain crab, *Pisidia longicornis*. This study raises questions about the perceived link between *S. spinulosa* reefs and enhanced biodiversity which represents a very real challenge to biodiversity protection legislation. *S. spinulosa* reefs can be considered as concentrations of species, often in elevated densities, that would likely be present in the wider area without them. It would be spatially efficient to protect these habitat types if the aim of conservation efforts was to preserve the range of species typically found in sedimentary habitats. However, the highest value of *S. spinulosa* reefs to humans probably lies in the enhancement of biomass and productivity that *S. spinulosa* reefs provide where they occur in certain habitat types, but the legislative structures to support these arguments, as well as the scientific evidence base, remains poorly developed.

The focus of marine conservation in the UK, and Europe, has for many years been on preserving biodiversity hotspots (JNCC 2013) based on the assumption that high biodiversity is commensurate with a healthy, functional and resistant marine environment (Stachowicz et al. 2002; Hooper et al. 2005; Cardinale et al. 2006; Cardinale et al. 2013). More recently there has been a move away from simply conserving biodiversity hotspots in favour of an MPA network that encompasses the full range of representative habitats and species (Payne et al. 2016) as well as to consider ecosystems in a more holistic way for example by identifying and measuring components which collectively give a measure of ecosystem functioning or 'health' (Tett et al. 2013). This is also reflected in the requirement to establish / work towards 'Good Environmental Status' as defined in the European Marine Strategy Framework Directive (2008) (Borja et al. 2011b; Borja et al. 2013). The original premise for the protection of *S. spinulosa* reefs was that this habitat supports and elevated biodiversity (including species that would not otherwise occur) and that it had suffered significant decline, primarily in the Wadden Sea (Riesen and Reise 1982; Reise and Schubert 1987). The results presented here could call into question the validity of the high conservation status awarded to *S. spinulosa* reefs, at least on the basis of elevated biodiversity. However, that this habitat acts to concentrate benthic species and hence biomass is likely to have some ecological significance which may be better recognised in the new wave of holistic conservation objectives. It should also be noted that we cannot be sure that the reefs included in this study represent stable, climax communities and hence it is possible that we have yet to document the full influence that this habitat can have on the wider ecosystem.

Examination of the gut content of demersal fish sampled from *S. spinulosa* reefs in the southern North Sea revealed that a number of species were feeding on *S. spinulosa* itself, whilst others were feeding on species that were very abundant on the reefs, including *Pisidia longicornis*. Fish samples were not available from adjacent sedimentary habitats to allow quantitative comparisons but comparisons with diets reported in the grey and published literature indicate that the reefs may have some influence on feeding behaviour as well as dietary composition, and this is an area that certainly warrants further investigation. A high abundance of juvenile flatfish was noted in association with *S. spinulosa* reefs in the southern North Sea leading suggesting that *S. spinulosa* reefs may also provide an important nursery habitat. The use of *S. spinulosa* reef habitat for feeding and as a nursery area for these species would qualify it as an Essential Fish Habitat (EFH), a concept developed to bring together disparate efforts to conserve the marine environment and manage fisheries in America (Peterson et al. 2000; Rosenberg et al. 2000). The concept of EFH is now starting to filter into UK marine conservation and management efforts, reflecting the paradigm shift from conserving specific species and habitats to a more holistic ecosystem approach (Bergmann et al. 2004; Tett et al. 2013; MMO 2016). This is the first time that a link has been made between *S. spinulosa* reefs and demersal fish and expanding this to explore the relationship more fully would help to inform future assessments of EFH which ultimately will feed into the UK marine plans (MMO 2016). A more complete understanding of the ecological value of *S. spinulosa* reefs is also likely to ease compliance amongst developers who are currently required to spend considerable sums of money identifying and monitoring any reefs that coincide with their activities.

The aspects of S. spinulosa reef ecology that have been investigated as part of this thesis are summarised in a conceptual model (Figure 7.2) which illustrates how the different components of research are linked with one another as well as the socio-political landscape.

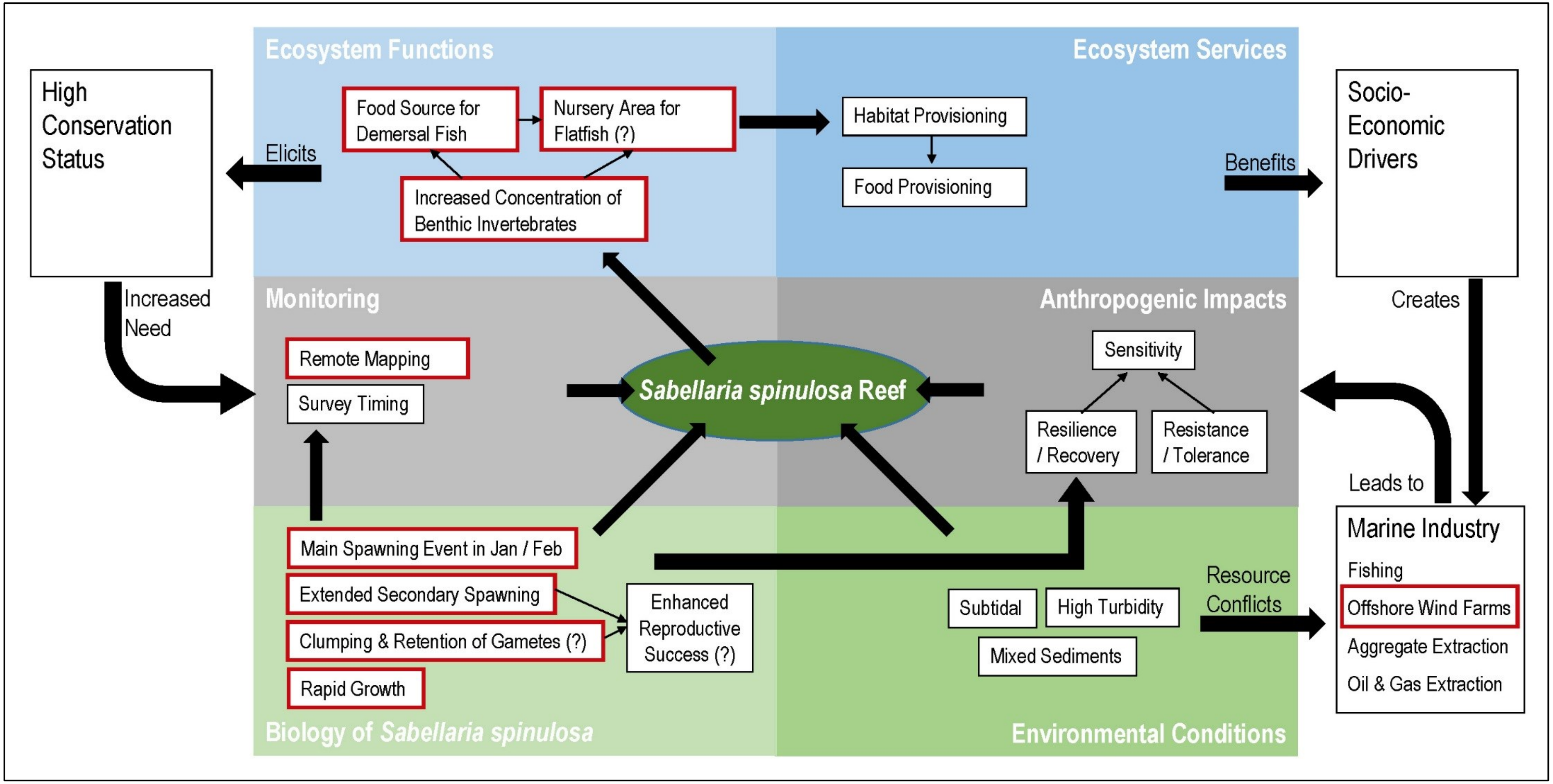


Figure 7.2 Conceptual model of *Sabellaria spinulosa* reef and its interactions with the natural and human environment. Aspects of reef ecology that have been studied as part of this thesis are highlighted in red.

7.2 Study Limitations

Sabellaria spinulosa reefs are a predominantly subtidal feature, meaning that they are logistically difficult and expensive to study. The biggest limitation common to all of the observations and investigations presented here is the low level of sample replication. None of these studies were carried out at more than one location, meaning that there is a limit to the extrapolative power. Similarly, there was little temporal replication. The surveys at the Thanet offshore windfarm site were repeated in three different years and larval sampling was undertaken at eight intervals over the course of 18 months at the Cutline site. However, examination of fish diets was carried out using fish collected on just one sampling event, as were studies into the relationship between the presence of *S. spinulosa* reefs and macrofaunal diversity in the eastern English Channel. It is likely that there will be an element of temporal variation both in the macrofaunal communities associated with *S. spinulosa* reefs and in the feeding behaviour of fish associated with the reefs. If the reefs are acting as a nursery for some flatfish species this is also likely to have a temporal element, and there may be certain times of the year where this function is more important than others.

Sampling was further limited by restrictions imposed because of the conservation status of this habitat. Some quantitative sampling of the reefs was carried out at the Hastings Shingle Bank which has provided a valuable insight into the relationship between reefs and the associated macrofauna. Quantitative grab sampling was not permitted at the Thanet Offshore Windfarm site and hence the associated impact assessment was limited to aspects of the reef that could be measured from remote observations collected using high resolution side-scan sonar and seabed imagery.

