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Conceptual Ecological Modelling of Shallow Sublittoral Mud Habitats to Inform Indicator Selection

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Summary

The purpose of this study is to produce a series of Conceptual Ecological Models (CEMs) that represent the shallow sublittoral mud habitat in the UK. CEMs are diagrammatic representations of the influences and processes that occur within an ecosystem. The models can be used to identify critical aspects of an ecosystem that may be developed for further study, or serve as the basis for the selection of indicators for environmental monitoring purposes. The models produced by this project are 'control diagrams', representing the unimpacted state of the environment, free from anthropogenic pressures.

It is intended that the models produced by this project will be used to guide indicator selection for the monitoring of this habitat in UK waters. CEMs will eventually be produced for a range of habitat types defined under the UK Marine Biodiversity Monitoring R&D Programme (UKMBMP), which, along with stressor models designed to show the interactions within impacted habitats, would form the basis of a robust method for indicator selection. This project builds on the work to develop CEMs for shallow sublittoral coarse sediment habitats (Alexander*.* 2014).

The project scope included the Marine Strategy Framework Directive (MSFD) predominant habitat type 'shallow sublittoral mud'. This definition includes those habitats that fall into the EUNIS Level 4 classifications A5.33 Infralittoral Sandy Mud, A5.34 Infralittoral Fine Mud, A5.35 Circalittoral Sandy Mud and A5.36 Circalittoral Fine Mud, along with their constituent Level 5 biotopes which are relevant to UK waters. A species list of characterising fauna to be included within the scope of the models was identified using an iterative process to refine the full list of species found within the relevant Level 5 biotopes.

A literature review was conducted using a pragmatic and iterative approach to gather evidence regarding species traits and information that would be used to inform the models and the interactions that occur within the shallow sublittoral mud habitat. All information gathered during the literature review was entered into a data logging pro forma spreadsheet which accompanies this report. Wherever possible, attempts were made to collect information from UK-specific peer-reviewed studies, although other sources were used where necessary. All data gathered was subject to a detailed confidence assessment. Expert judgement by the project team was utilised to provide information for aspects of the models for which references could not be sourced within the project timeframe.

A model hierarchy was developed based on groups of fauna with similar species traits which aligned with previous sensitivity studies of ecological groups. One general control model was produced that indicated the high level drivers, inputs, biological assemblages, ecosystem processes and outputs that occur in shallow sublittoral mud habitats. In addition to this, five detailed sub-models were produced, which each focussed on a particular functional group of fauna within the habitat: tube building fauna, burrowing fauna, suspension and deposit feeding infauna, mobile epifauna, scavengers and predators, and echinoderms and sessile epifauna. Each sub-model is accompanied by an associated confidence model that presents confidence in the links between each model component. The models are split into seven levels and take spatial and temporal scale into account through their design, as well as magnitude and direction of influence. The seven levels include regional to global drivers, water column processes, local inputs/processes at the seabed, habitat and biological assemblage, output processes, local ecosystem functions, and regional to global ecosystem functions.

The models indicate that whereas the high level drivers which affect each functional group are largely similar, the output processes performed by the biota and the resulting ecosystem functions vary both in number and importance between groups. Confidence within the

models as a whole is generally high, reflecting the level of information gathered during the literature review.

Important drivers that influence the ecosystem include factors such as wave exposure, depth, water currents, climate and propagule supply. These factors, in combination with seabed and water column processes, such as primary production, suspended sediments, water chemistry, temperature and recruitment define and influence the food sources consumed by the biological assemblages of the habitat, and the biological assemblages themselves. In addition, the habitat sediment type plays an important factor in shaping the biology of the habitat.

Output processes performed by the biological assemblage are variable between functional faunal groups depending on the specific fauna present and the role they perform within the ecosystem. Important processes include secondary production, biodeposition, bioturbation, bioengineering and the supply of propagules; these in turn influence ecosystem functions at the local scale such as nutrient and biogeochemical cycling, supply of food resources, sediment stability, habitat provision and in some cases microbial activity. The export of biodiversity and organic matter, biodiversity enhancement and biotope stability are the resulting ecosystem functions that occur at the regional to global scale.

Features within the models that are most useful for monitoring habitat status and change due to natural variation have been identified; as have those which may be useful for monitoring to identify anthropogenic causes of change within the ecosystem. Physical and chemical features of the ecosystem have mostly been identified as potential indicators to monitor natural variation, whilst biological factors have predominantly been identified as most likely to indicate change due to anthropogenic pressures.

Contents

1 Introduction

In order to manage the marine environment effectively, it is necessary for decision makers to have access to suitable tools for identifying the state of marine biodiversity, and, where a change in state occurs, to identify possible manageable causes of the change. The use of 'indicators' provides one such method, as a proxy for ecological status.

An indicator is a measurable factor that can be either qualified or quantified and which may be used to monitor the status of an ecosystem (e.g. Noon and McKelvey. 2006). Indicators can be related to any aspect of the marine environment, are typically straightforward to monitor, and provide crucial information about aspects of the target habitat that may otherwise be hard to measure. Indicators may include species, communities, habitat characteristics, or other biological properties, as well as physical or chemical properties of the environment.

The ICES Advisory Committee on Ecosystems[1] defines a good indicator as something easy to comprehend by specialists and non-specialists alike, sensitive and tightly linked in space and time to human activity, accurately measureable, with a low responsiveness to natural changes in the environment, based on currently available data and something that is widely applicable over large areas.

It is well known that indicator selection is no easy task (e.g. Noon and McKelvey. 2006), yet it is crucial to marine resource management. Indicators need to allow the robust assessment of status and enable change within marine ecosystems to be identified. However, it is necessary to be able to differentiate between natural and human induced variability in marine environments, and indicator selection needs to take this into account.

One such method proposed for selecting suitable indicators is the use of Conceptual Ecological Models (CEMs). CEMs allow current knowledge about the links in marine ecosystems to be drawn together in a diagrammatic way to highlight the ecological aspects of marine ecosystems that are important for monitoring (Gross. 2003; Maddox. 1999; Manley. 2000).

The present report is focussed on producing CEMs for the marine habitat 'Shallow Sublittoral Mud', following the former project where CEMs were established for 'Shallow Sublittoral Coarse Sediment Habitats' (Alexander. 2014). It is envisaged that CEMs will be produced for a selection of habitat types defined under the UK Marine Biodiversity Monitoring R&D Programme (UKMBMP). The models produced under this project will demonstrate the ecological components and processes that occur across spatial and temporal scales within non-anthropogenic impacted ecosystems (control models), which along with stressor models designed to show the interactions within impacted habitats (outside the scope of this project), will form the basis of a robust method of indicator selection.

1.1 Habitat Background

The Marine Strategy Framework Directive (MSFD) predominant habitat type 'Shallow Sublittoral Mud' is commonly found within UK waters and has the potential to support a large range of biodiversity. Sublittoral mud habitats are found in generally sheltered conditions of full and variable salinity and are characterised by cohesive muds, with fine- to very fine-grained sand fractions for certain habitats (Connor. 2004).

[1] www.ices.dk/community/groups/Pages/ACOM.aspx

This project uses the UK marine habitat classification (Connor. 2004), as translated in EUNIS (European Nature Information System[2]), to provide a structure to the study. The shallow sublittoral mud habitat covers four biological zones at EUNIS Level 4: infralittoral sandy mud and fine mud, defined as those areas between the mean low water line and the maximum depth at which 1% light attenuation reaches the seabed, circalittoral sandy mud and fine mud defined as the zone between which 1% light attenuation reaches the seabed and the bottom of the wave base (approximately 50-70m depth) (Cochrane. 2010; McBreen. 2011;). The distribution of EUNIS Level 4 biotopes that represent infralittoral and circalittoral mud habitats in the UK is shown in Figure 1.

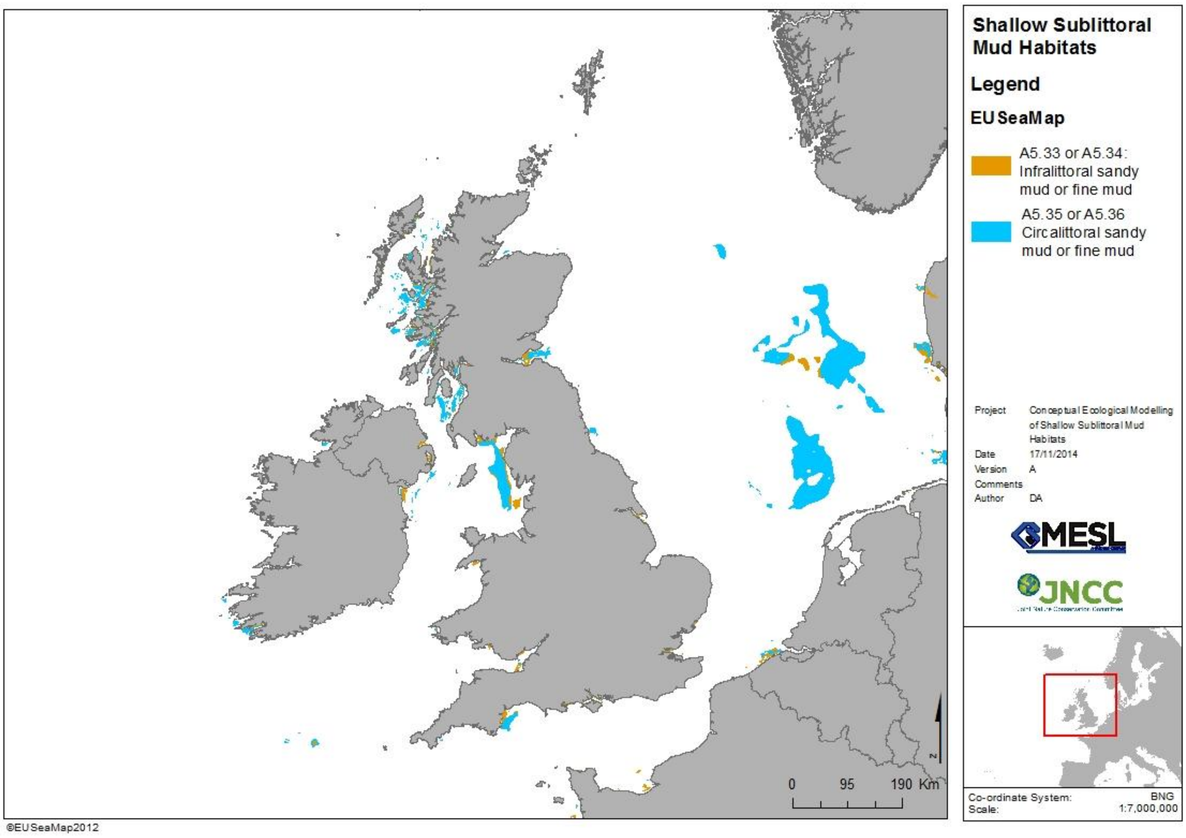

Figure 1. The distribution of shallow sublittoral mud habitats around the UK, split by infralittoral and circalittoral zones. Data is taken from the EUSeaMap broad-scale modelled habitat mapping project[3].

The Level 4 EUNIS habitats comprise the following Level 5 biotopes that have been included in the scope of this project (shown below according to EUNIS code, Marine Habitat Classification for Britain and Ireland v04.05 code shown in brackets) (Connor. 2004):

A5.33 (SS.SMu.ISaMu): Infralittoral sandy mud:

- **A5.331** (SS.SMu.ISaMu.NhomMac)- *Nephtys hombergii* and *Macoma balthica* in infralittoral sandy mud
- **A5.332** (SS.SMu.ISaMu.SundAasp) - *Sagartiogeton undatus* and *Ascidiella aspersa* on infralittoral sandy mud
- **A5.333** (SS.SMu.ISaMu.MysAbr) - *Mysella bidentata* and *Abra* spp. in infralittoral sandy mud
- **A5.334** (SS.SMu.ISaMu.MelMagThy) - *Melinna palmata* with *Magelona* spp. and *Thyasira* spp. in infralittoral sandy mud

[2] http://eunis.eea.europa.eu/
[3] http://jncc.defra.gov.uk/page-5020

- **A5.335** (SS.SMu.ISaMu.AmpPlon) - *Ampelisca* spp., *Photis longicaudata* and other tube-building amphipods and polychaetes in infralittoral sandy mud
- **A5.336** (SS.SMu.ISaMu.Cap) - *Capitella capitata* in enriched sublittoral muddy sediments

A5.34 (SS.SMu.IFiMu) - Infralittoral fine mud

- **A5.341** (SS.SMu.IFiMu.CerAnit) - *Cerastoderma edule* with *Abra nitida* in infralittoral mud
- **A5.342** (SS.SMu.IFiMu.Are) - *Arenicola marina* in infralittoral mud
- **A5.343** (SS.SMu.IFiMu.PhiVir) - *Philine aperta* and *Virgularia mirabilis* in soft stable infralittoral mud
- **A5.344** (SS.SMu.IFiMu.Ocn) - *Ocnus planci* aggregations on sheltered sublittoral muddy sediment

A5.35 (SS.SMu.CSaMu) - Circalittoral sandy mud

- **A5.351** (SS.SMu.CSaMu.AfilMysAnit) - *Amphiura filiformis*, *Mysella bidentata* and *Abra nitida* in circalittoral sandy mud
- **A5.352** (SS.SMu.CSaMu.ThyNten) - *Thyasira* spp. and *Nuculoma tenuis* in circalittoral sandy mud
- **A5.353** (SS.SMu.CSaMu.AfilNten) - *Amphiura filiformis* and *Nuculoma tenuis* in circalittoral and offshore sandy mud
- **A5.354** (SS.SMu.CSaMu.VirOphPmax) - *Virgularia mirabilis* and *Ophiura* spp. with *Pecten maximus* on circalittoral sandy or shelly mud
- **A5.355** (SS.SMu.CSaMu.LkorPpel) - *Lagis koreni* and *Phaxas pellucidus* in circalittoral sandy mud

A5.36 (SS.SMu.CFiMu) - Circalittoral fine mud

- **A5.361** (SS.SMu.CFiMu.SpnMeg) - Seapens and burrowing megafauna in circalittoral fine mud
- **A5.362** (SS.SMu.CFiMu.MegMax) - Burrowing megafauna and *Maxmuelleria lankesteri* in circalittoral mud
- **A5.363** (SS.SMu.CFiMu.BlyrAchi) - *Brissopsis lyrifera* and *Amphiura chiajei* in circalittoral mud

The EUNIS Level 5 biotope A5.345 (SS.SMu.IFiMu.Beg) – *Beggiatoa* spp. on anoxic sublittoral mud. was excluded from the habitat definition as it was found to be extremely rare in the UK and therefore not suitable to inform a general, UK wide CEM for the habitat type.