Reference sampling was also missing from a number of the studies presented here. Fish stomach data was only examined from fish retained from trawl samples on *S. spinulosa* reefs. This sampling was carried out on a serendipitous basis when *S. spinulosa* reefs were incidentally trawled as part of a much broader seabed characterisation exercise. Because this sampling was not planned before the research cruise there were limited resources on board with which to retain samples, and limited time in the schedule to process them on-board. The decision was made, therefore, to focus on fish associated with reef habitats knowing that there would be limited opportunities to sample reefs with this gear in the future. Whilst this data has proven to be valuable in ascertaining the role of *S. spinulosa* reefs in the marine ecosystem, samples taken from adjacent sedimentary habitats at the same time would have allowed for a more powerful and more in-depth analysis of the influence that this habitat has on fish feeding behaviour and diet.

Sample preservation also presented some challenges in this study, where samples were collected for one purpose but were subsequently used for multiple purposes. Grab samples collected from the Hastings Shingle Bank site, for example, were collected with the primary aim of investigating the macrofaunal communities, but the *S. spinulosa* themselves were subsequently used for cohort analysis. Anterior width proved to be the most useful metric to analyse population structure but it is possible that whilst the adults stop growing in width that they continue to grow in length – something that would be difficult to ascertain from the specimens used since many individual were damaged during sample processing. Had population dynamics been the main aim of the sampling the tubes could have been dissolved in acid which would have preserved the worms better. This method however, dissolves mollusc shells and the hard parts of crustaceans which would have made macrofaunal analysis very difficult.

7.3 Knowledge Gaps and Future Research Priorities

7.3.1 Natural Variation and Reef Dynamics

One of the major limitations to this study was the lack of repetition and the absence of any 'control reefs', that is, *S. spinulosa* reefs that are not being modified in some way by anthropogenic activity. In the absence of any control reefs the analytical power of studies like the ones presented here are significantly limited as it is impossible to differentiate between natural variance and anthropogenic influence. The ephemeral nature of *S. spinulosa* reefs is often stated as fact (Holt et al. 1995; Holt et al. 1998; Hendrick and Foster-Smith 2006; Hendrick 2007) and perhaps more worryingly is sometimes offered as a reason to reduce the specifications of monitoring programmes associated with MPAs and marine developments or to remove the requirement for them altogether (see for example: Jenkins et al. 2015). Despite the wide acceptance of their ephemeral nature there are currently no empirical data to support this theory. Anecdotal evidence does suggest that *S. spinulosa* reefs come and go, or shift from one area to another on an annual basis (Limpenny et al. 2010; Jenkins et al. 2015) as was noted in **Chapter 6**. However, all of these observations have been made in areas that are subject to the physical impacts of bottom trawling, an activity which *S. spinulosa* reefs are particularly vulnerable to (Gibb et al. 2014). Monitoring *S.*

spinulosa reefs that are pristine or that are subject only to minimal anthropogenic disturbance would allow us to establish the extent to which this habitat is ephemeral, and over what timescale. It would also allow us to establish whether or not *S. spinulosa* reefs exhibit a cycle of development and decay comparable to reefs built by its congener *S. alveolata* (Gruet and Bodeur 1995). Quantifying the natural variability that exists within this habitat in terms of its extent, patchiness and elevation, and associated faunal communities would allow us to put the results of studies such as those presented here into a meaningful context and ongoing monitoring of the 'control reefs' would provide reference points against which changes associated with marine developments, or those observed within MPAs, could be assessed.

It has been postulated by some (David Connor personal comms) that the *S. spinulosa* reefs we are observing today are a far cry from the climax reef communities observed in years gone by and it is possible, like so many aspects of the marine environment, that our perception of *S. spinulosa* reefs has suffered from the 'shifting baseline syndrome' first introduced by Pauly (1995) in relation to fisheries. The 'shifting baseline syndrome' essentially describes the way our collective perception of what a pristine environment looks like is diluted with each new generation, based on what they and the preceding generation have observed. The scientific community are only just starting to form a view of what a typical *S. spinulosa* reef looks like and this will be based primarily on observations made over the last 10-20 years, as before this time, the tools for observing these habitats remotely were poorly developed and only rarely utilised. Our view of what a typical *S. spinulosa* reef looks like will therefore also be based on our observations of reefs that have to some extent been modified by anthropogenic activities so it is very likely that what we consider to be 'healthy reefs' are in fact degraded. Monitoring *S. spinulosa* reefs in the absence of any anthropogenic disturbance would therefore be required to fully investigate the climax reef community.

This study has highlighted the potential to use *S. spinulosa* reefs within offshore windfarms as a proxy for pristine reefs, since the pressures from mobile fishing are much reduced (Ashley et al. 2014) and similar opportunities no doubt exist in other industries. The inclusion of closed 'Reference Areas' has also been proposed as part of the Marine Conservation Zone (MCZ) network, although the concept is still under discussion[2]. It is also likely that once the Common Fisheries Policy (CFP) reforms are actuated, and fishing activities start to be regulated within the UKs MPA network, that designated *S. spinulosa* reefs will be allowed to recover and MPA condition monitoring may then itself perform many of the functions of a control reef, outlined above. Another aspect of reef dynamics that has not been explored in this study, or elsewhere, is that of connectivity. This will become increasingly pertinent as the management of designated sites starts to take effect, since it will be necessary to determine whether damage to reefs that sit outside the MPA will have an impact on the integrity of the reefs within it. To date studies of connectivity have focussed on hydrodynamic modelling (Ayata et al. 2009), however, this method of assessment generally assumes that the species in questions is a broadcast spawner in the truest sense. Observations made here indicate that the gametes of *S. spinulosa* may stay loosely associated with the reef, possibly as a means of increasing fertilisation success. This possible reproductive adaptation would need to be researched further before connectivity of reefs could be modelled accurately based on hydrodynamics. It might also be useful to explore the potential application of genetic techniques to look at the relatedness of populations in different reef areas. This type of analysis has been applied successfully in a fisheries context (Prodöhl and Bailie 2015) but has yet to be tested on marine invertebrates.

Underpinning our understanding of reef dynamics is an understanding of the biology of the reef-builder itself. This study has demonstrated how a combination of larval sampling and histological examination of adult worms can be used to advance our understanding of the reproductive cycle of *S. spinulosa* and a series of targeted, geographically separate surveys, undertaken at monthly intervals would be a useful extension of this work. The precise nature and timing of the reproductive cycle of *S. spinulosa* have important management implications since they will have a significant influence on the species ability to recover from anthropogenic disturbances. Understanding when and if there are time which *S. spinulosa* habitats may be more sensitive to certain activities (i.e. during settlement periods) may also allow for more successful mitigation measures to be designed. Similarly, understanding the timing of the main spawning and settlement periods helps to inform the timing and interpretation of monitoring surveys.

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[2] https://www.gov.uk/government/publications/2010-to-2015-government-policy-marine-environment/2010-to-2015-government-policy-marine-environment#appendix-4-marine-protected-areas

7.3.2 Ecosystem Value

One of the main aims of this thesis was to explore the ecosystem functions of *S. spinulosa,* focusing on macrofaunal communities associated with the reefs as well as the use of the reefs by demersal fish. Examination of the associated macrobenthic communities revealed that the reefs increase the concentration of benthic invertebrates, in terms of both abundance and species. Biodiversity in its truest sense was not found to be enhanced by the presence of the reefs and, in contrast to most of the conservation literature, these reefs to not appear to support fauna that would not otherwise be present. This study looked at species composition and diversity indices derived from species abundance data which is a useful starting point for understanding the interactions between *S. spinulosa* reefs and the wider macrofaunal community. However, a useful extension of this work would be to explore the data further using different and more complex indices such as the AZTI Marine Biotic Index *(*AMBI*)* which provides a measure of benthic ecological quality (Borja et al. 2011a) or by applying functional traits to the data (Frid et al. 2008) Each of these measures would provide more information on the state of the reef and it how it is functioning within the ecosystem.

Serendipitous sampling undertaken as part of this study allowed for a preliminary assessment of the use of *S. spinulosa* reefs by demersal fish which indicated that most species were feeding either on the reef builder itself or on the crustacean communities that are known to be present in very high densities on the reefs (Limpenny et al. 2011; Pearce et al. 2011b). Comparisons were made with published records of fish stomach data but no quantitative comparisons were possible. If comparable data could be sourced, the analysis presented could be extended to explore further the possibility that the presence of S. spinulosa reefs influences the feeding behaviour of demersal fish and to begin to understand the extent to which these habitats support these higher trophic levels. This could be achieved by creating comparative food webs (Elliott et al. 2002) or testing for statistically significant differences in the diets of demersal fish. The feeding behaviour of the fish, in terms of specialisation, could also be examined through the construction of Costello or Tokeshi plots (Marshall and Elliott 1997)

The examination of stomach contents has its limitations in terms of understanding the degree to which demersal fish are utilising *S. spinulosa* reef to feed, since, with the exception of the reef builder itself, it is impossible to determine where the prey items have originated from. Many of the fish examined here were, for example, feeding on the long-clawed porcelain crab, *Pisidia longicornis*. This species has been recorded in very high densities in association with *S. spinulosa* reefs. However, *P. longicornis* is a crevice dwelling crab and hence the high abundance of this species on the reef may not translate to a high abundance of available prey. This species is also known to occur in the mixed gravelly sediments adjacent to the reefs. Stable isotope analysis might help to determine whether or not prey are being consumed from the reef or from nearby sediments, but it may also be necessary to observe fish feeding in-situ by deploying a seabed camera trap. Holt et al. (1998) postulated that flatfish were able to crunch up the tubes of *S. spinulosa* to obtain the worms and this hypothesis could also be tested through the use of seabed cameras. The presence or absence of sediment in the guts of fish eating *S. spinulosa* (not recorded in this study) could also provide useful evidence of the feeding mechanisms employed by these species to exploit the reef.

This study has shown that some demersal fish species feed upon *S. spinulosa* and many more feed on prey items that are abundant on the reefs created by *S. spinulosa*. The prevalence of *S. spinul*osa in the diet of juvenile flatfish (dab, plaice and Dover sole) and the high ratios of juvenile flatfish to adults also suggests that this habitat could be used a nursery ground by these species and that they perhaps utilise the gaps in the reef as areas of refuge. Establishing the use of *S. spinulosa* reefs as a nursery for flatfish and other demersal fish species would be best achieved using a Baited Remote Underwater Video (BRUV) system as this could be deployed for a day or two at time and would not cause any undue damage to the reef itself.

7.3.3 Sensitivity to Anthropogenic Disturbance

Surveys of *S. spinulosa* reefs at the Thanet offshore windfarm site, carried out before and after construction, indicate that the reefs have not been adversely impacted by the construction and operation of the wind farm, and could even benefit from the presence of the turbines, which are thought to reduce pressures from bottom trawling. Similarly, a survey of the Hastings Shingle Bank aggregate extraction site demonstrated that *S. spinulosa* reefs had colonised an area where dredging activities had ceased for only a few months (Pearce et al. 2007) It is however, impossible to put these observation into context without any ‘control reefs’ or without a better understanding of the impacts of fishing. *S. spinulosa* reefs are generally considered to be sensitive to bottom trawling and indeed the physical impact of a single trawl pass is evident in sidescan sonar data collected from this habitat (**Figure 7.1**). However, *S. spinulosa* reefs do continue to exist in the eastern English Channel and the southern North Sea despite relatively high levels of commercial fishing (Breen et al. 2015). This suggests that, whilst fishing pressure may be preventing *S. spinulosa* reefs from developing into continuous stable reef features or climax communities (see earlier discussion), the reefs are able to tolerate current fishing levels to a certain degree. It is unlikely to be possible to explore the tolerance of *S. spinulosa* reefs to different levels of fishing in an experimental way because of the sampling restrictions placed on this habitat. However, there may be opportunities to monitor *S. spinulosa* reefs for which fishing pressures have been removed, through MPA management measures or some other mechanism, and in doing so it may be possible to ascertain what the impact of previous fishing activity was.

There is anecdotal evidence that *S. spinulosa* is tolerant of high levels of turbidity and even that it thrives in these conditions, for example, reefs have been identified in close proximity to an active aggregate extraction area (**Chapter 4**). Laboratory experiments have also found that *S. spinulosa* is tolerant of certain levels of burial (Last et al. 2011b) but these studies have yet to be linked to sedimentation levels experienced by reefs in the wild. Increased turbidity and sedimentation levels are associated with almost any anthropogenic activity occurring in the marine environment it would therefore assist in the management of this habitat if the tolerance of the reefs investigated more fully, and in-situ. Because it is the habitat that is of interest, rather than the reef builder itself it would also be pertinent to look at latent impacts on the reef community so as to fully understand the implications of burial events.

The temperature tolerance of *S. spinulosa* is undoubtedly broad, however in light of the predicted temperature changes associated with climate change (Hiscock et al. 2004; Bulling et al. 2010) this would seem a pertinent area for future research. Bamber and Irving (1997) reported that *S. alveolata* maintained higher metabolic rates and tube-building activity in the vicinity of the cooling water outflow of Hinkley point, which is usually 8 to 12°C above ambient water temperatures. Assuming *S. spinulosa* would have the same response to temperature fluctuations caused by global warming, this could cause an increase in the metabolism and tube building activity which could expand the distribution and size of reefs built by this species. *S. spinulosa* was identified as having a very broad biogeographical range (Achari 1974), although all of the species identifications to date have been based on morphological features of the worm. Genetic analysis of *S. spinulosa* specimens collected from around the world would not only serve to confirm the geographical range of this species but in turn this may also provide further clues with regards to the species tolerance to different climates and its likely response to future climate change.

7.4 Conclusions

Despite the limitations associated with subtidal sampling, this study has gone some way towards elucidating the relationship between *S. spinulosa* reefs and the associated macrofauna. Although it has been widely accepted, until now, that *S. spinulosa* reefs enhance biodiversity this study has found that their ecological value is actually in their ability to increase macrofaunal biomass, rather than biodiversity. The relatively high biomass of *S. spinulosa* reefs translates to an important prey resource for demersal fish which may be particularly important for juvenile flatfish. *S. spinulosa* was also previously assumed to have essentially the same reproductive cycle as its congener *S. alveolata,* but this study has demonstrated a significant difference in that female *S. spinulosa* were frequently found to contain eggs in all stages of development at the same time, in contrast with *S. alveolata* where egg development has been observed to be synchronous (Culloty et al. 2010). *S. spinulosa* would therefore appear to be much better adapted to environmental change and to have a much greater capacity to recover from physical damage. This is, perhaps, a trait that has evolved in response to a life in a dynamic environment. Studies of *S. spinulosa* reefs at an offshore windfarm site have demonstrated the ability of this habitat to recover from the physical damage of construction and to be able to withstand longer-term impacts from fishing. There is however, some evidence to suggest that both the extent of the reef and the diversity of macrofauna associated with them was limited by commercial fishing. Given that none of the reefs included in this study were protected from commercial fishing activities and most were also exposed to physical impacts originating from other offshore developments, including aggregated extraction and the construction of offshore windfarms, it is possible, if not likely, that the climax reef community has yet to be documented. As marine conservation legislation continues to develop examples of this habitat are beginning to be afforded protection from all sources of anthropogenic disturbance. This presents a unique and highly valuable opportunity to study the successional development of *S. spinulosa* reefs and to gain a more complete understanding of their influence and ecological functioning in the marine ecosystem in the absence of any anthropogenic disturbance.

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Repeated mapping of reefs constructed by *Sabellaria spinulosa* Leuckart 1849 at an offshore wind farm site

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ABSTRACT

Sabellaria spinulosa reefs are considered to be sensitive and of high conservation status. This article evaluates the feasibility of using remote sensing technology to delineate *S. spinulosa* reefs. *S. spinulosa* reef habitats associated with the Thanet Offshore Windfarm site were mapped using high resolution sidescan sonar (410 kHz) and multibeam echo sounder ($<1\ m^2$) data in 2005 (baseline), 2007 (pre-construction baseline) and 2012 (post-construction). The *S. spinulosa* reefs were identified in the acoustic data as areas of distinct irregular texturing. Maps created using acoustic data were validated using quantitative measures of reef quality, namely tube density (as a proxy for the density of live *S. spinulosa*), percentage cover of *S. spinulosa* structures (both living and dead) and associated macrofauna derived from seabed images taken across the development site. Statistically significant differences were observed in all physical measures of *S. spinulosa* as well the number (S) and diversity (H') of associated species, derived from seabed images classified according to the presence or absence of reef, validating the use of high resolution sidescan sonar to map these important biogenic habitats. High precision mapping in the early stages allowed for the micro-siting of wind turbines in a way that caused minimal damage to *S. spinulosa* reefs during construction. These habitats have since recovered and expanded in extent. The surveys undertaken at the Thanet Offshore Windfarm site demonstrate the importance of repeat mapping for this emerging industry, allowing habitat enhancement to be attributed to the development whilst preventing background habitat degradation from being wrongly attributed to the development.

1. Introduction

The global environmental benefits of offshore wind energy developments are undisputed and there is considerable political support for the continued expansion of this industry (Baltas and Dervos, 2012; Brennand, 2004; Portman et al., 2009; Saidur et al., 2010). As in any industry however, there are environmental impacts associated with construction, operation and decommissioning activities and it is vital that these are given due consideration. The UK currently has the largest installed offshore wind capacity in the world, exceeding 3GW (BVG Associates, 2013). Predicted expansions in the industry could see this figure rise to 18 GW by 2020. There has been a greater than tenfold increase in the generation capacity of wind turbines since the first wind farm was installed in UK waters, although this has not resulted in an equivalent reduction in the overall size of each development. The footprint of individual wind farms has steadily increased in-line with the UK governments renewable energy targets (Brennand, 2004). Under Round 1 of the UK's offshore wind farm development scheme, administered in December 2000, sites ranged from 4 to 45 km^2 (mean 13 km^2) (4C Offshore, 2013). Under Round 2 of the scheme, development sites ranged in size from 8 to 230 km^2 (mean 70 km^2) (4C Offshore, 2013). Many of the Round 1 and Round 2 sites were subsequently extended and nine significantly larger zones were designated for offshore wind development under Round 3 in January 2010. The Round 3 zones range in size from 162 km^2 (Rampion Offshore Wind Farm) to 8660 km^2 (Dogger Bank) (4C Offshore, 2013). The ambition is that the larger Round 3 zones will

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ultimately house multiple adjacent wind farms that will collectively produce a total output of 33 GW. The rate at which the offshore wind industry is developing and the fact that these developments are occurring against a backdrop of unprecedented levels of anthropogenic disturbance (Blaber et al., 2000; Cardoso et al., 2008; Kaiser et al., 2006; Merchant et al., 2012; Royal Commission on Environmental Pollution, 2004; Tappin et al., 2010) makes environmental consideration all the more important.