1.2 Project Aims

The aim of this project is to produce a series of Conceptual Ecological Models (CEMs) to demonstrate the ecological links, drivers, processes and ecosystem functions that occur in shallow sublittoral mud habitats. The models reflect the non-impacted state of the ecosystem (i.e. a state that is exclusive of anthropogenic influence) and will act as control models indicative of the natural state and variability of the environment.

The specific project objectives were as follows:

1. Collate and review available information on the environmental and ecological aspects of shallow sublittoral mud habitats, along with associated confidence and knowledge gap analyses.

2. Create a hierarchical set of control models to represent shallow sublittoral mud habitats and relevant subsystems.
3. Produce a list of key ecological aspects of the habitat which would be most useful for monitoring habitat status and change due to natural variation.
4. Describe how the driving influences and output processes of the habitat are likely to respond to pressures and identify those which may be useful for monitoring to identify anthropogenic causes of change.

2 Literature Review

An initial literature review was designed and conducted to provide necessary information to inform the model building. Information on the following topics was gathered:

- Environmental drivers of the habitat/biotopes (physical and chemical) including factors such as natural variation (e.g. seasonal/annual), prevailing conditions and connectivity with other habitats.
- Species composition within the biotopes, detailing species of conservation importance, key characterising taxa, those which provide specific functions, as well as spatial distribution and temporal variability.
- Biological traits of the key species identified, including features such as life history, environmental preference, feeding habitat and growth form.
- Ecosystem functions provided by the habitat and its associated species, whether physical, chemical or biological and an assessment of the spatial and temporal scales at which these functions occur.

In order to effectively conduct the literature review, key elements for the project were defined as follows:

- **Environmental Driver** – the physical, biological and chemical controls that operate on an ecosystem, shape its characteristics and determine its faunal and floral composition across all spatial scales.
- **Ecosystem Function** – the physical, chemical and biological outputs of the ecosystem that are interconnected with other biotic and abiotic cycles.
- **Ecosystem Process** – the processes through which the flora/fauna and ecosystem are able to provide ecosystem functions.
- **Species Trait** – a biological characteristic of a certain taxa relating to their life history, ecological interactions or environmental preference.
- **Habitat/Biotope Composition** – the physical, chemical and biological characteristics of the environment which support a particular ecological community. The biotopes included within the scope of this project (i.e. those contained within sublittoral mud habitats) are shown in Section 1.1.

Information was initially gathered on the physical, chemical and biological characteristics of each biotope by consulting both the Marine Habitat Classification for Britain and Ireland hierarchy[4] (Connor. 2004) and the European Environment Agency European Nature Information System (EEA EUNIS) Habitat Type Classification[5].

[4] http://jncc.defra.gov.uk/marine/biotopes/hierarchy.aspx
[5] http://eunis.eea.europa.eu

2.1 Species Selection

Aside from the differentiation between light attenuation and wave exposure in the infralittoral and circalittoral biological zones, the large-scale environmental drivers for each biotope are thought to be largely similar to each other. The key and most variable aspect of the models is therefore the characterising fauna themselves.

An initial review of all taxa associated with the project biotopes yielded a list of 155 species (Connor. 2004). To help focus the task within the allotted timescales, the list of species to be included in the scope of the project was refined to the key characterising taxa representative of all the project biotopes. Fauna were selected for inclusion based on the biotope description criteria below (adapted from the methodology developed in Alexander*.* 2014 and Tillin & Tyler-Walters. 2014):

- **Title species**: Fauna named in biotope title, e.g. *Nephtys hombergii, Macoma balthica,* etc*.*
- **Description species**: Species identified as particularly characterising in the biotope descriptive text but not included within the biotope title.

Alexander*.* 2014 also selected example taxa from the full species list to represent groups named in the biotope titles, for example, venerid bivalves and cumaceans. For the sublittoral mud habitats, the description species covered groups named in the biotope titles, such as sea pens and burrowing megafauna.

Alternative methods of reducing the list, for example, grouping fauna by major taxonomic group or using a higher taxonomic classification, were ruled out due to the potential loss of critical information on relevant ecosystem processes and/or functions, and the likelihood that species level information would still be required for effective results. The methodology used was modified from that presented in Alexander. 2014 due to the differing complexity of biotopes between sediment habitats.

The Excel Add-In TREx (Taxonomic Routines for Excel) was used to check taxonomic information (spelling and name changes) about the species selected. TREx was also used to identify whether any of the total of 155 identified species were of conservation importance or were alien species to the UK. This check resulted in one sea urchin species (*Echinus esculentus*) that may be found in Circalittoral Sandy Mud being added to the selection list. *Thyasira* spp. was excluded from the final species list despite being named in a biotope title. This was due to the extremely limited geographical distribution of *Thyasira* spp. and habitat A5.352 '*Thyasira* spp. and *Nuculoma tenuis* in circalittoral sandy mud'.

A revised list of 53 benthic species to be considered within the immediate scope of the project was taken forward for review in the literature, as shown in the accompanying 'Species Selection' worksheet and in Appendix 1.

2.2 Species Traits Selection

Species traits are an essential consideration within the model, impacting the ecosystem functions and feedback loops within the habitat. A comprehensive list of biological traits was collated from the MarLIN Biological Traits Information Catalogue (BIOTIC) database (MarLIN 2006) and further supplemented with other traits considered to be important by the project team for informing the models. This resulted in a list of 47 species traits which was further refined based on other comparable studies (e.g. Van der Linden. 2012; Bolam. 2014; Tillin & Tyler Walters. 2014) and through expert opinion to give a manageable list of 21 relevant traits for inclusion in the project. The list of 21 traits is shown in the data logging spreadsheet (worksheet 4. Trait Selection in the Sublittoral mud CEM literature review and ancillary information spreadsheet), including a short justification for the inclusion of each trait.

2.3 Literature Gathering

In tandem with the process to select biological traits for consideration, an initial literature search was conducted to identify i) the key environmental drivers likely to affect shallow sublittoral mud habitats; ii) the ecosystem processes and functions that the constituent taxa and biotopes are likely to produce; and iii) the interactions that may occur between components and levels of the final models. This information was initially identified using peer-reviewed review papers as the preferred literature source with the highest reliability. These were then supplemented with information from other sources.

Multiple electronic databases (Science Direct, Web of Knowledge, Wiley Online Library) were searched using a list of key words (included in Appendix 2) which ensured that all databases were thoroughly interrogated, and allowed a systematic approach to the literature review.

A ‘grey literature’ search (i.e. literature that has not been peer-reviewed, such as articles, theses, technical reports, agency publications etc.) was also undertaken following the same process as that for peer-reviewed information. The grey literature search was conducted using the Google and Google Scholar search engines and Government agency websites (such as JNCC, Natural England, Cefas, MarLIN, etc.).

Where possible, an attempt was made to utilise sources relating to information from the UK, in some cases, the search was widened beyond the UK to locate information relevant to the research topic. The implications of this are discussed in the confidence assessment presented in Section 2.5.

Taxonomic nomenclature checks revealed that several of the species names listed under the biotope descriptions are no longer accepted in the scientific community. A cross reference with the World Register of Marine Species (WORMS) database[6] indicated that a number of taxa have changed nomenclature. These are listed below:

- *Tharynx marioni* recently changed to *Aphelochaeta marioni*
- *Euclymene oerstedii* is now known as *Euclymene oerstedi*
- *Goniada maculate* is now known as *Goniada maculata*
- *Myriochele oculata* is now known as *Galathowenia oculata*
- *Pectinaria koreni* is now known as *Lagis koreni* but is often called *P. koreni* in literature
- *Spio fuliginosus* is now known as *Malacoceros fuliginosus*
- *Mysella bidentata* is now known as *Kurtiella bidentata* and is often called this in literature
- *Nuculoma tenuis* is now known as *Ennucula tenuis*
- *Rhodine loveni gracilior* is now known as *Rhodine gracilior*

As such, the search terms were varied accordingly, taking into account all known names to search for literature. Species names described in the Marine Habitat Classification for Britain and Ireland v04.05 (Connor. 2004) and EUNIS descriptions have been used throughout this project, even when some names may have changed nomenclature, to ensure that this project is consistent with the classification scheme that the habitat is defined by.

[6] http://www.marinespecies.org/

2.4 Data Logging Pro-forma

Information collated during the literature review was entered into a data logging spreadsheet for ease of reference, and to allow an evaluation of the number of sources gathered to inform the literature gap analysis. These tables were developed in conjunction with the project steering group and accompany this report (Sublittoral Mud CEM Literature Review and Ancillary Information- Version 1.0). The information logged was divided into the following sections (worksheets):

- **Habitat Characterisation**: Physical and chemical characterising information for each biotope type using information from the EUNIS classification and Marine Habitat Classification for Britain and Ireland (both based on Connor. 2004).
- **Faunal Traits Matrix**: Trait information for each of the selected species. Data was entered in such a way with one row in the spreadsheet representing information gathered from one particular source per taxon, thus there are multiple lines per characterising taxon. The reference code of each source is included at the end of each row.
- **Faunal Traits Summary**: Summary of the level of information gathered for each species, used to inform the gap analysis.
- **Interactions Matrix**: Information collated on relevant environmental drivers, ecosystem functions and ecosystem processes relevant to the project habitat. Information on relevant interactions was built up by reviewing the referenced information to establish a list of topics for research. Each piece of information contains metadata on the focus aspect (the model level the information informs), the specific model component the information relates to (temperature, bioturbation, etc.), and the final model links that the information will inform. Details on the source limitations (used to inform confidence), as well as the direction and magnitude of the interaction (based on expert opinion and the referenced information) are also included.
- **Reference Summary**: Source information, full reference, abstract, summary of relevant material extracted and source confidence. Each reference was given a unique code used to identify the source throughout all sheets.

In addition to the above information, the pro forma also presents the full species list from all biotopes, the species selection information, a rationale for each of the traits used in the project and a list of definitions and standard categories used in the literature review.

2.4.1 Magnitude and Direction of Influence

In order for the models to fully show how individual components within the ecosystem link to each other, it was necessary to describe the direction and magnitude of influence between components. This was achieved according to the criteria presented in Tables 1 and 2 for each link represented in the models. Direction of interaction was simple to assign based on literature evidence and expert judgement, whereas the magnitude of the interaction was based solely on expert judgement according to the criteria presented. A direction of interaction was only described for output processes and ecosystem functions. Driving factors on the biological components of the habitat could be both positive and negative, thus were not assigned a direction.

Table 1. Assessment of direction of interaction (Alexander. 2014).

Direction of Interaction	Definition
Positive	The CEM component being considered has a positive/enhancing influence on the component it is linked to, e.g. the presence of bioturbation in a habitat links to enhanced biogeochemical cycling.
Negative	The CEM component being considered has a negative/destabilising influence on the component it is linked to, e.g. the presence of bioturbation in a habitat links to reduced sediment stability.
Feedback	The CEM component being considered has an influencing effect on a higher level driver, e.g. the local ecosystem function 'nutrient cycling' feeds back to 'water chemistry and temperature'.

Table 2. Assessment of magnitude of interaction (Alexander. 2014).

Magnitude of Interaction	Requirement
Low	Low level of connection or influence between ecosystem components. Removal of the link would likely not lead to significant changes in the ecosystem.
Medium	Some degree of connection or influence between ecosystem components. Removal of the link may lead to moderate changes in the ecosystem.
High	Strong connection or influence between ecosystem components. Removal of the link would lead to significant changes in the ecosystem.

2.5 Literature Review Confidence Assessment

Confidence in the data gathered and in the models produced by this project is a key consideration. Confidence has been assessed in a number of ways. The confidence matrix utilised for individual evidence sources is shown in Tables 3a-c. This uses parameters such as source quality (peer-reviewed/non peer-reviewed) as shown in Table 3a, and applicability of the study (whether the source is based on data from the UK and relates to specific model features or not) as shown in Table 3b.

The confidence assessment also has provisions for assigning confidence to 'expert opinion' judgements. Overall confidence is based on the lowest common denominator in confidence from the two source tables, as shown in Table 3c (for example. a source with a high quality score and a medium applicability score would have an overall confidence of medium). Confidence classifications were entered into the relevant column in the Reference Summary worksheet for each source.

Confidence in the individual sources gathered as part of the literature feeds into confidence in the resulting models produced by this project. Confidence in the models and the methodology applied is described in Section 5.

Table 3a. Confidence assessment of quality for individual evidence sources (Alexander. 2014).

Individual Source Confidence	Quality Requirement
High	Peer reviewed Or grey literature reports by established agencies
Medium	Does not fulfil 'high' confidence requirement but methods used to ascertain the influence of a parameter on the habitat / biotope are fully described in the literature to a suitable level of detail, and are considered fit for purpose Or expert opinion where feature described is a well-known/obvious pathway
Low	Does not fulfil 'medium' requirement for level of detail and fitness for purpose but methods used to ascertain the influence of a parameter on the habitat / biotope are described Or no methods adopted and informed through expert judgement

Table 3b. Confidence assessment of applicability for individual evidence sources (Alexander. 2014).

Individual Source Confidence	Applicability Requirement
High	Study based on UK data Or study based on exact feature listed (species, biotope or habitat) and exact CEM component listed (e.g. energy at the seabed)
Medium	Study based in UK but uses proxies for CEM component listed Or study not based in UK but based on exact feature and CEM component listed
Low	Study not based on UK data Or study based on proxies for feature listed and proxies for CEM component listed

Table 3c. Overall confidence of individual evidence sources based on combining both quality and applicability, as outlined separately above (Alexander. 2014).

Overall Source Confidence		**Applicability Score**		
		Low	Medium	High
Quality Score	Low	Low	Low	Low
	Medium	Low	Medium	Medium
	High	Low	Medium	High

3 Summary of Literature Review

Over 200 peer-reviewed and grey literature sources were reviewed as part of this project. The information gathered during the literature review is detailed and summarised in the accompanying data logging pro forma spreadsheet. Specific evidence on ecosystem interactions or species traits which inform the models is presented and discussed throughout Section 4.

The majority of biological traits information was obtained from peer-reviewed and grey literature (such as the MarLIN BIOTIC database) and from taxonomic identification books and keys. Predominantly, the information obtained from journals was research that had been carried out internationally from comparable temperate regions, but in most cases can still be applied to UK species. During the literature review, it became apparent that information was more readily available for larger, common species, or those which are commercially exploited, but less so for rare and smaller interstitial species. Larger faunal species such as *Amphiura filiformis, Echinocardium cordatum, Brissopsis lyrifera* and *Nephrops norvegicus* were well researched, as were many of the tube dwelling polychaete worms such as *Arenicola marina, Lagis koreni* and *Spiophanes bombyx.* Fewer sources were available for species such as *Microprotopus maculatus* and smaller interstitial species such as *Galathowenia oculata.*

Due to the paucity of information relating to driving factors on specific biotopes, a focus was given to generic drivers likely to affect all shallow sublittoral mud habitats. A degree of expert opinion has been used to infer the linkages between some key environmental driving factors and the biological communities. Many of the identified sources relating to environmental drivers were overarching papers that did not relate to a specific location or range. Preference was given to sources describing ecosystem function in shallow sublittoral mud habitats in the UK, although it was not always possible to find suitable information. In some cases, information has been taken from comparable habitats (such as intertidal mud habitats), using comparable taxa likely to perform the same functions, and from comparable global locations. This has been reflected in the 'limitations in evidence' column in the data logging spreadsheet (worksheet 7. Interactions Matrix in the Sublittoral mud CEM literature review and ancillary information spreadsheet) and in the source confidence score. Information for the majority of interactions was taken from peer-reviewed articles, with either a high or medium confidence level.

The results of the conservation status checks indicated that the majority of the species selected are assumed to be native to the UK, and one taxon, *Echinus esculentus,* is of conservation importance (listed as 'Near Threatened' on the IUCN Red List[7]).

The literature review undertaken as part of this project is intended to be an iterative process, and was designed so that it can easily be updated in the future.

3.1 Knowledge Gap Assessment

Overall, a high level of information was gathered to inform the project as part of the literature review. An iterative knowledge gap assessment was undertaken in order to evaluate the nature of this data and to identify any areas where additional effort was needed to gather evidence to inform the models.

The 'Faunal Traits Summary' worksheet in the accompanying spreadsheet indicates the degree of evidence that has been sourced for species trait information. The majority of

[7] http://www.iucnredlist.org/details/7011/0

faunal traits have a high level of information recorded. Information on basic traits, such as typical food types and size, are complete for all taxa covered by the project. Less information was sourced for more complex aspects, such as species connectivity to other habitats/species, physiographic or tidal stream preference and whether a taxon is likely to have a naturally highly variable population. In some cases, expert opinion has been used to input trait information, as indicated in the 'Faunal Traits Summary' tab. Expert opinion carries a lower confidence score (see Table 3a).

Information gathered on the ecosystem interactions which occur in sublittoral mud habitats has been incorporated into the confidence assessments associated with each of the models produced by this project, as described in Section 4.2. Those interactions that are well informed by multiple sources have a high associated confidence. Where literature evidence could not be sourced, expert judgement has been used to inform interactions between ecosystem components (see Section 4.2). Expert judgement carries a lower confidence score (see Table 6) but is considered appropriate for those traits and interactions deemed to be well known / understood, despite a lack of references (whether actual or could not be sourced within the project timescales). This is fully highlighted in the confidence models that accompany each conceptual ecological model (see Section 6). It is important to note that the level of information sourced during the literature review (and thus the associated confidence assessment) was a factor of the time and resource limitations of the project. This is further discussed in Section 5.

Literature sources detailing the interactions between high-level environmental drivers are relatively uniform across all biotopes, owing to the broad level of information found. Information regarding ecosystem processes and functions was largely species specific. As with species trait information, some sources have been taken from comparable habitats outside of the UK, although predominantly within the Temperate Northern Atlantic marine eco-region (Spalding. 2007), or are based on comparable species. Generally, few gaps in the literature were identified, and none which could not be informed by expert judgement (see Section 6 for confidence assessment).

Due to the iterative nature of the project, models were constructed using the initial evidence gathered. Based on the associated early-stage confidence assessments, focussed literature searches were then undertaken to target specific areas where evidence was lacking, and the models updated as part of the gap-filling exercise.

4 Model Development

4.1 Model Design

The Conceptual Ecological Models (CEMs) developed for shallow sublittoral mud habitats are designed to represent both an overarching general model for this habitat, as well as more detailed sub-models that cover specific sub-components of the habitat. To aid easy understanding of the models, a standard format was developed based on a model hierarchy to facilitate consistent presentation of parameters, interactions and temporal / spatial scales.

4.1.1 Model Hierarchy

General Model

A general shallow sublittoral mud habitat model has been created as an overarching design to indicate the general processes that occur within the ecosystem across all relevant biotopes listed in Section 1.1. This does not address the individual species identified within each biotope, but instead considers the sublittoral mud habitat as a whole.

Sub-Models

The sub-models were designed to show a greater level of detail about specific ecological aspects of the shallow sublittoral mud habitat and therefore to inform the selection of monitoring aspects at a meaningful ecological scale.

Functional groups of the sublittoral mud habitat were identified for the key characterising species selected for each habitat type. The selection process drew heavily upon a set of ecological groups described by Tillin and Tyler-Walters (2014). Tillin and Tyler-Walters described ten ecological groups from characterising species of 33 sublittoral sedimentary biotopes. Due to the large degree of species overlap between biotopes, it was deemed more useful to divide the species into ecological functional groups and develop models based on these rather than the individual biotopes, which would result in duplication and more complex models. The ecological groups were distinguished by using both biological traits and habitat preferences, supported by ordination and clustering analyses. In some instances, expert judgement was applied where analyses did not place species into discrete clusters.

Two ecological groups described by Tillin and Tyler-Walters (2014) were not included as part of the CEM sub-models as no key characterising species from the sublittoral mud habitat belonged to these groups: Ecological group 2 (Temporary or permanently attached surface dwelling or shallowly buried larger bivalves) and Ecological group 7 (Very small to small, short lived (<2 years) free-living species defined on size and feeding type).

Based on the study carried out by Tillin and Tyler-Walters (2014), eight of the ten ecological groups were used to categorise the selected shallow sublittoral mud species (Section 2.1) into five functional groups (Table 4) of the sublittoral mud habitats, each of which form the basis of a sub-model, as identified in Figure 2.

Table 4. Relationship between the CEM sub-models of the shallow sublittoral mud habitat CEM and the ecological groups defined by Tillin and Tyler-Walters (2014).

Ecological Groups described by Tillin and Tyler-Walters (2014)	CEM Sub-Model
Group 5: Small-medium suspension and/or deposit feeding polychaetes	Tube-building Fauna
Group 5: Small-medium suspension and/or deposit feeding polychaetes	Burrowing Fauna
Group 6: Predatory polychaetes	
Group 10: Burrowing soft bodied species	
Group 9: Burrowing hard-bodied species	
Group 4: Infaunal very small to medium sized suspension and/or deposit feeding bivalves	Suspension and deposit feeding infauna (non-burrowing)
Group 3: Mobile epifauna, mobile predators and scavengers	Mobile Epifauna, mobile predators and scavengers
Group 1: Temporary or permanently attached epifauna	Echinoderms and attached Epifauna
Group 8: Echinoderms	

Ecological Group 5 (Small-medium suspension and/or deposit feeding polychaetes) was divided into two sub-models in order to create separate sub-models for the tube-building and the burrowing fauna as they can differ in ecosystem output processes, for example, burrowing fauna have a greater sediment reworking potential in comparison to tube-builders (Quieros*.* 2013).

Ecological Groups 9 (Burrowing hard-bodied species) and 10 (Burrowing soft-bodied species) were grouped into the same functional group as many ecosystem output processes will be similar for both ecological groups.

The matrix presented in Appendix 3 details the selected species against the allocated biotope classifications and sub-model, therefore allowing a rapid reference guide to the models and which species / biotopes they cover.

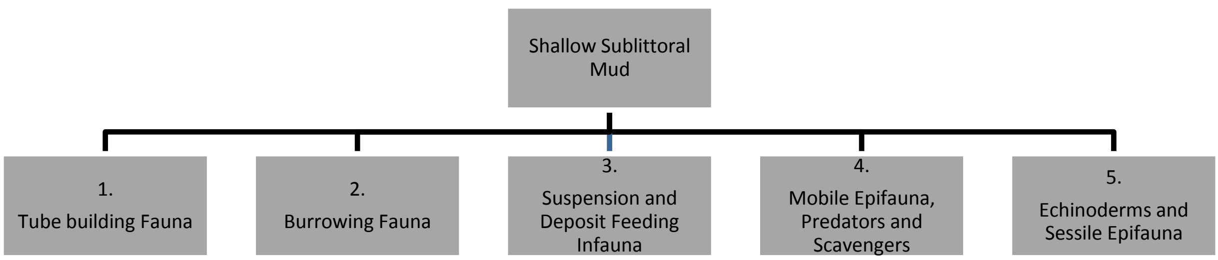

Figure 2. Shallow sublittoral mud habitat CEM hierarchy. The top level of the flowchart represents the general control model, with the six sub-models each documenting a specific functional group within this habitat.

Following the approach developed by Alexander (2014), the ecological groups which have been allocated to one sub-model (Table 4) will still be discussed separately by introducing different subdivisions into the sub-model relating to either feeding activity or taxonomic classification.

No differentiation is made in the hierarchy for fauna specifically related to the infralittoral or circalittoral zones due to the large degree of crossover apparent in drivers and functions within the habitats at the different biological zones. The matrix presented in Appendix 3 indicates which species characterise which biotopes (as defined by this project), and indicates how each model relates to individual biotopes.

4.1.2 Model Levels

Each model is broken down into several component levels which address differing spatial scales of input and output processes. The models and sub-models are defined as a series of seven levels as shown below.

Driving Influences:

- **1. Regional to Global Drivers** – high level influencing inputs to the habitat which drive processes and shape the habitat at a large-scale, e.g. water currents, climate etc. These are largely physical drivers that impact on the water column profile.
- **2. Water Column Processes** – processes and inputs within the water column that feed into local seabed inputs and processes, e.g. suspended sediment, water chemistry and temperature etc.
- **3. Local Processes/Inputs at the Seabed –** localised inputs and processes to the ecosystem that directly influence the characterising fauna of the habitat, e.g. food resources, recruitment etc.