In a widely cited review of the potential impacts of offshore renewable energy developments Gill (2005) identified numerous sources of likely environmental damage. Abbasi and Abbasi (2000) concluded that the adverse environmental impacts associated with renewable energy sources could be as strongly negative as the impacts of conventional energy sources. In contrast, there is a growing body of thought that offshore renewable energy developments may enhance the marine environment by creating artificial reef habitats, by acting as aggregation devices for fish and by forming *de-facto* marine reserves by excluding other sea users (Ashley et al., 2014; Inger et al., 2009; Reubens et al., 2011, 2013;Wilhelmsson et al., 2006; Wilhelmsson and Malm, 2008; Wilson, 2007; Wilson and Elliott, 2009). This is of course dependent on the environment being given careful consideration during the planning and design phases and would only apply where developments occur in non-pristine environments.

Knowledge of the distribution, quality and quantity of habitats and species, is fundamental to our ability to protect them (Jackson et al., 2001). Historically, distribution records were based entirely on point observations and samples but this changed with the wide acceptance of remote sensing techniques in the early 1990s. Remote sensing techniques, most notably sidescan sonar and multibeam echo sounding (MBES) systems are now considered the tool of choice when mapping large areas of the seabed (Coggan et al., 2007). These survey tools are able to ensonify large areas of the seabed with 100% coverage at a resolution finer than 1 m^2 (Anderson et al., 2008). Sidescan sonar and MBES data can be used to define roughness characteristics, acoustic properties and morphological features of the seabed which in turn can be used to map habitat boundaries (Brown and Blondel, 2009). In recent years this mapping process has been taken a step further with the incorporation of biological ground-truthing. Acoustic signatures have been found to behave as reliable surrogates of biotopes, and with sufficient ground-truthing can be used to create full coverage biotope maps with moderate to high levels of confidence (Brown and Collier, 2008; Ierodiaconou et al., 2011; Micallef et al., 2012). A number of studies have demonstrated the utility of very-high resolution acoustic data in mapping discrete biological features such as the reefs formed by the tube-worm *Lanice conchilega* (Degraer et al., 2008), the horse mussel *Modiolus modiolus* (Lindenbaum et al., 2008; Wildish et al., 1998) and seagrass beds (Ardizzone et al., 2006).

Aggregations of the tubiculous polychaete *S. spinulosa* were identified within the Thanet Offshore Windfarm site during baseline characterisation surveys in 2005 (Marine Ecological Surveys Ltd., 2005). Where this species forms reef structures, it is considered to be a conservation priority both at a national and European level. *S. spinulosa* reefs are included in the Habitats Directive definition of reef habitats 1070 and may also be afforded protection as features of broader physiographic habitats listed under the directive such as Estuaries (European Commission, 2007). *S. spinulosa* reefs are also listed in the OSPAR list of threatened and/or declining habitats (OSPAR Commission, 2008) and are identified as Habitats of Principal Importance under Section 42 of the English Natural Environment and Rural Communities (NERC) Act 2006. Despite being listed as a habitat of significant conservation importance the definition of what constitutes an *S. spinulosa* reef remains a topic of much discussion (Gubbay, 2007; Hendrick and Foster-Smith, 2006). The Habitats Directive defines reefs as concretions which arise from the sea floor (European Commission, 2007) whilst the OSPAR definition is based on per cent cover (30% on mixed substrate, 50% on rock) but also notes that the habitat should be thick and persistent and support an epibiota that is distinct from surrounding substrates (OSPAR Commission, 2008). Gubbay (2007) and Hendrick and Foster-Smith (2006) noted that extent, elevation and patchiness are important attributes for defining an *S. spinulosa* reef and both advocate the use of a sliding scale of “reefiness”. Pearce et al. (2007) noted a potential relationship between an irregular acoustic signature and the presence of *S. spinulosa* aggregations that are likely to qualify as reefs of conservation significance based on the aforementioned definitions (Gubbay, 2007; Hendrick and Foster-Smith, 2006; European Commission, 2007; OSPAR Commission, 2008). The aim of this paper is to test the relationship between the textured signature observed in acoustic data and the presence of *S. spinulosa* reefs that may qualify for statutory protection.

Although the *S. spinulosa* aggregations identified at the site were not protected by any formal conservation designations, the wind farm developer and the UK statutory nature conservation bodies (Natural England and the Joint Nature Conservation Committee (JNCC)) decided at an early stage that it would be favourable to protect the best examples of this habitat during the construction phase. The work presented here is one of the first examples of an integrated environmental assessment, where conservation agencies and marine scientists have worked with the developer to facilitate an environmentally responsible construction process. It presents the first attempt to map *S. spinulosa* reef extent and distribution over time in relation to a new offshore wind farm development, representing an important step forward in our ability to map, monitor and manage sensitive marine habitats in the face of increasing anthropogenic activity.

2. Materials and methods

2.1. Study area

The Thanet Offshore Windfarm site is located 12 km off Foreness Point in Kent, in the English southern North Sea (Fig. 1), occupying an area of approximately 35 km^2 in water depths ranging from 15 to 27 m CD (Chart Datum). The site is mesotidal during neap tides, with an estimated tidal range of 2.5 m and macrotidal during spring tides, with an estimated tidal range of 4.3 m (Royal Haskoning, 2005). The Thanet site is also exposed to northerly and easterly waves generated from the North Sea, as well as waves generated from in the English Channel that can propagate from the south. Locally generated waves caused by winds blowing across the Thames Estuary from west to north westerly directions are also significant (Royal Haskoning, 2005).

The near surface geology at the site can be divided into three core units: Cretaceous chalk bedrock to the south, exposed in places but dipping towards the north; Tertiary units overlying the chalk, including Thanet Sand, Woolwich Beds and Harwich Formation exposed at the Drill Stone Reef and in several other places across the site; and Sand and gravel lag, including deposits in paleo-channels cut into the Tertiary units and the chalk (Royal Haskoning, 2005). Surficial sediments at the site range from sand to sandy gravels with a small area of gravel in the far north west. Much of the wind farm site is characterised by sand with megaripples trending in an east-west direction (Gardline Geosurvey Ltd., 2007, 2012). The sand waves typically reach a maximum height of 3 m and are asymmetrical with the lee to the south, indicating that the predominant current is in a southerly direction (Gardline Geosurvey Ltd., 2012). To date there have been no studies on the mobility of these sand waves although it is assumed that some degree of

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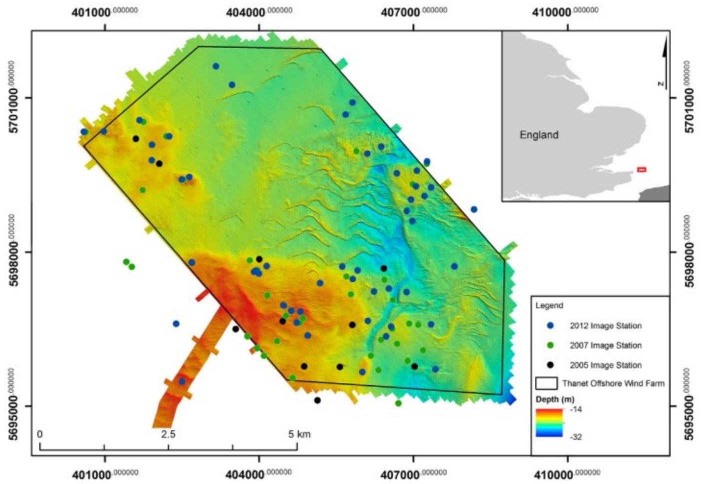

Fig. 1. Chart showing the Thanet Offshore Windfarmsite and the sampling stations sampled with a fresh water lens camera in 2005, 2007 and 2012 (Marine Ecological Surveys Ltd, 2005, 2007, 2012). Sampling stations are overlaid on the 2012 digital elevation model (DEM) derived from high resolution multibeam echo sounder data (Gardline Geosurvey Ltd., 2012).

migration occurs as has been observed at other sites across the North Sea (Royal Haskoning, 2005).

The sedimentary processes occurring at the Thanet Offshore Windfarm site are dominated by the tidally driven current regime which typifies the southern North Sea (Pietrzak et al., 2011). High turbidity levels (monthly average Suspended Particulate Matter (SPM) $> 20\,\text{g}\,\text{m}^{-3}$) are observed year round, peaking between January and April, when the erosion of cliffs along the English coasts is also at its greatest (Pietrzak et al., 2011). High tidal currents (peak spring tides of 1.0 m/s) and inputs from the Thames estuary and the East Anglian Plume (Holt and James, 1999) are all thought to contribute to the high turbidity levels experienced at this site (Pietrzak et al., 2011).

2.2. *Data collection and preparation*

2.2.1. *Acoustic surveys*

Acoustic data were collected from the Thanet Offshore Windfarm site using side-scan sonar and MBES, in order to delineate *S. spinulosa* aggregations. Surveys were carried out in 2005, 2007 and 2012, corresponding to a baseline characterisation survey, a pre-construction baseline survey and a post-construction monitoring survey. The acoustic survey carried out in 2005 was concentrated in the south of the development site as *S. spinulosa* records from baseline macrofaunal sampling were limited to this area. In subsequent surveys the whole site was surveyed using acoustics to ensure the full extent of this habitat was captured.