Defining Habitat:

- **4. Habitat and Biological Assemblage** – the characterising fauna and sediment type(s) which typifies the habitat. For the sub-models, fauna are categorised into functional groups and sub-functional groups as necessary. Example taxa characterising each group are named in the models, however for the full list of fauna related to each grouping, please see Appendix 3.

Outputs:

- **5. Output Processes –** the specific environmental, chemical and physical processes performed by the biological components of the habitat, e.g. biodeposition, secondary production etc.
- **6. Local Ecosystem Functions –** the functions resulting from the output processes of the habitat which are applicable on a local scale, whether close to the seabed or within the water column, e.g. nutrient cycling, habitat provision etc.
- **7. Regional to Global Ecosystem Functions** – ecosystem functions that occur as a result of the local processes and functions performed by the biota of the habitat at a regional to global scale, e.g. biodiversity enhancement, export of organic material etc.

4.1.3 Model Components

Each model level is populated with various components of the ecosystem, shown in boxes that are coloured and shaped according to the model level they form. Model components are informed by the literature review and in some cases, expert judgement. Definitions of model components split by model level are presented in Table 5.

Table 5. Descriptions of the components which form various levels of the models. Note that for the general model some parameters have been grouped together to facilitate presentation and to summarise the key processes which occur within the habitat.

DRIVING INFLUENCES	
1. Regional to Global Drivers	
Propagule Supply	Supply of larvae, spores and/or regenerative body fragments
Geology	Underlying rock or substratum
Depth	Distance between water surface and sea bed
Wave Exposure	Hydraulic wave action
Water Currents	Movement of water masses by tides and/or wind
Climate	Short term meteorology and long-term climatic conditions
2. Water Column Processes	
Primary Production	The production of new organic substances through photosynthesis
Suspended Sediment	Particles of sediment which have become elevated from the seabed and are being kept suspended by turbulence within the water column
Light Attenuation	The penetration of light in the water column
Water Chemistry & Temperature	The chemical and physical characteristics and composition of the water column, excluding dissolved oxygen. This parameter is inclusive of salinity, nutrients, chemicals in the water column and water temperature
Dissolved Oxygen	The dissolved oxygen concentration in the water column above the seabed. Dissolved oxygen was separated from Water Chemistry as it is an important driving force for the sublittoral mud habitats.
3. Local Processes/Inputs at the Seabed	
Recruitment	The process by which juvenile organisms join the adult population. Combines settlement and early mortality
Food Sources	Types of food ingested by the fauna represented in the models
- Plankton	Microscopic plants and animals which inhabit the water column (for the purposes of this study, phytoplankton and zooplankton have been grouped together)
- POM (Particulate Organic Matter)	Non-living material derived from organic sources within the water column
- Detritus	Organic waste and debris contained within seabed sediments
- Phytobenthos	Plants and algae attached to the seabed
- Carrion	Dead and decaying animal flesh
- Living Prey	Live prey items such as benthic infauna or interstitial fauna
Seabed Mobility	Movement of sediment on the seabed
4. Habitat and Biological Assemblage (Tillin and Tyler-Walters, 2014)	
Tube Building Fauna	Tubicolous fauna which construct and live in tubes made from sedimentary material on the surface of the seabed
Burrowing Fauna	Burrowing soft- (e.g. Polychaetes) and hard- bodied (Crustaceans) fauna living within the sediments
Suspension and Deposit feeding	Very small to medium sized suspension and deposit feeding

Infauna	bivalves and smaller infauna
Mobile Epifauna, Predators and Scavengers	Mobile scavenging and predatory crabs, polychaetes and molluscs
Echinoderms and Sessile Epifauna	(Sub-) surface urchins, free-living interface suspension/deposit feeding brittle stars and sea cucumbers and permanently attached (sessile) larger, longer-lived surface fauna
OUTPUTS	
5. Output Processes	
Secondary Production	Amount of biomass created as a direct result of consumption
Biodeposition	The process by which filter feeding organisms capture particulate matter from the water column and deposit into the sediments
Bioturbation	Sediment re-working by marine fauna
Bioengineering	Faunal modification of the natural habitat, e.g. tube building, burrow creation etc
Supply of Propagules	The production and transportation of larvae, spores or body fragments capable of regeneration
6. Local Ecosystem Functions	
Food Resources	The growth of prey items as a food resource for other organisms
Nutrient Cycling	Cycling of organic and inorganic nutrients that involves processing into a different chemical form
Biogeochemical Cycling	The cycling of organic carbon and nitrogen other than nutrients
Sediment Stability	Cohesion of sediments into a stable form more resistant to disturbance
Habitat Provision	Provision of living space for other organisms through surface attachment of increased habitat complexity
Microbial Activity Enhancement	Enhanced growth and activity of microbial organisms (e.g. bacteria, diatoms and protozoa) within the sediment
7. Regional to Global Ecosystem Functions	
Export of Biodiversity	Export of biodiversity, including propagules, outside of the habitat
Export of Organic Matter	Export of organic material outside of the habitat, such as food sources etc.
Biodiversity Enhancement	Enhancements in biodiversity within the habitat resulting from increased sediment stability and habitat provision
Biotope Stability	Stability of the habitat through the habitat provision and increased sediment stability (including carbon sequestration)

4.1.4 Model Interactions

Each model component listed above is linked to one or more other components at either the same model level or a different level, using an arrow that is formatted according to the type of interaction.

The links in the general model reflect driving influences, as well as positive and negative influences and feedback loops. However, the general model does not indicate the magnitude of influence for each interaction. This is a result of the general model summarising information from the habitat as a whole where multiple functional groups are being considered. Thus, in some cases, conflicting information on magnitude of influence of one component on another would need to be presented, which is not achievable.

The strength of influence between sub-model components is indicated by the thickness of the connecting line and is based on the magnitude scoring matrix presented in Table 2. Driving influences are shown in uniform black within the models, whereas outputs are coloured to indicate whether they are positive or negative in accordance with Table 1. Feedback within the models is indicated with a dashed line.

For ease of presentation, several models make use of brackets to indicate factors affecting inputs to, or outputs from, several functional groups of organisms. Where brackets are employed, it is implied that the arrows leading to or from the brackets are related to all faunal groups and species contained within.

In order to differentiate between driving factors that are most relevant in the infralittoral zone and those which are most relevant in the circalittoral zone, coloured markers have been added to each component at levels 1 and 2 of the models. The main variation between the infralittoral and circalittoral zones is in relation to light attenuation, primary production and wave exposure.

4.1.5 Natural Variability

Natural variability of the main environmental drivers is indicated on the models by graduated circles. The degree of natural variability is based on the following three factors:

- Potential for intra-annual (e.g. seasonal) variability
- Potential for inter-annual disturbances and variability
- Frequency of extreme disturbances e.g. storm events

Natural variability is assigned a score of 1-3 where 1 is low, 2 medium and 3 high. Scores are based on an expert judgement estimate of the above criteria and are indicated on the models for environmental drivers and inputs at levels 1-3.

The most variable aspect of each model is the biological assemblage. Ultimately, as each of the sub-models is a component of the same broad-scale habitat and simply focuses on a sub-selection of the fauna present, the main physical environmental drivers and water column processes that affect each model component are highly similar. Food sources are a major source of variation in the models, and are defined by the sub-selection of fauna being addressed. The fauna covered in each model characterises the output processes, and in turn the ecosystem functions at the local to global scales.

4.2 Model Confidence

The confidence of each individual source of evidence for interactions between model components is assigned in accordance with the method detailed in Section 2.5. As more than one source is often used to inform the overall / final interaction confidence, a separate method was devised to combine these.

The combined confidence for the interactions from multiple sources is scored in accordance with the protocol presented in Table 6. This assesses the number of sources related to one particular link within the model, the level of agreement between them and differentiates between sources of information.

Wherever possible, the links in each of the models are informed by evidence gathered as part of the literature review. However some links are informed by expert judgement in cases where no references could be identified within the project timescales. In these cases, confidence can only be medium (for those relationships certain to exist), or low (for those relationships which possibly exist but are not evidenced). No high confidence links can exist when expert judgement has been applied.

Table 6. Combined confidence assessment of relationship between CEM components.

Combined relationship confidence	Requirement if one literature source only	Requirement if more than one literature source	Requirement if expert judgement applied
Low	Single source is low confidence	Strong disagreement between sources for both magnitude and direction AND low-medium confidence scores for individual sources	Relationship is considered to exist based on experience of project team
Medium	Single source is medium confidence	Majority agreement between sources for either magnitude or direction AND low-medium confidence scores for individual sources OR minority agreement between sources AND high confidence source used to provide information in CEM	Relationship is strongly thought to exist based on the experience of the project team and is well established and accepted by the scientific community
High	Single source is high confidence	Agreement between sources on both magnitude and direction AND majority individual sources are medium to high confidence	N/A

For each model produced, an additional diagram has been created that shows the confidence scores for each interaction. This shows the same structure and components as the main model but the arrow style is altered to allow the degree of confidence to be emphasised and readily understood. The width of each link between model components indicates the confidence levels low, medium or high; the colour indicates whether it is based on the literature review or expert judgement.

Confidence results are presented in Section 5. No associated confidence model has been produced for the general model due to the difficulties of presenting conflicting confidence assessments for several functional groups summarised into one model.

4.3 Model Limitations

The produced models are conceptual designs that have been created for the specific habitats and selected species only. As a result, not every existing link within the ecosystem is presented. Only links that are regarded as potentially important for habitat monitoring purposes, and for which supporting evidence exists or expert opinion can sufficiently inform, are shown. Some minor links and those for which no substantial evidence exists (below low confidence) are therefore not presented. Omissions of aspects of the models for which evidence exists but the links are not shown for various reasons are discussed in each section.

It is also important to note that the models presented in this report are based only upon the selected species which have been identified as important for characterising the biota of the project biotopes. Other species (and functional groups) may be present within the relevant habitat biotopes that are subject to alternative influences and produce different ecosystem functions; however these have not been included within the scope of this project as they have not been deemed as particularly characteristic (see Section 2.1 for details of how species were selected).

Changes in nomenclature and taxonomic classification have been recorded for certain species since the biotope classifications were published (as detailed in Section 2.3). For ease of comparison with the biotope descriptions, the models presented in this report refer to those species names listed in the biotope descriptions (Connor. 2004).

Confidence in the models is influenced by the extent of the literature review, time and budgetary constraints of the project. This is further discussed in Section 5.

5 Model Results

Each of the models produced is described and discussed in the following paragraphs of this report and included in Appendices 4 -14. The models should be interpreted in consultation with the biotope/model matrix presented in Appendix 3. Reference should also be made to the 'Habitat Characterisation' worksheet in the spreadsheet that accompanies this report for details of the physical parameters which define the habitat and each constituent biotope.

The biological assemblage of each sub-model is described first, followed by the ecosystem drivers and ecosystem functions. The biological assemblage is considered the defining element of each sub-model and thus explains the variation between sub-models. As such, the accompanying text does not necessarily exactly follow the model structure. Ecosystem drivers and functions are described in a logical and pragmatic way, so that those which are linked are defined in turn, rather than described by model level.

Each sub-model has been described in such a way that it can be interpreted independently from all other sub-models. It should also be noted that information presented under each model heading is tied to the confidence assessments presented in Section 6. References for the information discussed are shown where literature sources have been found to back up the statements being made.

5.1 General Control Model and Common Model Components

The general control model indicates the processes, interactions, influences and links that occur in shallow sublittoral mud habitats. The general model is intended to give an overview of the habitat, with the sub-models providing an in-depth view of specific components of the habitat which can be used for monitoring purposes.

The general model provides information on the large-scale environmental drivers that affect the ecosystem, all of which are common to each of the sub-models. The output processes and resulting ecosystem functions at both the local and regional/global scale have been summarised in the general model to some extent for the purposes of presentation. General information common to all the sub-models is discussed in the context of this section, and is not repeated under each specific sub-model heading, unless there is specific variance or a feature of interest which is particularly relevant to that model (such as local processes/inputs at the seabed, food sources, etc.).

5.1.1 Ecosystem drivers

Regional to Global Drivers

The majority of ecosystem drivers relate to the physical environment in the general model, especially at the regional to global scale. Several of the drivers are critical in defining the nature of the habitat itself (such as depth), whereas others are crucial in shaping the subsequent faunal complement and resulting output processes.

Depth is one of the major defining factors of shallow sublittoral mud habitats with a high relevance in both the circalittoral and infralittoral zones (Basford*.* 1990). Increasing depth has a negative influence on key water-column processes, significantly affecting light attenuation (Devlin. 2009), temperature (Munn, 2004) and sediment oxygen uptake (Middelburg and Soetaert. 2004).

Shallow sublittoral mud habitats can be found within the depth range of the wave base (the maximum depth to which wave energy causes motion in the water column). Water depth therefore has a major influence on habitat and exposure to wave action (Brown. 2002a; Connor. 2004;). The effect of wave disturbance is far more prominent in the shallow waters of the infralittoral zone (Masselink and Hughes. 2003; Brown. 2002a). Wave exposure is a crucial factor defined in the biotope classifications (see worksheet 2. Habitat Characterisation in the Sublittoral mud CEM literature review and ancillary information spreadsheet for biotope-specific details) and varies for shallow sublittoral mud habitats from 'moderately exposed' to 'extremely sheltered' (Connor. 2004). Increased wave exposure generally enhances the resuspension, erosion and sorting of cohesive muds, increasing the concentration of suspended sediment in the water column and affecting the seabed mobility (Masselink and Hughes, 2003; Brown. 2002a). Wave exposure can also have an influence on the water column chemistry, temperature and dissolved oxygen availability by increasing mixing activity (Brown. 2002b). A moderate natural variability is defined for wave exposure, based on meteorological conditions including seasonal variation, cyclical fluctuations and the frequency of extreme events. For example, severe autumn storms can increase the impact of wave exposure, mixing of the water column and breakdown of summer thermoclines in deeper waters (Diaz and Rosenberg. 1995).

Water currents include both wind mediated flows and tides (Reiss. 2009). Currents are an important factor for shallow sublittoral mud habitats as they facilitate the transportation and deposition of fine sediment particles (suspended sediment) and together with wave action affect seabed mobility (Brown. 2002a). They also create a transport mechanism for the circulation of temperature and nutrients and sustain the supply of food and propagules to the seabed (Chamberlain. 2001; Biles. 2003; Hiscock. 2004). Bottom water circulation distributes dissolved oxygen in the water column and transfers oxygen from the surface to the seabed (Diaz and Rosenberg. 1995). Although water currents do vary naturally in magnitude and direction through the seasons and annually (both tidal and non-tidal flows), variability is low in comparison to other components.

Propagule supply is a major driver at the regional to global scale, and the only biological ecosystem driver. This driver also forms part of a feedback loop, indicating the importance of recruitment, which is necessary for the persistence of habitats. Connectivity to the same or other habitats is likely to be a key influence on propagule supply where larvae from associated or adjacent habitats are responsible for local recruitment. Propagule supply links to recruitment at the local input level of the models and drives the biological assemblages. In turn this recruitment is driven by propagules from reproductively active organisms in this habitat or from other habitats, completing the feedback loop. It is also likely that the supply of propagules acts as a source of food and nutrients for some species. Propagule supply has high natural variability as it is dependent on a large number of different physical and biological factors. Temperature is an important environmental factor affecting the planktonic larval duration and development (Brennand. 2010), while water currents mainly facilitate the distribution of larvae (Qian. 1999; Hiscock. 2004). All impacting factors have not been shown on the models in an effort to minimise unnecessary complexity.

Geology is an environmental driver at the regional to global scale as it forms the physical basis of the benthic habitat. The physical properties of bed rock and post-glacial drift material have an influence on suspended sediments and sediment type.

Climate is an important driver in the ecosystem and represents both long-term and short-term meteorological conditions within the model. Influenced by global, regional and local atmospheric and oceanographic conditions, this model component particularly influences water chemistry, dissolved oxygen, temperature and primary production (Eppley. 1972; Hiscock. 2006). The climate is described as a driver with a moderate natural variability, taking into account the seasonal variation, cyclical fluctuations and the frequency of extreme events.

Water Column Processes

At the second model level (water column processes), five components link the regional/ global drivers to local inputs at the seabed.

Primary production by phytoplankton is a crucial base to the biological aspects of the shallow sublittoral mud habitat, and a key driver of prey sources (Hiscock. 2006). Larger macrophytes are less common in sublittoral mud habitats due to the high sediment mobility often associated with the habitat and the lack of suitable attachment surfaces. However, littoral and sublittoral seagrass (*Zostera* spp.) beds are an important habitat occurring in medium to fine sandy muds (Connor. 2004) which will greatly contribute to the overall photosynthesis due to the connectivity between habitats. Primary production is a temperature, nutrient (water chemistry) and light dependent process providing energy to drive plankton and marine food webs (Hiscock. 2006; Devlin. 2009). Primary production predominantly occurs in the shallow waters of the infralittoral zone, (e.g. Jones. 2000). As the top of the circalittoral zone is defined as receiving 1% light attenuation (Connor. 2004), primary production will be very low within this zone (e.g. Lalli and Parsons. 2006). Light attenuation itself is driven by depth and suspended sediments in the water column (Masselink and Hughes. 2003; Brown. 2002a; Devlin. 2009).

Photosynthesis is the most important source of dissolved oxygen in the marine environment, while wave and wind exposure facilitate the uptake of dissolved oxygen from the atmosphere and mixing into the water column (Brown. 2002b). Water chemistry and temperature is a large component of the model incorporating many aspects. Properties include salinity, temperature, nutrients and dissolved organic material, mainly influenced by wave exposure, water currents, depth and climate (e.g. Dutertre. 2012; Brown. 2002b). In addition to primary production, water chemistry and temperature link to biological components such as food sources and the biological assemblage of the habitat, based on the need of organisms for dissolved components in the water column (nutrients, calcium carbonate etc.) and specific temperature requirements (Cusson and Bourget. 2005; Bolam. 2010). A feedback loop from biogeochemical cycling (a local ecosystem function) to water chemistry and dissolved oxygen signifies the re-supply of organic chemicals to the water column (e.g. Libes. 1992). Water chemistry, temperature and dissolved oxygen have a moderate natural variability, based on environmental drivers and the potential for seasonal and long-term changes.

Suspended sediments are mainly influenced by wave exposure, water currents and to a lesser degree geology, directly affecting light attenuation through turbidity of the water column. An increased suspension of fine sediments can influence the filter-feeding mechanisms of suspension feeding infauna (Rhoads and Young. 1970).

Local Processes and Inputs at the Seabed

Local processes and inputs at the seabed directly impact the physical and biological nature of the habitat on a smaller scale. Food sources are a key driving factor for biological communities. Due to the diverse nature of fauna that inhabit shallow sublittoral muddy habitats, there are a considerable number of specific food resources which need to be considered in the models, and these are presented in detail within the distinct sub-models, rather than the general model.

Seabed mobility is a proxy for the extent to which the habitat is affected by natural physical disturbance. Environments with a high degree of seabed mobility are likely to be characterised by fauna tolerant to mobile sediments and sediment movement. Fauna that require stable sediments, such as burrowing bivalves, tube-dwelling fauna and sessile epifauna are not likely to flourish in highly mobile environments due to the potential for smothering and difficulties in finding food. Filter feeding fauna, straining food particles from the water column, are likely to require some degree of current flow in order for transport of particulate food sources to be maintained, although currents that are too strong could result in a highly mobile seabed, with decreased sediment stability, and harsher living conditions (Nybakken. 2001; Masselink and Hughes. 2003; Lalli and Parsons. 2006).

Sediment type is one of the key drivers influencing infaunal communities at the habitat level (Ellingsen. 2002; Seiderer and Newell. 1999; Middelburg and Soetaer. 2004; Basford. 1990; Cooper. 2011). The sublittoral mud habitats defined in the UK contain sediments with varying percentages of fine mud, sand and clay (Connor. 2004). The sediment grain size will directly impact the biological assemblage as some functional groups have specific niche sediment requirements. In sandy mud or fine-mud habitats deposit feeders attain higher densities in comparison to suspension feeders as the resuspension of fine sediments is stressful for suspension feeders due to the clogging of filtering structures (Rhoads and Young. 1970). The mineralisation of organic matter is much slower in muddy sediments compared to coarse sediments, creating a rich bacterial community in the fine cohesive sediments (Braeckman. 2014). Infaunal species dominating sublittoral muds have mainly adapted to the anaerobic conditions within these sediments (Diaz and Rosenberg. 1995; Pretterebner. 2012). One important adaptation is the ability to burrow into the substrate or to create tubes which facilitate the transportation of oxygen into deeper sediment layers (Nybakken. 2001). Finer-grained muddy sediments are typically less diverse in comparison to coarser-grained sediments and tend to contain a lower abundance of organisms (Cooper. 2011).

Sediment type itself is influenced by multiple factors, including wave exposure, water currents, underlying geology, seabed mobility and to some extent the fauna itself (e.g. Brown. 2002a). The underlying geology may be an important driver of sediment type, however many sediment deposits found in UK waters are likely to be the product of Pleistocene (or similar) drifts (e.g. Limpenny. 2011; Tappin. 2011) which may rest on unrelated geological formations. As a result, surface sediments may be unconsolidated and could be prone to movement or winnowing (Masselink and Hughes. 2003). Should this occur on a large scale, the underlying geology may be vastly different to the surface sediments.

5.1.2 Ecosystem Outputs

The output processes described in this section are those that are applicable to the habitat as a whole at a general level. As output processes and ecosystem functions are heavily influenced by the characterising fauna of each habitat, the sub-models should be referred to for specific interactions (and references) related to one particular functional group. Output processes from shallow sublittoral mud habitats can be broadly split into four main categories: secondary production, sediment processing, habitat modification and supply of propagules.

Secondary production is a key process occurring within the sublittoral mud habitat. Energy from lower trophic levels is converted to higher trophic levels through energy transfer (Lalli and Parsons. 2006), which in turn provides ecosystem functions at the local scale by driving nutrient cycling (Nybakken. 2001; Lalli and Parsens. 2006). This is a major influencing factor in increasing food and prey availability within the habitat.

Sediment processing refers to biological reworking of sediments, and incorporates actions such as bioturbation and biodeposition. Habitat modification is defined as the biological modification of the natural environment, through processes such as tube or reef building or the creation of permanent burrows. Supply of propagules is the product of reproduction and transport by currents, which feeds back to recruitment at the input level.

Output processes lead to ecosystem functions at the local scale, and in some cases at the regional to global scale. Nutrient and biogeochemical cycling are two crucial functions performed by shallow sublittoral mud and are heavily influenced by sediment processing (Probert. 1984; Kristensen. 2000; Mermillod-Blondin. 2011; Norling*.* 2007). These occur in part due to the representative fauna themselves through natural processes (such as uptake of nutrients, decay etc.) and secondary production (Mermillod-Blondin. 2011; Norling*.* 2007). These processes are also undertaken in part by microbial activity, both naturally occurring as well as occurring as a function of the other biological features of the habitat, such as increased microbial activity in the tubes and burrows of certain taxa (Mermillod-Blondin. 2011; Kristensen*.* 2012). Microbial activity leads to nitrogen and carbon fixation, which feeds back to water chemistry as an ecosystem input (Bertics*.* 2010). Reworking of sediments through bioturbation allows oxygen to penetrate into deeper sediment layers, encouraging chemical exchange within the sediments and increasing the rates of nutrient and biogeochemical cycling (Kristensen*.* 2012).

Sediment stability is likely to be affected by the output processes of sediment processing and habitat modification. Consolidation of sediments by fauna is achieved in several ways, such as tube building, compacting sediment and mucus lining when burrowing or through biodeposition (Probert. 1984; Ziervogel and Forster. 2006; Woodin*.* 2010). It should be noted however that sediment processing also has the potential to negatively affect sediment stability through reworking activities which destabilise the sedimentary environment (Meadows*.* 2012).

Habitat provision is the result of bioengineering of the natural environment (building of tubes and burrows) and the colonisation of species which are found within the habitats themselves by symbiotic or commensal organisms (Vader. 1984; Pretterebner. 2012). This in turn has the potential to enhance biodiversity up to the regional and global scale, as well as contributing to the overall maintenance of the habitat (Meadows. 2012).

There are four regional to global scale ecosystem functions resulting from shallow sublittoral mud habitats. The export of both organic matter and biodiversity are provided for by the supply of propagules, secondary production and biodeposition. Biotope stability and biodiversity enhancement are directly influenced by sediment stability and habitat provision (Nybakken. 2001; Lalli and Parsons. 2006).

5.1.3 Connectivity to other habitats

Connectivity to other habitats is a key part of the marine ecosystem (Connor*.* 2004) although difficult to represent within the conceptual models.

There are various marine habitat types around the UK which may be found in close proximity to shallow sublittoral mud habitats and which do not exist in isolation, for example littoral mud (Connor. 2004). In terms of ecosystem drivers, connectivity is important for certain aspects of the models such as supply of propagules, nutrient cycling, temperature, and food resources. All components are likely to be affected to some degree by adjacent habitat types, depending on the spatial scales involved.

Connectivity to other habitats is also a factor to be considered at the ecosystem function level. Several of the identified regional to global ecosystem functions concern the export of matter or biodiversity from the sublittoral mud habitat to other habitat types. This represents factors such as propagule and biomass supply to adjacent habitats, and increased species richness from the varied habitats.

As such, it should be kept in mind that whilst the models presented as part of this project detail the ecological processes which occur in shallow sublittoral mud habitats, the habitats should not be thought of as operating in isolation, and connectivity to other habitats is likely to be key to maintaining their health.

5.2 Sub-model 1. Tube-Building Fauna

5.2.1 Biological assemblage

The tube-building fauna sub-model represents fauna in the shallow sublittoral mud habitats that construct and live in rigid tubes made of fine-grained sand and shell particles (e.g. *Owenia fusiformis*) or highly fragile tubes formed by mucus and fine particles (e.g. *Spiophanes bombyx*) (Noffke. 2009). Some species construct and live in a single tube throughout their lifecycle while others construct larger reefs and tube mats (e.g. *Ampelisca* spp.).