2.2.1.1. 2005 Baseline characterisation survey. In July/August 2005 sidescan sonar data were collected using a GeoAcoustics Dual Frequency sidescan sonar system, set at its highest frequency (410 kHz) in order to record fine scale seabed features. The sonar fish was towed at a depth of 10–12 m below the surface, equivalent to between 7 and 15 m above the seabed, and the transceiver was set to transmit 8 pings per second. A minimum of 100% coverage was achieved by running north-south survey lines at 150 m intervals, with the data range set to between 75 and 85 m. Infill lines were run at 75 m intervals where time allowed, finally providing > 200% coverage of over 60% of the area surveyed. In addition, two east-west cross-lines were run. Horizontal positioning accurate to approximately ± 1 m was achieved for the recorded vessel track using a CSI dGPS MAX 12-channel parallel differential GPS receiver. The differential corrections used by the receiver were supplied by the IALA beacon system. The sonar tow fish position was calculated using recorded vessel position, vessel heading (from the ships compass) and measured cable 'out' between the vessel and the sonar tow fish. Accuracy of calculated tow fish position is estimated to be ± 3 m. Navigation, data logging, real-time quality control, display and post-processing were carried out using C-View Navigation and C-View Seabed Data Management software packages (C-Products Ltd).

2.2.1.2. 2007 Pre-construction baseline survey. A pre-construction baseline survey was carried out in August/September 2007 across the whole Thanet Offshore Windfarm site. Geophysical surveys were undertaken across the site using a combination of sidescan sonar and MBES. The EdgeTech 4200FS side-scan sonar fish was flown at an approximate height 7.5–10 m above the seabed. The sonar range was set at between 75 m and 100 m and data coverage of between 100% and 400% was achieved across the site. Sidescan sonar data was exported to Coda and digital recorder for post processing and interpretation. MBES data were simultaneously collected using a vessel mounted Simrad EM3002D system. Bathymetry data were processed using Caris HIPS and SIPS (version 7.1) software to produce a depth profile gridded at a horizontal resolution of 1 m^2 and a backscatter layer to aid in the determination of habitat boundaries. Velocity profiles were undertaken at 24 h intervals throughout the survey using a Valeport SV&T probe. Positioning was managed using Gardline's Voyager5 navigation software integrated with the Seatex Seapath 200 positioning and orientating system for heave pitch, roll and yaw corrections. Differential corrections were provided by Fugro Starfix.

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2.2.1.3. 2012 Post-construction monitoring survey. The first in a series of planned post-construction monitoring surveys was undertaken at the site in April 2012, approximately 18 months after the construction of the turbines had been completed. Geophysical surveys were undertaken across the whole site using a combination of sidescan sonar and MBES with the same specifications as the 2007 pre-construction baseline survey.

2.2.2. Ground-truthing sampling

Ground truth sampling surveys were undertaken shortly after each of the acoustic surveys allowing time for a preliminary interpretation of the acoustic data to be undertaken. As *S. spinulosa* reefs are considered to be sensitive to physical damage, direct samples were not collected to groundtruth the acoustics in all but the first baseline survey, although they were collected from adjacent sedimentary habitats as part of more general environmental assessment work (Marine Ecological Surveys Ltd., 2005, 2007, 2012). Ground-truthing was carried out using a drop-down camera system fitted with a fresh-water lens, especially designed to collect images in highly turbid environments as occur at this site (Marine Ecological Surveys Ltd., 2005). Images collected in 2005 were excluded from all analyses as the quality and resolution was insufficient to estimate tube density, % cover or to facilitate the identification of associated fauna. The poor quality and resolution of seabed images taken in 2005 was a result of very high turbidity levels. The freshwater lens camera system was also in a very early stage of development which will also have contributed to the poor quality of the images acquired. The results reported here are therefore limited to those obtained from the seabed images collected in 2007 and 2012. Positioning accurate to approximately ±1 m was achieved for the ground-truth sampling using a differential GPS receiver. Between 3 and 5 images were collected at each sampling site.

2.2.2.1. Tube counts. Estimates of *S. spinulosa* density were determined using the open source image processing software, Image J® (Schindelin et al., 2012). The number of tube openings were used as a proxy for the density of live *S. spinulosa* as animals were completely retracted in the majority of photographs obtained. Image J® standard methods for particle counting were adapted for *S. spinulosa* density estimations. The process involved image smoothing and sharpening and overlaying a reference grid. Tube openings were counted using the Image J cell-counting utility. Counts for each image were repeated 3 times and the mean calculated. As this method relies on high quality images with low background noise, images collected in 2005 could not be analysed using this method and 50 of the 268 images collected in 2007 and 2012 also had to be excluded from the analysis due to high levels of background noise, poor focus and/or high turbidity levels.

2.2.2.2. Per cent cover calculations. The total per cent cover of *S. spinulosa* structures, including dead and broken tubes, was estimated for each image collected in the 2007 and 2012 surveys. Working on the assumption that any structures that were intact and growing vertically were living, the per cent cover of live *S. spinulosa* structures was also estimated. A grid was overlaid on each image in Photoshop, and a series of reference images were produced to aid the consistency of estimations.

2.2.2.3. Macrofaunal abundance. All macrofauna visible in the seabed images were identified to the highest possible taxonomic resolution (species level where possible) and their abundance recorded. Colonial species that cannot be accurately enumerated were recorded as present or absent (1 or 0 respectively). The World Register of Marine Species (WoRMs; http://www.marinespecies.org/) was used to ensure consistency in the species nomenclature.

2.3. Habitat mapping

The acoustic data were interpreted to provide estimates of the distribution and extent of *S. spinulosa* reefs within the Thanet Offshore Windfarm site using the presence of an irregular surface texture noted by Pearce et al. (2007), (Fig. 2). The side-scan sonar data formed the primary data source for mapping the extent and distribution of *S. spinulosa* reefs, although digital elevation models (DEMs) produced from the MBES data, and the associated backscatter data, were used to further aid the delineation of reef boundaries. Since the irregular texturing produced by *S. spinulosa* habitats cannot definitively be distinguished from other biogenic structures, ground-truthing data were used to verify the species responsible for the putative reefs. For example, during the 2007 surveys an area initially identified as potential *S. spinulosa* reef was subsequently identified as a mussel bed formed by the blue mussel, *Mytilus edulis*. This habitat only occupied a small area, was only captured at one ground-truthing station, and has been excluded from the current study.

2.3.1. Verification of acoustic reef classification

The detection of *S. spinulosa* reefs using acoustic data was verified using quantitative measures of *S. spinulosa* tube density and % cover of *S. spinulosa* structures derived from seabed images. For each measure, values within stations were averaged, and then pairwise differences between stations were calculated using Euclidean distance. A permutational dispersion test (Anderson, 2006) revealed that the variance in density was significantly different between the two habitat classes and hence the density data was $\text{Log}(x+1)$ transformed, before being averaged. The resulting resemblance matrices were analysed using a 2-way permutation-based analysis of variance (PERMANOVA; Anderson, 2001, McArdle and Anderson, 2001) to determine the significance of differences between acoustically-derived habitat classes (*S. spinulosa* reef and sediment) and years (2007 and 2012). This procedure is formally equivalent to standard Analysis of Variance, but the flexibility and robustness of the permutation approach avoids the necessity for variables to fulfil standard normality assumptions.

2.4. Impact assessment

The influence of the wind farm development on the *S. spinulosa* reefs and adjacent sedimentary habitats was investigated by calculating the relative extent of reefs recorded in the acoustic data in 2005, 2007 and 2012, and by examining the associated macrofaunal communities. Quantitative macrofaunal abundance data extracted from the seabed images collected in 2007 and 2012 were used to calculate a range of univariate measures of community structure. These were: S, number of taxa; N, number of individuals; H', Shannon's diversity and J, Pielou's J', an evenness measure. Sample values were averaged within sampling stations, pairwise differences calculated between stations, and the resulting resemblance matrix analysed using 2-way PERMANOVA. A permutational dispersion test (PERMDISP; Anderson, 2006) revealed that the variance in S was significantly different between the two habitat classes and hence a $\text{Log}\,(x+1)$ transformation was applied before the number of species (S) was averaged by station.

Differences in the faunal composition between 2007 and 2012 and between the different acoustic habitat classes were also investigated using a 2-way PERMANOVA carried out on a Bray–Curtis similarity matrix calculated using untransformed, station-averaged macrofaunal abundance data. Finally, a one-way SIMPER analysis was carried out on the same data, using a combined factor of habitat class and year, to ascertain which taxa were responsible

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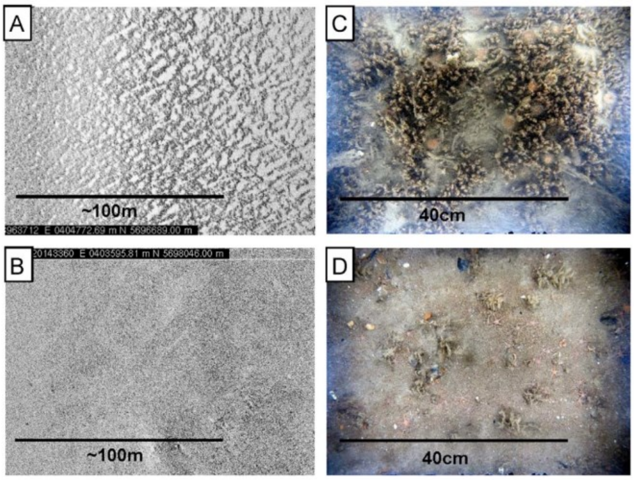

Fig. 2. High resolution (410 kHz) sidescan sonar snapshot images (EdgeTech 4200FS) of (A) *Sabellaria spinulosa* reef; (B) Flat sedimentary habitats within the Thanet Offshore Windfarm site in 2012; (C) seabed image taken at the same location as A; and (D) seabed image taken at the same location as B.

for the observed differences (Clarke and Gorley, 2006; Clarke and Warwick, 2001).