Three main functional groups were identified within this model:

- Polychaetes e.g*. Lagis koreni, Owenia fusiformis, Polydora ciliata, Pygospio elegans*
- Phoronida e.g. *Phoronis muelleri*
- Amphipods e.g. *Photis longicaudata, Ampelisca tenuicornis*

A full species list of the selected taxa which constitute these functional groups, and a breakdown of the biotopes they represent are presented in Appendix 3.

This group represents species that are all mainly characterised by their bioengineering potential. Most species are suspension or deposit feeders or can switch between both feeding methods. Suspension (filter) feeders separate particulate organic matter and plankton from the water column whereas deposit feeders typically consume detritus and organic matter in the surrounding sediment. Certain species will also consume small living prey e.g. protists, meiobenthos and bacteria.

5.2.2 Ecosystem Drivers

As described in the general model, propagule supply is an important biological driver of the tube-building fauna sub-model. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN, 2006) suggesting that connectivity to other habitats nearby could be an important consideration. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

Near-bed current flows affect the settlement of tube-building larvae. Water currents form an important factor in determining where this functional group can establish itself in a certain area together with the active larval substrate selection (Qian. 1999). Relatively strong hydrodynamics can reduce larval settlement due to the erosion of larvae from the seabed (Qian. 1999; Coates*.* 2013). As tube-building fauna are partially filter feeders, water currents are likely to also interact with the supply of particulate food sources.

Seabed mobility is a moderate driver for this model. High levels of sediment mobility will likely prohibit colonisation by tube building fauna, as a relatively stable environment is required for successful habitat construction (Holt. 1998). This is likely to be at least in part influenced by a feedback loop from the sediment stabilising ecosystem function performed by tube builders. Some fauna could acquire a degree of suspended sediment to construct their tubes, however most tube-building fauna select sediment particles from the seabed itself and do not rely on suspended particles (Noffke. 2009).

Primary food sources for tube-building fauna are plankton within the water column (both phytoplankton and zooplankton), Particulate Organic Matter (POM) and detritus (MarLIN, 2006; Fauchald. 1979). Phytoplankton is heavily influenced by factors affecting primary production, such as light attenuation (Jones. 2000), climate, water column chemistry and temperature, including nutrient content (Hiscock. 2006; Lalli and Parsons. 2006; Hily. 1991). Other larger scale drivers such as water currents and wave exposure (promoting water column mixing) are also likely to influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Lalli and Parsons. 2006; Jones. 2000; Hily. 1991; Eppley. 1972). Phytoplankton is likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make plankton of limited importance at the top of the circalittoral zone (Hily. 1991). Zooplankton abundance is likely to be intrinsically tied to phytoplankton abundance (e.g. Nybakken. 2001) although it will also be influenced by other factors, including reproduction of benthic and epibenthic fauna (producing propagules and larvae in the water column), POM and water column chemistry (dissolved oxygen in particular) (Levinton. 2001; Nybakken. 2001; Lalli & Parsens. 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsens. 2006). POM and detritus are important food sources in both the infralittoral and circalittoral zones (Nybakken. 2001; Lalli and Parsens. 2006; MarLIN. 2006). Detritus, the organic matter contained within seabed sediments or on the seabed, is influenced by a number of factors, including abundance of marine life (Nybakken. 2001; Brown. 2002a; Lalli and Parsens. 2006). Not all the factors influencing detritus are indicated on the model for the sake of simplicity. Some of the tube-building fauna also feed on living prey such as meiobenthos, bacteria, protists and small invertebrates (MarLIN. 2006), suggesting again an important connectivity between different habitats.

5.2.3 Ecosystem Outputs

The key output processes performed by tube-building fauna are secondary production, biodeposition, bioturbation, bioengineering and propagule supply.

Habitat modification through the construction of tubes (bioengineering) is one of the most important output processes in this model. The degree of bioengineering is highly variable between species with certain taxa creating individual fragile mucus tubes (e.g. *Spiophanes bombyx*) and others building strong tubes (e.g. *Owenia fusiformis*) or mats (e.g. *Ampelisca tenuicornis*) which are able to form dense aggregations.

The habitat modification and creation of sedimentary tubes has a large influence on several local ecosystem functions in the shallow sublittoral mud habitat. The tubes enhance the habitat provision for other organisms increasing the colonisation of both macro- and meiofaunal species (Dobbs and Scholly. 1986; Bolam and Fernandes. 2003; Larson. 2009; Rigolet. 2014) and by providing a refuge to species which are otherwise highly susceptible to predation (Larson. 2009; Rigolet. 2014). The tubes of *Phoronis* provide for example a refuge for small clams from predation by shore crabs (Larson. 2009). Tube-building fauna create a positive feedback loop to recruitment by providing a settlement surface for larval and postlarval benthic organisms (Qian, 1999) and by creating a favourable and sheltered environment for the larval settlement of many benthic species (Bolam and Fernandes. 2003).

Tube-builders also create favourable conditions for the microbial activity in and around their tubes (Passarelli. 2012), increasing the biogeochemical cycling of nutrients and oxygen in the shallow sublittoral mud (Meadows*.* 2012). Microbes can then add stability to the mud habitats by increasing the adhesion between sediment particles (Probert. 1984).

At high densities, tube-building fauna stabilise the surrounding sediment by trapping sediment particles between their tubes (Woodin. 2010; Van Hoey. 2008; Pandolfi. 1998; Kirtley and Tanner. 1968), which feeds back to seabed mobility. However, solitary tubes can have a negative effect on the sediment stability by creating local water turbulence and sediment erosion (Paterson and Black. 1999; Probert. 1984). A feedback loop is created due to the alteration of the local water flow pattern above the sediment interface (Rigolet. 2014; Paterson and Black, 1999). When present in high abundances, tube reefs can have a negative feedback to water currents by reducing the velocity of the near-bed water flow due to an enhanced shear stress at the seabed (Holt*.* 1998). Decreased water flows can then result in increased passive biodeposition to the seabed (Bolam and Fernandes. 2003).

Biodeposition is another key output process performed by the three functional groups of the tube-building fauna model. Biodeposition involves the trapping of sediment particles and POM from the water column and transport to the seabed. Biodeposition modifies the nutrient and biogeochemical cycling of the sediments (Libes. 1992; Kristense. 2012) by contributing to the sediment organic matter content (Pillay and Branch. 2011). These processes are linked to the export of organic matter at a wider scale and to water column chemistry through a feedback loop. Furthermore, the biodeposits of the tube-building fauna create a food source for other organisms e.g. meiofauna and have a positive influence on the habitat provision by stabilising sediments (Bolam and Fernandes. 2003).

The active sediment reworking and bioturbation potential of tube-building fauna is limited as most species, once settled, live in fixed tubes restricting them to movements within their tubes (Quieros*.* 2013). Both the building of tubes and body movements within them (e.g. feeding activity) enhance the biogeochemical fluxes in sublittoral muds, transporting oxygen and organic matter to deeper sediment layers (Rigolet. 2014; Braeckman*.* 2010) and creating a feedback loop to water chemistry, temperature and dissolved oxygen.

Tube-building fauna are important secondary producers, consuming primary producers, particulate matter and to a lesser extent small living prey. In turn, most tube-building fauna are prey items for species belonging to higher trophic levels, such as crustaceans, gastropods and fish (Sheader. 1998; MarLIN. 2006; Kaiser and Spencer. 1994; Lopezjamar. 1984). Food processing through secondary production contributes to the nutrient cycling within the ecosystem.

The tube-building fauna provide four regional to global ecosystem functions that are based on the output processes and local ecosystem functions in the model; Export of biodiversity through the supply of propagules, export of organic matter through food resources and nutrient cycling, biodiversity enhancement and biotope stability through the enhanced stabilisation of the sediment and habitat provision.

5.3 Sub-model 2. Burrowing Fauna

5.3.1 Biological assemblage

The burrowing fauna model represents the largest group of fauna considered in the shallow sublittoral mud habitat sub-models. The movement of these species can range from freely burrowing in the sediment (e.g. *Nephtys hombergii*) to those inhabiting a semi-permanent fixed burrow (e.g. *Nephrops norvegicus*). This group mainly contains crustaceans and polychaetes divided into two main groups (Tillin and Tyler-Walters. 2014):

Burrowing hard-bodied species

- Predatory Crustaceans e.g. *Nephrops norvegicus*
- Deposit Feeding Crustaceans e.g. *Callianassa subterranean, Calocaris macandreae*

Burrowing soft-bodied species

- Predatory Polychaetes e.g. *Hediste diversicolor, Nephtys hombergii*
- Other Polychaetes e.g. *Arenicola marina, Scoloplos armiger*
- Other Infauna e.g. *Labidoplax media, Leptosynapta bergensis*

A full species list of the selected taxa which constitute these functional groups, and a breakdown of the biotopes they represent are presented in Appendix 3.

Predatory crustaceans and polychaetes are those species which actively hunt other infauna within the sediments or at the sediment-water interface. Non-predatory species are mainly deposit feeders, consuming detritus or particulate organic matter (POM) within or on the surface of the sediments. A small number of the burrowing species are both suspension and deposit feeders, consuming suspended plankton from the water column and detrital material in the sediments (MarLIN. 2006).

5.3.2 Ecosystem Drivers

In common with other models, propagule supply is an important biological driver of the burrowing fauna sub-model. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN. 2006) suggesting that connectivity to other habitats nearby could be an important consideration. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop. Near-bed current flows effect the settlement of faunal larvae and form one of the main controlling factors in determining where this functional group can establish itself in a certain area together with active larval substratum selection (Qian. 1999).

Driving influences directly acting on the biological assemblage include seabed mobility, water chemistry, temperature, and dissolved oxygen (Nybakken. 2001; Lalli and Parsens. 2006). Sediment type (Basford*.* 1990) and the availability of food sources (MarLIN. 2006) are driving forces with the highest influence on the burrowing fauna in the shallow sublittoral mud.

The primary food source of predatory polychaetes and crustaceans mainly consists of other infaunal species such as smaller crustaceans, molluscs and polychaetes (MarLIN. 2006; Fauchald and Jumars. 1979). The living prey is also comprised of other burrowing fauna represented in this model, indicated by direct links between the faunal compartments and the feedback loop from food resources. For the suspension and deposit feeding species the primary food sources are plankton within the water column (both phytoplankton and zooplankton), POM and organically derived detritus in the surrounding sediments (MarLIN. 2006; Fauchald and Jumars. 1979). Phytoplankton is heavily influenced by factors affecting primary production, such as light attenuation, climate, and water column chemistry and temperature, including nutrient content (Hily. 1991; Lalli and Parsons. 2006; Jones*.* 2000; Hiscock*.* 2006). Other larger-scale drivers such as water currents and wave exposure (promoting water-column mixing) are also likely to influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley. 1972; Hily. 1991; Lalli and Parsons. 2006; Jones*.* 2000). Phytoplankton is likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make plytoplankton of limited importance at the top of the circalittoral zone (Hily. 1991). Zooplankton abundance is likely to be intrinsically tied to phytoplankton abundance (Nybakken. 2001) although will also be influenced by other factors, including reproduction of benthic and epibenthic fauna (producing propagules and larvae in the water column), POM and water column chemistry (dissolved oxygen in particular) (Levinton. 2001; Nybakken. 2001; Lalli and Parsens. 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli and Parsens. 2006). POM and detritus are important food sources in both the infralittoral and circalittoral zones (Nybakken. 2001; MarLIN. 2006; Lalli and Parsens. 2006).

5.3.3 Ecosystem Outputs

The major local output processes performed by burrowing fauna are bioturbation and bioengineering. Each of the sub-functional groups represented in the model engage in bioturbation to some degree (Quieros. 2013), with the thalassinidean decapod crustaceans (e.g. *Calocaris macandreae*) considered as the most effective bioturbators in the shallow sublittoral mud habitat (Reise. 2002). This reworking and overturning of the sediment is a particularly key process undertaken by the predators and the fauna burrowing freely through the sediments (Mermillod-Blondin. 2011; Quieros. 2013). Bioturbation leads to the bioirrigation of sediments, increasing the potential for nutrient and biogeochemical cycling (Pillay and Branch. 2011; Kristensen. 2012), which in its turn stimulates bacterial growth rates and microbial decomposition processes (Probert. 1984). In shallow sublittoral muds, burrowing is an important activity to ventilate the burrows ensuring the sediment is oxygenated to a much greater depth (Jones. 2000; Pinn and Atkinson. 2009). The increased depth of the aerobic habitat creates a larger surface area available for the colonisation of other organisms such as microorganisms, meiofauna and other macrofauna (Probert, 1984; Reise. 2002; Volkenborn and Reise. 2006), positively maintaining the shallow sublittoral mud habitat. Bioturbation is linked with mainly positive ecosystem functions (Norling. 2007; Bertics. 2010; Mermillod-Blondin. 2011), however excessive bioturbation can destabilise sediments and increase the erosion potential by increasing the re-suspension of fine surficial sediments (Paterson and Black. 1999; Woodin. 2010; Meadows. 2012). This effect is directly expressed by a feedback loop from bioturbation to suspended sediment.