3. Results

3.1. Verification of acoustic reef classification

3.1.1. Sabellaria spinulosa density

The density of *S. spinulosa* tubes recorded in seabed images was higher in areas identified as *S. spinulosa* reef than in adjacent sedimentary habitats (Fig. 3a). The range of *S. spinulosa* densities was notably higher in 2012, both within and outside areas that were identified as reef, and much higher densities of *S. spinulosa* were recorded in adjacent sediments in 2012. This suggests that the reef habitats became patchier over this time period, and the increase in *S. spinulosa* density in adjacent sediments could be a precursor to future reef development. Although differences in *S. spinulosa* densities on and off acoustically defined reef habitats were significant, whilst differences between years were not (Table 1), there is a decrease in the median density of *S. spinulosa* within reefs between 2007 and 2012, driven by a small number of stations sampled in 2007 with densities of >6000 individuals per image. The tubes identified in these images were very small (<0.5 mm in diameter) indicating that this was a new settlement. Tube openings with this diameter were not recorded at any other stations or in any other year.

3.1.2. Per cent cover of S. spinulosa structures

The total % cover of *S. spinulosa*, including dead and broken structures, and the % living *S. spinulosa* structures, were found to differ significantly on and off acoustically-defined areas of reef (Table 1). A marginally significant difference was also detected in the total % cover between years. The relationship between the acoustic reef classification and the % living *S. spinulosa* (Fig. 3b) is similar to that observed with tube density (Fig. 3a). The relationship between the acoustic reef classification and the total % cover of *S. spinulosa* (Fig. 3c), which includes dead and broken up structures, followed the same general trend but there was a larger overlap between classes.

3.2. Effect of the wind farm development on benthic habitats

3.2.1. S. spinulosa reef extent

Acoustically-derived maps of the extent and distribution of *S. spinulosa* reefs in 2005, 2007 and 2012 (Fig. 4) show that although there were differences in the areas surveyed between 2005 and 2012 there was a considerable level of change in the distribution and extent of *S. spinulosa* reefs during this time (Fig. 4; Table 2). Between the baseline characterisation survey undertaken in 2005 and the pre-construction survey carried out in 2007 there was a marked decrease in the extent of *S. spinulosa* reef in the southern sector of the development site. However, a new area of reef was detected in the north of the site which was of roughly equivalent extent. As this area was not covered by the 2005 high resolution acoustic survey it is impossible to know whether or not the reef was present at that time. An increase in reef extent was recorded between the 2007 pre-construction survey and the 2012 post-construction survey, both in the southern sector and across the site as a whole. The *S. spinulosa* reefs in the southern sector increased in extent by 0.42 km^2 during this time and the across the site as a whole there was an increase of 0.32 km^2.

3.2.2. Macrofaunal diversity

In both 2007 and 2012 numbers of species (S) and Shannon Weiner's diversity (H') were significantly higher in samples taken from within acoustically defined areas of *S. spinulosa* reef than in samples taken from areas identified as being sedimentary habitats (Tables 3 and 4). These two indices also increased between 2007 and 2012. Differences in the numbers of individuals (*N*) and Pielou's evenness (*J'*), a measure of the equitability of species abundance, between samples taken on and off acoustically defined areas of reef were not significant (Table 4).

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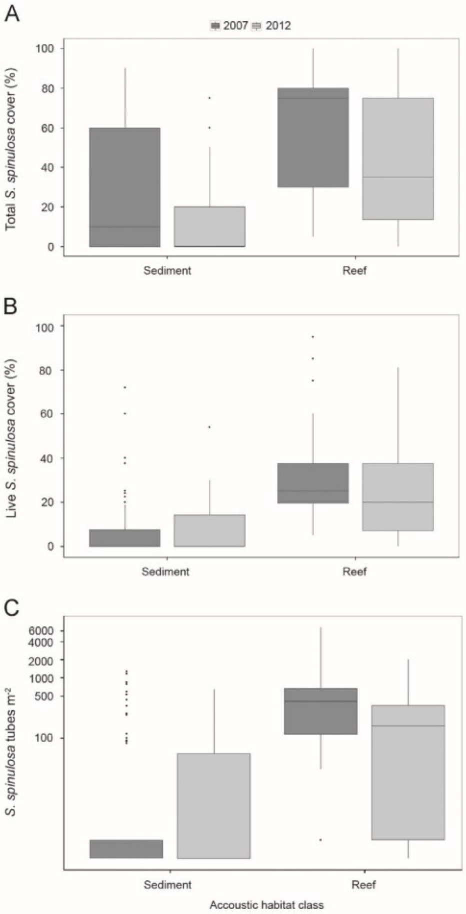

Fig. 3. Box plots showing (A) the density of *S. spinulosa* tube openings, (B) total % cover and (C) % cover of living *S. spinulosa* structures recorded in seabed images taken within acoustically defined *S. spinulosa* reefs and adjacent sedimentary habitats in 2007 and 2012 within the Thanet Offshore Windfarm site (Fig. 2). Each of the boxes represents the interquartile range of densities recorded whilst the central line represents the median value. The upper and lower limits of the density records (Median ± 1.5 × IQR) define the limits of the whiskers and any outlying values (< or > Median ± 1.5 × IQR) are represented by a dot.

3.2.3. Community composition

To determine whether observed differences in diversity reflected differences in community composition, the Bray–Curtis resemblance matrix derived from macrofaunal abundance data was analysed using permutational analysis of variance (Table 5). There were statistically significant differences between the macrofaunal communities associated with each acoustic habitat class, and between 2007 and 2012. SIMPER analysis (Table 6) showed that the relative abundance of fauna present was driving the differences between the acoustically defined habitat classes and between 2007 and 2012. Whilst differences in the abundance of individual taxa recorded in each habitat and year class exist, the taxa present remain broadly comparable across all classes.

A number of attached epifaunal taxa including anemones belonging to the genus *Sagartia*, and hydroids belonging to the genera *Obelia* and *Halecium* were more abundant in samples taken from *S. spinulosa* reefs than in samples taken in sedimentary habitats. These taxa were also more abundant in 2012 than in 2007. Colonial animals such as the hydroids were only recorded as being present (1) or absent (0), so the differences observed in these taxa are likely to be more ecologically significant than the numbers presented in Table 6 suggest. Some mobile species, such as the brittle star *Ophiura albida*, the pink shrimp *Pandalus montagui* and the hermit crab *Pagurus berhardus*, also increased in abundance between sediment habitats and reefs, and between 2007 and 2012. In contrast, the queen scallop, *Aequipecten opercularis*, was all but absent from the *S. spinulosa* reef habitat in 2012 despite being present in high numbers in 2007.

The common starfish, *Asterias rubens*, and the long clawed porcelain crab, *Pisidia longicornis*, were both more abundant on the *S. spinulosa* reefs than in adjacent sedimentary habitats but their abundance showed little change between 2007 and 2012. This indicates that the presence of reef has a greater influence on the distribution of these species than other elements of the environment that changed between 2007 and 2012. Conversely, a dramatic increase in the abundance of the anemone *Sagartiogeton laceratus* was observed between 2007 and 2012 in sedimentary habitats, indicating that this species may be responding positively to changes in environmental conditions that occurred during this time.

4. Discussion

4.1. Mapping S. spinulosa habitats using high resolution acoustic data

Sidescan sonar technology has been shown to be effective in the detection of small-scale seabed features such as seagrass beds, horse mussel beds and *Lanice conchilega* beds through the discrimination of textural differences on the seafloor (Ardizzone et al., 2006; Degraer et al., 2008; Lindenbaum et al., 2008; Wildish et al., 1998; additional examples are given in other papers contained within the marine renewable energy Special Issue). This paper demonstrates that this technology can also be used to

Table 1

Summary of a series of Permutational Multivariate Analysis of Variance (PERMANOVA) tests carried out on Log $(x+1)$ transformed, station averaged *S. spinulosa* tube density and station averaged live and total *S. spinulosa* cover (%) derived from seabed images collected across the Thanet Offshore Windfarm site in 2007 and 2012 in acoustically defined *S. spinulosa* reefs and adjacent sedimentary habitats. A 2-factor crossed design was tested using Type I (sequential) sums of squares with permutations under a reduced model. The test results for interactions between habitat class and year (Habitat X Year) are also provided. The Pseudo-F (*F*) test statistic is provided alongside the probability (*P*) of obtaining that test statistic, generated using permutations. Significant results ($P \leq 0.05$) are highlighted with an asterisk.