Habitat modification through the construction of semi-permanent to permanent burrows (bioengineering) is a second important output processes in this sub-model (Levinton. 2001; MarLIN. 2006). The complexity of the burrows varies from species to species, but most burrows contain two entrances through which an influx of oxygen rich water is pumped into the burrow by the organism and an efflux of dissolved nutrients and prey filtered out (Nybakken. 2001; Reise. 2002). These micro-habitats within the sediments serve several functions above those directly benefiting the host organism, including the provision of a habitat for associated organisms, increasing sediment stability through the creation of compacted or mucus-lined sediment tunnels which increases shear stress resistance of sediments and restricts lateral inflow of water in the burrows (Probert. 1984). These stable environments can provide an extended and protected platform for biogeochemical cycling bacteria to colonise along the burrow walls (Munn. 2004; Papaspyrou. 2005; Meadows. 2012), allowing greater oxygen penetration into the seabed (Levinton. 2001; Nybakken. 2001; Lalli and Parsens. 2006). The presence of extensive burrows and increased seabed rugosity of burrowing may also serve to reduce current flow at the seabed and restrict shear bed stress (Jones. 2011). In turn, this can lead to increased habitat stability, biotope maintenance and biodiversity enhancement across larger spatial scales.

Biodeposition is another key output process performed by filter feeding burrowing fauna that pumps seawater through their burrows in order to feed (Norkko. 2001). Particulate matter is strained from the water column by the fauna and subsequently deposited into sediments through the excretion of waste material (Levinton, 2001; Nybakken, 2001).

Burrowing fauna are important secondary producers, consuming other fauna, primary producers and organic material, and in turn serve as an important food resource for multiple other organisms such as flatfish, crustaceans and larger polychaetes (Francour, 1997; Fauchald and Jumars. 1979; Levinton. 2001; Nybakken. 2001; MarLIN. 2006; Jones. 2000). As some organisms serve as a food source within this model, a feedback loop exists from food resources up to the local processes level (MarLIN. 2006; Jones. 2000). Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale.

In common with other models, the supply of propagules is another key output process. A large proportion of the burrowing fauna have planktotrophic larvae (MarLIN. 2006), indicating that connectivity to other habitats is likely to be important. Supply of propagules as an output process links back to recruitment as an input feature, and also links to the export of biodiversity at the regional to global scale.

5.4 Sub-model 3. Suspension and Deposit Feeding Infauna

5.4.1 Biological assemblage

The suspension and deposit feeding infauna sub-model contains fauna that are typically positioned at the sediment-water interface or shallowly buried (e.g. *Abra alba*) (Tillin and Tyler-Walters. 2014). Two main functional groups were identified within this model:

- Bivalves e.g. *Abra alba, Macoma balthica, Mysella bidentata*
- Other Infauna e.g. *Thysanocardia procera*

A full species list of the selected taxa that constitutes these functional groups, and a breakdown of the biotopes they represent are presented in Appendix 3.

Most species are suspension or deposit feeders or can switch between both feeding methods. Suspension (filter) feeders separate particulate organic matter and plankton from the water column while deposit feeders typically consume detritus and organic matter in the surrounding sediment.

5.4.2 Ecosystem Drivers

In common with other models, propagule supply is an important biological driver of suspension and deposit feeding infauna. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN. 2006) suggesting that connectivity to other habitats nearby could be an important aspect. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

Water chemistry, sediment type (Basford. 1990) and the availability of food sources (MarLIN, 2006) are driving forces with a large influence on the suspension and deposit feeding infauna in the shallow sublittoral mud habitat.

Concentrations of fine sediments can influence the filter-feeding mechanisms of suspension feeding infauna (Rhoads and Young. 1970). Certain bivalves (e.g. *Cerastoderma edule*) have adapted to elevated suspended sediment concentrations by producing large amounts of mucus which loosely binds sediment particles together and ejects them as pseudo-faeces through their inhalant siphon (Ciutat. 2006).

Primary food sources for suspension and deposit feeding infauna are plankton within the water column (both phytoplankton and zooplankton), POM and detritus (MarLIN, 2006; Fauchald and Jumars. 1979). Phytoplankton is heavily influenced by factors affecting primary production, such as light attenuation, climate, and water column chemistry and temperature, including nutrient content (Hily. 1991; Lalli and Parsons. 2006; Jones*.* 2000; Hiscock*.* 2006). Other larger-scale drivers such as water currents and wave exposure (promoting water column mixing) are also likely to influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley. 1972; Hily. 1991; Lalli and Parsons. 2006; Jones. 2000). Phytoplankton is likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make phytoplankton of limited importance at the top of the circalittoral zone (Hily. 1991). Zooplankton abundance is likely to be intrinsically tied to phytoplankton abundance (Nybakken. 2001) although will also be influenced by other factors, including reproduction of benthic and epibenthic fauna (producing propagules and larvae in the water column), POM and water column chemistry (dissolved oxygen in particular) (Levinton. 2001; Nybakken. 2001; Lalli and Parsens. 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli and Parsens. 2006). POM and detritus are important food sources in both the infralittoral and circalittoral zones (Nybakken. 2001; MarLIN. 2006; Lalli and Parsens. 2006). As suspension feeders, water currents are likely to interact with the supply of particulate food sources. Other driving influences directly acting on the biological assemblage include seabed mobility, temperature and dissolved oxygen (Nybakken. 2001; Lalli and Parsens. 2006).

5.4.3 Ecosystem Outputs

Biodeposition is a key output process performed by filter feeding infauna. Sediment particles and POM are trapped from the water column, deposited into the sediments through the excretion of waste material, creating a stabilising effect (Levinton. 2001; Nybakken. 2001). In response to elevated suspension sediment concentrations, certain bivalves (e.g. *C. edule*) produce large amounts of mucus which loosely binds sediment particles together and ejects them as pseudofaeces through their inhalant siphon (Ciutat*.* 2006). This process further increases biodeposition rates onto the seabed. Biodeposition modifies the nutrient and biogeochemical cycling of the sediments (Libes. 1992; Kristensen*.* 2012) by contributing to the sediment organic matter content (Pillay and Branch. 2011). These processes are linked to the export of organic matter at a wider scale and to water column chemistry through a feedback loop.

Another important output process is active sediment reworking (bioturbation) through the physical shallow burrowing and ploughing activities that are related to the feeding activity of the infauna. Bioturbation leads to the bioirrigation of sediments, increasing the potential for nutrient and biogeochemical cycling (Pillay and Branch. 2011; Kristensen*.* 2012), which in its turn stimulates bacterial growth rates and microbial decomposition processes (Probert.1984). In shallow sublittoral muds, burrowing movements are an important activity to ventilate the burrows ensuring the sediment is oxygenated to a much greater depth (Pinn and Atkinson. 2009; Jones*.* 2000) and extending the habitat of smaller organisms (e.g. foraminifera, nematodes) (Braeckman*.* 2011). In turn, these processes can lead to increases in biodiversity enhancement and biotope maintenance across larger spatial scales.

Bioturbation is mainly linked with positive ecosystem functions (Norling*.* 2007; Bertics*.* 2010; Mermillod-Blondin*.* 2011), however excessive bioturbation by cockles (*Cerastoderma edule*) can destabilise sublittoral mud habitats in particular by creating burrows and furrows which increases the bed roughness (Ciutat*.* 2006). The increased bed shear-stress will then reduce the near-bed water-flow velocity creating a feeback loop back to the regional to global ecosystem-driver water currents (Ciutat. 2007).

The suspension and deposit feeding infauna are important secondary producers, consuming primary producers and organic material, and in turn serving as an important food resource for many other organisms such as fish, crustaceans and polychaetes (Levinton, 2001; MarLIN. 2006; Nybakken. 2011; Jones. 2000; Francour. 1997; Fauchald and Jumars. 1979). Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale. As the deposit feeding infauna consume POM and detritus a feedback loop exists from the export of organic matter to food sources.

In common with other models, the supply of propagules is another key output process. A large proportion of the suspension and deposit feeding infauna have planktotrophic larvae (MarLIN. 2006); indicating that connectivity to other habitats is likely to be important. Supply of propagules as an output process links back to recruitment as an input feature, and also links to the export of biodiversity at the regional to global scale.

5.5 Sub-model 4. Mobile Epifauna, Predators and Scavengers

5.5.1 Biological assemblage

The mobile epifauna, predators and scavengers sub-model (Tillin and Tyler-Walters. 2014) includes those species which actively hunt or scavenge other infauna within the sediments or at the sediment-water interface. Three main functional groups were identified within this model:

- Crustaceans e.g. *Carcinus maenas, Pagurus bernhardus*
- Molluscs e.g. *Philine aperta*
- Polychaetes e.g. *Pholoe inornata*

A full species list of the selected taxa which constitute these three functional groups, and a breakdown of the biotopes they represent are presented in Appendix 3.

5.5.2 Ecosystem Drivers

In common with other models, propagule supply is an important biological driver of suspension and deposit feeding infauna. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN. 2006) suggesting that connectivity to other habitats nearby could be an important consideration. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

Seabed mobility and suspended sediment is likely to have a smaller driving influence on mobile epifauna, predators and scavengers in comparison to other ecological groups as most species are highly adaptable to physical disturbance (Kaiser. 1998).

Sediment type is expected to have a smaller influence for many mobile epifauna, predators and scavengers as they have a wide range of substratum preferences (Basford. 1990); however this is highly variable between species and their distribution is likely to be indirectly linked to sediment type. For example, the hermit crab *Pagurus bernhardus* will appear in substrates ranging from large boulders to fine-grained sand while the sand slug *Philine aperta* is limited to fine muddy sand (MarLIN. 2006).

The final key driving influencing on mobile epifauna, predators and scavengers is food resources. The primary food source in this model consists of carrion and living prey, such as crustaceans, molluscs and polychaetes (MarLIN. 2006; Fauchald and Jumars. 1979). These sources of food can be the product of other functional groups found within the habitat, indicated by the feedback loop in the model. The shore crab *Carcinus maenas* for example also preys upon its own species (MarLIN. 2006).

Organic detrital matter in seabed sediments or on the seabed, is also an important food source for scavenging fauna such as the hermit crab *Pagurus bernhardus* (MarLIN. 2006). Organic detritus in the marine environment is influenced by a number of factors, including the abundance of marine life (Nybakken. 2001; Lalli and Parsens. 2006; Brown. 2000a). Not all the relevant factors influencing detritus availability are indicated on the model for the sake of simplicity.

Microphytobenthos, small marine algae attached to sediment grains, are likewise a source of food for crustaceans such as *Carcinus maenas* (MarLIN. 2006). Phytobenthos is likely to be affected by similar habitat characteristics as phytoplankton, including light attenuation and water chemistry and temperature (Levinton. 2001). Seabed mobility is also expected to play an influencing role in the distribution of marine plants, with high energy environments potentially prohibiting plant growth and attachment (link not shown on model as marine plants are not thought to be a key characterising biological component of the shallow sublittoral mud habitat). Microphytobenthos will only be present in the infralittoral zone where light attenuation is great enough to permit photosynthesis.

5.5.3 Ecosystem Outputs

Secondary production is a key process occurring within the shallow sublittoral mud habitat, whereby energy from lower trophic levels is converted to higher trophic levels through energy transfer (Lalli and Parsons. 2006). This in turn provides ecosystem functions at the local scale by driving nutrient cycling (Nybakken. 2001; Lalli and Parsens. 2006), and is a major influencing factor in increasing food and prey availability within the habitat. In terms of wider regional to global ecosystem functions, secondary production ultimately leads to both export of organic matter and export of biodiversity. Food resources in shallow sublittoral mud habitats may be negatively affected by a high population of active predators.

Mobile epifauna, predators and scavengers moderately rework (bioturbate) the sublittoral mud (Schratzberger and Warwick. 1999). Scavengers such as crabs continuously disturb and aerate the sediment through their ploughing feeding movements, which increases the potential for biogeochemical cycling and enables smaller organisms (e.g. nematodes) to penetrate to deeper layers of the sediment (Reise. 2002; Schratzberger and Warwick. 1999). Excessive bioturbation can have a destabilising effect on sublittoral muds (Ciutat. 2006). Hermit crabs also offer additional habitat provision to symbionts and epibiota (Pretterebner. 2012), enhancing the biodiversity at regional to global ecosystem levels.

As in other models, the supply of propagules is another key output process. A large proportion of the fauna represented in this sub-model have planktotrophic larvae (MarLIN. 2006), indicating that connectivity to other habitats is likely to be important. Supply of propagules as an output process links back to recruitment as an input feature, and also links to the export of biodiversity at the regional to global scale.