	Acoustic habitat class		Year		Habitat class × Year	
	F	*P*	*F*	*P*	*F*	*P*
S. spinulosa tube density (Log $(x+1)$)	35.73	0.001*	0.05	0.827	0.48	0.477
Live *S. spinulosa* cover (%)	27.76	0.001*	0.66	0.43	1.22	0.265
Total *S. spinulosa* cover (%) (including dead and broken up structures)	12.30	0.002*	4.45	0.045*	0.0001	0.987

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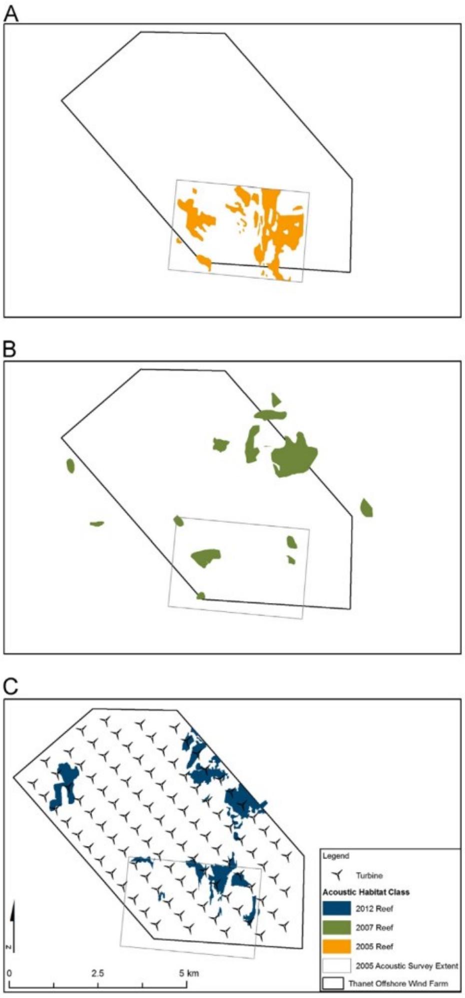

Fig. 4. Charts showing the distribution and extent of *S. spinulosa* reefs identified within the Thanet Offshore Windfarm site in 2005 (A), 2007 (B) and 2012 (C) using high resolution sidescan sonar and multibeam echo sounder data (Gardline Geosurvey, 2007, 2012; Marine Ecological Surveys Ltd., 2005, 2007, 2012). Also shown are the extent of the reduced 2005 acoustic survey and the turbines installed at the site in 2011.

Table 2
Summary of the extent (km^2) of *S. spinulosa* reef identified within the Thanet Offshore Windfarm site using high resolution sidescan sonar data (see also Fig. 2). Note that only the southern sector of the site was surveyed using high resolution sidescan sonar in 2005.

	Southern sector			Whole site	
	2005	2007	2012	2007	2012
Sabellaria spinulosa Reef (km^2)	2.57	0.48	0.90	2.59	2.91

Table 3
Mean values of macrofaunal diversity indices (S=No. Species, N=No. Individuals, *H'*=Shannon's diversity and *J'*=Pielou's evenness) calculated from macrofaunal abundance data obtained from seabed images collected in each of the acoustically defined habitat classes (*Sabellaria spinulosa* reef and sedimentary habitats). *S. spinulosa* abundances were excluded from this analysis.

		S		*N*		*H'*		*J'*	
		2007	2012	2007	2012	2007	2012	2007	2012
Mean	*S. spinulosa Reef*	3.00	4.74	14.85	15.20	0.69	1.05	0.68	0.74
	Sediment	1.70	3.77	5.90	20.42	0.41	0.81	0.75	0.61

Table 4
Summary of a series of Permutational Multivariate Analysis of Variance (PERMANOVA) tests carried out on station averaged diversity indices calculated for macrofaunal abundance data from seabed images collected across the Thanet Offshore Windfarm site in 2007 and 2012 in acoustically defined habitat classes (*Sabellaria spinulosa* reef and sedimentary habitats). A 2-factor crossed design was tested using Type I (sequential) sums of squares with permutations under a reduced model. The test results for interactions between habitat class and year (Habitat X Year) are also provided. The Pseudo-F (*F*) test statistic is provided alongside the probability (*P*) of obtaining that test statistic, generated using permutations. Significant results ($P \leq 0.05$) are highlighted with an asterisk.

	Acoustic habitat class		Year		Habitat Class × Year	
	F	*P*	*F*	*P*	*F*	*P*
S	24.53	0.001*	22.67	0.001*	0.13	0.714
N	1.63	0.216	4.75	0.032*	3.37	0.062
H'	17.79	0.003*	13.4	0.004*	0.03	0.851
J'	0.51	0.469	0.89	0.362	2.87	0.091

Table 5
Summary of a Permutational Multivariate Analysis of Variance (PERMANOVA) test carried out on station averaged macrofaunal abundance data from seabed images collected across the Thanet Offshore Windfarm site in 2007 and 2012 within and outside acoustically defined areas of *S. spinulosa* reef. A 2-factor crossed design was tested using Type I (sequential) sums of squares with permutations under a reduced model. The test result for the interaction between habitat class and year (Habitat X Year) is also provided. The Pseudo-F (*F*) test statistic is provided alongside the probability (*P*) of obtaining that test statistic, generated using permutations. Also shown are the degrees of freedom (*df*), sums of squares (SS) and mean squares (MS). Significant results ($P \leq 0.05$) are highlighted with an asterisk.

Source	*df*	SS	MS	Pseudo-F	*P*
Acoustic Habitat Class	1	7751	7752	2.66	0.011*
Year	1	14,531	14,531	4.98	0.001*
Habitat Class × Year	1	5334	5334	1.83	0.062
Residual	62	180,800	2916		
Total	65	2,084,200			

reliably detect *S. spinulosa* reefs. In addition, high resolution multibeam backscatter and bathymetry data were used to supplement the sidescan sonar data interpretation and these methods were also found to be successful in distinguishing the textural differences between *S. spinulosa* reefs and surrounding sediments.

S. spinulosa aggregations are visible in both high resolution sidescan sonar and backscatter derived from MBES data as an irregular texturing of the seafloor. The precise physical qualities of *S. spinulosa* reefs that generate the irregular acoustic signature is not yet fully understood, but it seems likely that it is a combination of both physical and biological factors. The high rigidity of the tube structures would result in areas of high reflectivity in the acoustic data, as has been observed in other polychaete reefs (Degraer et al., 2008). Conversely the high volume of biological material associated with *S. spinulosa* reefs, both in terms of the reef-building organisms

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Table 6
The average abundance (n) of the taxa that collectively contribute to 90% of the dissimilarity between the different acoustic habitat classes and the different years. Determined through a SIMPER analysis on untransformed, station averaged macrofaunal abundance recorded from seabed images. Note *S. spinulosa* itself was excluded from this analysis.

Taxa	Sediment		Reef	
	2007	2012	2007	2012
Ophiura albida	3.19	8.18	2.67	5.97
Sagartia spp.	1.05	1.43	2.81	3.84
Aequipecten opercularis	0.13	0.08	6.56	0.43
Pagurus bernhardus	0.08	0.58	0.26	0.79
Pandalus montagui	0	0.18	0.15	0.75
Sagartiogeton laceratus	0.15	7.67	0.59	0.1
Obelia spp.	0	0.32	0.04	0.57
Asterias rubens	0.19	0.17	0.33	0.34
Pisidia longicornis	0.03	0.02	0.52	0.32
Halecium spp.	0.03	0.3	0.04	0.36
Pomatoceros spp.	1.13	0.2	0.19	0.11
Hydrallmania falcata	0	0.25	0	0.04

themselves and the associated fauna, would result in low reflectivity in the acoustic data, as observed in the acoustic signature of seagrass beds (Ardizzone et al., 2006). This combination of high- and low-reflectivity attributes of the reefs is likely to be, at least partially, responsible for the irregular texturing observed in the acoustic signature which is characteristic of these habitats.

Significant differences in tube density and percentage cover (living and total) between samples taken on and off the reefs identified in acoustic data, supports this hypothesis. Furthermore, as differences in percentage live cover and tube density between samples collected from the *S. spinulosa* reefs and from adjacent sediments were more pronounced than differences in total cover, which includes broken structures, it seems likely that healthier reefs will be more detectable using these acoustic techniques. Tube densities and per cent living cover will be highly correlated with each other as only erect tubes can be counted reliably using automated image counting techniques, and these are likely to be alive. Both tube density and per cent living cover are also likely to be correlated with the biomass of *S. spinulosa*, which may explain the stronger relationship with the acoustic signatures. However, it is also possible that aspects of the non-living *S. spinulosa* cover such as tube degradation or horizontal positioning could be responsible for the weaker relationship observed with the acoustic signatures.

Fine sediment, known to collect in the gaps in Sabellariid reef structures (Cunningham et al., 1984; Kirtley and Tanner, 1968; Pandolfi et al., 1998) may also contribute to the variable reflectivity observed in the acoustic signature but this aspect was not measured during the current study. Well-developed *S. spinulosa* aggregations, in terms of size and elevation, are visible not only in the MBES backscatter data but also in the digital elevation model (DEM), indicating that a component of the irregular signature observed may be caused by variations in the height of these structures as well as by differences in reflectivity.

4.2. New insights into the impacts of offshore wind farm developments

In addition to demonstrating the ability of high resolution acoustic data to detect and delimit *S. spinulosa* reefs, this study provides new insights into the response of these and adjacent sedimentary habitats to an offshore wind farm development. Offshore wind farms have previously been reported to increase biomass by acting as an artificial reef (Krone et al., 2013; Wilhelmsson et al., 2006; Wilson and Elliott, 2009) and by acting as fish aggregation devices (Reubens et al., 2011, 2013). It has also been postulated by some authors that these developments could act as de-facto marine reserves (Inger et al., 2009). This study provides some evidence for the latter. *S. spinulosa* reef habitats were found to have increased in extent by 0.32 km^2 18 months after construction at the site had been completed. The absence of any significant *S. spinulosa* reef losses during and after construction indicates that the micro-siting of turbines was effective at this site, and that these habitats have not been negatively impacted by the development.

A decrease in reef extent (2.09 km^2) was observed in the southern sector of the development site, between the 2005 baseline survey and the 2007 pre-construction survey. The reduction in reef extent in the absence of any construction activities associated with the wind farm development is indicative of a habitat with a high level of natural variability. However, these changes in extent may be attributable to other anthropogenic pressures acting on this area, such as commercial fishing. Commercial fishing, and towed bottom gear in particular, is widely accepted as having detrimental impacts on the benthos (Cook et al., 2013; Kaiser et al., 2006) and scars which are very likely to have been caused by paired beam trawlers were noted in the high resolution acoustic data collected across this site in 2005 and 2007 (Marine Ecological Surveys, 2005, 2007). It is therefore impossible to separate the natural variation in reef extent and distribution from the physical effect of fishing activities that occurred in this area between 2005 and 2007. Future monitoring surveys of the Thanet Offshore Windfarm site may provide important information to help tease apart these aspects of reef ecology.

The diversity of macrofauna supported by both *S. spinulosa* reefs and adjacent sedimentary habitats was significantly higher in 2012 (post-construction) than in 2007 (pre-construction). In the absence of any non-impacted reference sites it is impossible to attribute the enhancements observed to the presence of the wind farm unequivocally. However, this area was known to be targeted by commercial beam trawlers prior to the construction of the wind farm and it is likely that this source of anthropogenic disturbance has been reduced. Although there are no legislative barriers to commercial fishing in the Thanet Offshore Windfarm site, and the turbine locations were designed to allow trawling in the area to continue, it is likely that construction works will have reduced fishing effort in this area. It is possible therefore that a short-term reduction in these activities may be responsible for the increase in macrofaunal diversity and increase in abundance of epifauna associated with *S. spinulosa* reefs in this area. Whether or not the presence of the Thanet Offshore Windfarm has influenced the use of this site by commercial fishermen, beyond the construction phase, has yet to be established.

4.3. The importance of repeat mapping in support of offshore wind farm developments

This study demonstrates the application of seabed mapping using acoustics for environmental impact assessment, and also demonstrates the importance of these technologies to an emerging offshore industry. The Thanet Offshore Windfarm development exemplifies pro-active environmental consideration through the life of the development. Conservation agencies and environmental consultants were involved in the environmental impact assessment from an early stage, and this has facilitated the protection of an important benthic habitat during construction through influencing the placement of turbines and cables. Early indications are that this wind farm has not had any detrimental effects on the *S. spinulosa* reefs or the adjacent sedimentary habitats. Increases in reef extent and macrofaunal diversity indicate this development may be having a positive influence on the

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benthos, although the mechanisms driving the observed changes, and their longevity have yet to be established.

Repeated baseline surveys are rare in environmental impact assessment work, but this paper goes some way towards demonstrating their potential importance to both the developer and to science in general. It has been widely postulated that *S. spinulosa* aggregations are ephemeral in nature (Hendrick and Foster-Smith, 2006; Holt et al., 1998) but there have been no studies to date that demonstrate this unequivocally. The 2005 and 2007 surveys undertaken at this site are perhaps the first record of this habitat having moved and changed in extent, although the cause of this change cannot be determined at this time. The change in *S. spinulosa* distribution and extent between the baseline survey and the pre-construction survey also has important implications for the developer. Had the pre-construction survey not been carried out, micro-siting of the turbines would have been somewhat fruitless as the reefs identified in 2005 were no longer present in 2007 and new reefs had been detected elsewhere in the site. Perhaps more critically, the two baseline surveys allow the effects of the development to be put into the context of the natural background variability of this habitat. Decreases in the extent of *S. spinulosa* reefs were noted between the first and second baseline survey. Had this not been recorded these losses could have been attributed wrongly to the construction of the wind farm, and increases in the extent of *S. spinulosa* reefs following the construction of the wind farm would also have gone undetected.

4.4. *Limitations*

The data presented in this article were collected as part of the licensing procedures for wind farm developments in the UK, and were therefore subject to stringent budgetary and timing constraints. The surveys were designed to meet regulatory requirements, which are a compromise between "best science" and the financial burden placed on the developer. This inevitably means that there are imperfections in the survey design. In this case the most notable gap in the survey design is the lack of any reference areas outside the boundary of the wind farm. Had reference sites been placed in suitable areas outside the wind farm boundary a better understanding of temporal and spatial variability in reef extent and quality could have been gained, it would have been possible to place the findings reported here, in a more robust context of background variation. This ultimately would have made the findings of this study more scientifically robust.

The acoustic data collected as part of this study was acquired by two different contractors, using different equipment. Even in the two years where the data were collected by the same contractor using the same equipment (2007 and 2012) the interpretation was undertaken by different individuals. The use of different equipment and different personnel introduces a number of sources of potential error. Time-series data are a very valuable commodity in the marine environment (Frost et al., 2006) unfortunately, where data are collected as part of a licensing and/or monitoring requirement the error levels associated with requirements to reduce costs and deliver outputs within short timescales may significantly reduce their scientific value. Efforts to standardise the way that acoustic data are collected across Europe will help to reduce levels of error and subjective differences in interpretation between contractors and scientists (Coggan et al., 2007). There is also a considerable amount of research currently underway to develop mechanisms of automated acoustic data classification which may ultimately remove the subjectivity of manual interpretation and allow for much more homogeneous time-series assessments (Brown and Collier, 2008; Brown et al., 2011; McGonigle et al., 2009).

It was not possible to use the seabed images collected in 2005 because of the poor image quality, caused in part by the very high levels of turbidity experienced at this site. As photographic technology advances it is likely that our ability to monitor the environment remotely will also advance. However, there are limitations to this sampling technique which will not change. For example, it is not possible to identify all taxa to species level from seabed images alone. Many species, including colonial hydroids, can only be identified reliably to the species level using a stereo-microscope because important morphological differences are not visible to the human eye. Other taxa, such as tubiculous polychaetes, cannot be identified to the species level because the animals themselves are concealed within their tubes. In this study the identification of sea anemones was particularly problematic. *Sagartia* spp. could not be identified to species as this requires detailed examination their anatomy (e.g. tentacle positioning) as well as knowledge of the substrate upon which they are attached. The latter could not be determined reliably from all images because of the high level of habitat heterogeneity. The authors are confident that both *S. elegans* and *S. troglodytes* were present across the site but could not separate these species consistently. In many instances the loss of species-specific information will not be significant but in this instance it is likely that failure to detect differences in the relative abundance of these two species may have masked important information about the environmental changes that occurred between 2007 and 2012.

Seabed imagery is also limited to the assessment of epifaunal taxa, as most infauna will not be visible from the surface of any given substrate. Grab sampling would have facilitated a more complete assessment of the faunal assemblages in the area, and the potential impacts of the wind farm development. Statutory advice is to avoid direct (destructive) sampling of *S. spinulosa* habitats as this is thought to be more damaging than using remote sampling systems. However, there is no evidence to support this assertion as most drop-camera systems come into direct contact with the seabed and it is likely that they also cause some damage to the habitat. Evidence collected from an aggregate extraction site in the English Channel (Pearce et al., 2007) indicates that these habitats are able to recover from physical disturbance in a very short period of time. A limited amount of direct sampling would therefore be unlikely to cause long-lasting damage to the habitat, and the contributions this could make to its future management are thought to outweigh the risks.

Evidence presented here indicates that offshore wind farms may have positive impacts on benthic communities, possibly through the exclusion of other more damaging activities such as fishing. However, this study only considers one site, and only one post-construction survey has been undertaken to date. The effects of the Thanet Offshore Windfarm site on associated benthic assemblages may not yet have been fully realised, and we cannot yet be confident that the apparent enhancements in *S. spinulosa* reef habitat extent and diversity are attributable to the development. The impacts of offshore developments may also be very site specific, so caution should be exercised when extrapolating the results presented here to other wind farm sites.

5. Conclusions

High resolution acoustic data have been shown to successfully discriminate *S. spinulosa* reefs from surrounding sedimentary habitats. Significant differences in the density of *S. spinulosa* tubes, and both living and total per cent cover of *S. spinulosa* structures, were observed between reef and non-reef habitats delineated using high-resolution acoustic imaging, validating the use of this survey technique in environmental assessment work.

The extent of *S. spinulosa* reefs identified within the Thanet Offshore Windfarm site increased between the pre-construction

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survey in 2007 and the post-construction survey in 2012, indicating that the wind farm may be providing some protection to this habitat. The diversity of macrofauna associated with the *S. spinulosa* reefs at the site was greater than that observed in adjacent sedimentary habitats, suggesting that increasing the extent of this habitat will have a positive impact on the benthic biodiversity at this site. An increase in the diversity of macrofauna associated with both the *S. spinulosa* reefs and the sedimentary habitats at this site between 2007 and 2012 provides evidence that the wind farm may be having a positive influence on the benthos although the mechanism for this is not yet clear. Future monitoring surveys, ideally incorporating reference sites, would be needed to determine the full effect of this development on the benthos and to separate any effects of the wind farm from the natural variability in the system and the effects of commercial fishing.

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