5.6 Sub-model 5. Echinoderms and Sessile Epifauna

5.6.1 Biological assemblage

The echinoderms and sessile epifauna model represents one of the most disparate groups of species (Tillin and Tyler-Walters. 2014) and can be divided into two sub-functional groups:

Echinoderms

- Ophiuroids e.g. *Amphiura filiformis*
- Holothurians e.g. *Ocnus planci*
- Echinoids e.g. *Brissopsis lyrifera, Echinocardium cordatum, Echinus esculentus*

Sessile Epifauna e.g. *Sagartiogeton undatus, Virgularia mirabilis*

A full species list of the selected taxa which constitute these functional groups, and a breakdown of the biotopes they represent are presented in Appendix 3.

Within the echinoderm group most species are suspension feeders, deposit feeders or grazers of which some can switch between feeding methods. The sessile or permanently attached epifauna are passive suspension feeders mainly filtering the water column for POM and plankton.

5.6.2 Ecosystem Drivers

Water chemistry, sediment type (Basford. 1990), suspended sediment and the availability of food sources (MarLIN. 2006) are likely the most important driving forces on the echinoderms and sessile epifauna in the shallow sublittoral mud habitat.

An increased suspension of fine-grained sediments can influence the filter-feeding mechanisms of the suspension-feeding echinoderms and sessile epifauna (Rhoads and Young. 1970).

The primary food sources for suspension feeding echinoderms (e.g. *Amphiura filiformis*) and sessile epifauna is plankton within the water column (both phytoplankton and zooplankton) (MarLIN. 2006; Fauchald and Jumars. 1979). Phytoplankton is heavily influenced by factors affecting primary production, such as light attenuation, climate, and water column chemistry and temperature, including nutrient content (Hily. 1991; Lalli and Parsons. 2006; Jones. 2000; Hiscock. 2006). Other larger-scale drivers such as water currents and wave exposure (promoting water column mixing) are also likely to influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley. 1972; Hily. 1991; Lalli and Parsons. 2006; Jones. 2000). Phytoplankton is likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make phytoplankton of limited importance at the top of the circalittoral zone (Hily. 1991). Zooplankton abundance is likely to be intrinsically tied to phytoplankton abundance (Nybakken. 2001) although will also be influenced by other factors, including reproduction of benthic and epibenthic fauna (producing propagules and larvae in the water column), POM and water column chemistry (dissolved oxygen in particular) (Levinton. 2001; Nybakken. 2001; Lalli and Parsens. 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli and Parsens. 2006). For suspension feeders, particularly passive filtering epifauna, water currents will be highly important for the supply of particulate food sources (Levinton. 2001).

POM and organic detritus are also important food sources for deposit feeders in both the infralittoral and circalittoral zones (Nybakken. 2001; MarLIN. 2006; Lalli and Parsens. 2006). Certain deposit feeding echinoderm species (e.g. *Brissopsis lyrifera*) also consume small living organisms on or within the sediment.

Grazing echinoderms (e.g. *Echinus esculentus*) scrape over the seabed to consume microphytobenthos or sessile organisms such as bryozoan crusts to retain inorganic particles such as sand grains (MarLIN. 2006).

In common with other models, propagule supply is an important biological driver in the echinoderm and sessile epifauna model. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN. 2006) suggesting that connectivity to other habitats nearby could be an important consideration. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

5.6.3 Ecosystem Outputs

Echinoderms and sessile epifauna are important secondary producers, consuming primary producers and organic material, and in turn serving as an important food resource for multiple other organisms such as fish, crustaceans, molluscs and polychaetes (Francour, 1997; Levinton. 2001; MarLIN.2006; Nybakken. 2011; Fauchald and Jumars. 1979; Jones. 2000). Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale. Since the echinoderms consume POM and organic detritus, a feedback loop exists from the export of organic matter to food sources.

Within the echinoderm sub-functional group, burrowing ophiuroids and echinoids contribute greatly to the sediment reworking (bioturbation) and habitat modification (bioengineering) (Quieros. 2013). The reworking and overturning of the sediment is a particularly key process undertaken by fauna freely burrowing through the sediments (Mermillod-Blondin. 2011; Quieros. 2013). The burrowing ophiuroid *Amphiura filiformis* contributes to the total oxygen flux into the sediment by disturbing the boundary layer flow and moving particles while sweeping the sediment surface in circles (Vopel. 2003). This process increases the potential for nutrient and oxygen cycling in the sublittoral mud (Kristensen. 2012), creating a feedback loop to the water column chemistry and dissolved oxygen (Hughes. 1998; Lohrer. 2004).The increased depth of the aerobic habitat creates a larger surface area available for the colonisation of other organisms (Probert. 1984; Reise. 2002), positively maintaining the sublittoral mud habitat. The bivalve *Tellimya ferruginosa* and amphipod *Urothoe marina* are for example commensal species of the burrowing echinoderm *Echinocardium cordatum* as adult specimens live freely in and around their permanent burrows (Hayward and Ryland. 1995; Fish and Fish. 1996). Echinoderms also provide a direct habitat to other organisms (e.g. polychaete worms, isopods, copepods and young bivalves) that live in or around their spines (Fish and Fish. 1996). These processes thus enhance the biodiversity and biotope stability at regional to global ecosystem levels.

Excessive bioturbation activity, mainly due to the feeding activity of echinoderms (e.g. deposit feeding and grazing), can also increase the potential for erosion of the shallow sublittoral mud due to the loosening of surface sediments (Ciutat. 2007) which in its turn creates a feedback loop to suspended sediment.

Biodeposition is a key output process performed by the filter feeding epifauna and the selective suspension feeding ophiuroids. Sediment particles and POM are trapped from the water column and subsequently deposited into sediments through the excretion of waste material, stabilising the sediment through natural sedimentation (Levinton. 2001; Nybakken.

2001). Biodeposition modifies the nutrient cycling of the sediments (Libes. 1992; Kristensen . 2012) by contributing to the sediment organic matter content (Pillay and Branch. 2011). This process is linked to the export of organic matter at regional to global ecosystem levels.

In common with other models, the supply of propagules is another key output process. Most echinoderms have planktotrophic larvae (MarLIN. 2006), indicating that connectivity to other habitats is likely to be important. Supply of propagules as an output process links back to recruitment as an input feature, and also links to the export of biodiversity at the regional to global scale.

6 Confidence Assessment

The confidence models that form a supplement to this report are included in Appendices 10-14. The confidence models replicate the components and layout of each of the sub-models described in Section 5. No confidence assessment has been undertaken for the general model due to the conflicting information that would need to be displayed. To form the confidence models, ancillary information (such as natural variability and biological zone) has been removed from the model structure and the connecting links between model components have been weighted to indicate strength of confidence supporting the links, and coloured according to whether literature evidence or expert opinion informs each connection. As detailed in Section 4.2, the confidence of these links is divided into two types within the models, informed by either literature sources or expert opinion, following the pro forma shown in Table 6.

In general, a good level of literature has been sourced to inform the models, thus confidence is relatively high for each sub-model. Expert judgement has been used to inform some links within each model where necessary, which has resulted in lowered confidence in some instances. Confidence within these models is constrained by the scope of the project, as well as time and resource limitations. Should any new information be collated on shallow sublittoral mud habitats in the future, the confidence models can easily be updated.

Confidence is generally high for the environmental drivers at the top of the models (levels 1 to 4), with a medium to high confidence level based on literature review. The main exception to this is the links between propagule supply and recruitment, which are mainly informed by expert judgement with a medium confidence level. The links between food sources and the biological assemblage are well informed by literature review and have high confidence.

The output processes were generally well researched, creating a medium to high confidence level based on literature review in most models. Links to the local ecosystem functions and regional/global ecosystem functions (Levels 6 and 7) are partially informed by expert opinion in certain places for all models, owing to the limited level of literature available.

Confidence was largely dependent on how well a particular functional group and its ecosystem functions had been studied. For example, the tube-building and burrowing fauna sub-models have a generally high confidence level reflecting the large amount of literature and research that has been carried out on the relevant species and their importance within the ecosystem. In the suspension and deposit feeding sub-model, output processes from the sipunculid *Thysanocardia procera* and oligochaete Tubificoides were restricted and had a lower confidence due to the limited literature available on the ecosystem functioning of these taxa.

7 Monitoring habitat status and change due to natural variation

Using the information gathered during the literature review and presented in the models, the CEM components of shallow sublittoral mud habitats that are most useful for monitoring habitat status in the context of natural variation in the environment have been identified. Identification of these components will allow monitoring programmes to take account of how the habitat is varying naturally, so that any changes detected can be put within this context. These components have been identified through assessment of the model components and their interactions and are presented in Table 7.

Selected habitat components have a large magnitude of effect on the structure and functioning of the habitat, a generally low level of natural variability and operate at relevant spatial and temporal scales to reflect change in the habitat. It should be noted that no consideration has been given to the monitoring methodology or practicality of including these features in a monitoring programme at this stage.

A short rationale is presented for each potential monitoring component in Table 7. Confidence in the model components has been assigned based on the protocols presented in Sections 2.5 and 4.2.

The information presented in Table 7 is based on expert judgement and current understanding of levels of natural variability assigned to each factor (see Section 4.1.5), which is generally poor.

There may be other factors which are useful for monitoring to determine habitat change in the context of natural variation; however those presented are considered the key components identified by this project.

Table 7. Key ecological aspects of shallow sublittoral mud habitats that would be most useful for monitoring habitat status and change due to natural variation.

Habitat Component	Rationale	Confidence	Relevant Models
Sediment Type	Natural variation in sediment composition over time is likely to be relatively low, although it is known to occur (e.g. from studies of reference areas in proximity to aggregate extraction sites). Any alteration to sediment particle-size distribution is likely to have a potentially large impact on benthic fauna (Basford. 1990; Seiderer and Newell. 1999; Cooper. 2011), and in turn on other factors in the ecosystem (such as sediment stability, suspended sediments etc.). Changes in sediment composition are likely to affect fauna predominantly at a local scale although effects will be directly tied to the spatial change in sediment type. As such, it is thought that sediment type is a crucial factor to monitor in terms of identifying changes in habitat status due to natural variation.	High (supported by large amount of literature evidence)	All
Burrowing Fauna	Burrowing fauna form the largest group in the sublittoral mud conceptual ecological model. By constructing permanent to semi-permanent burrows the fauna have profound effects on the surrounding environment due to their bioturbation and bioengineering activities (Pillay and Branch. 2011;	High (largely informed by literature evidence)	Sub-model 2

	Jones. 2000). A natural decrease in abundance of burrowing fauna would have a direct effect on the local to regional diversity together with a decrease of the biogeochemical cycling (particularly oxygen) in the mud (Pinn and Atkinson.2009; Jones . 2000).		
Tube-building Fauna	Tube-building fauna form an important functional group within the shallow sublittoral mud habitat, producing numerous ecological functions not performed to the same degree by any other group (e.g. bioengineering and biodeposition). Some aggregations of tube-building fauna are known to vary naturally over time (Limpenny. 2010; Pearce . 2013). Evidence shows that reef aggregations containing a higher number of live worms provide a greater output of associated ecosystem functions such as habitat provision and sediment stability (Bolam and Fernandes. 2003; Passarelli. 2012). A natural decrease in the abundance of the tube building fauna would likely have a large magnitude of effect at the local (and possibly wider) scale on other functional faunal groups and ecosystem functions.	Medium (largely informed by literature evidence)	Sub-model 1
Light Attenuation	Light attenuation is predominantly dependent on water turbidity and depth. Whilst turbidity undergoes frequent short term fluctuations, e.g. from tidal flows and seasonal changes, annual turbidity levels have a low level of natural variability; however, when changes do occur they will likely have a large magnitude of impact. Any change in light attenuation will impact primary production and food sources for fauna (Masselink and Hughes, 2003; Brown. 2002a; Devlin. 2009).	Medium (largely informed by literature evidence)	All
Water Chemistry and Temperature	Water chemistry and temperature are influencing factors on fauna as well as primary production (and food sources), and as such are key components in the habitat (Cusson and Bourget. 2005; Bolam. 2010). Natural variation in water chemistry and temperature is likely to be relatively low (aside from seasonal variation), but impacts of change have the potential to be large when they do occur, and across a variety of scales. Water temperature and nutrient content are all potential key sub-components that could be targets for monitoring programmes.	Medium (informed by expert judgement and literature evidence)	All
Dissolved Oxygen	Dissolved oxygen in the water column of shallow sublittoral mud habitats has a moderate natural variability with main impacts of change related to water currents, wave exposure and changes in primary production.	Medium (informed by expert judgement and literature evidence)	All
Benthic Infauna	Benthic infauna is a crucial part of the shallow sublittoral mud habitat; the species are influenced by numerous factors and perform several key functions within the habitat (MarLIN. 2006). Infauna is considered to be a good aspect for monitoring habitat status and change due to natural variation given the relatively low-moderate natural variation likely to be exhibited by the fauna itself under a non-	Medium (informed by both expert judgement and literature evidence)	Sub-models 1 - 5

	stressed scenario. Changes in the main driving influences on the habitat (such as recruitment, sediment type, food sources etc.) would likely lead to large changes in infaunal dynamics, which in turn would affect output processes and ecosystem functions across a variety of scales. It may be pragmatic to select specific species from within the main functional group that could serve as indicators for specific habitats (those species listed in model/biotope matrix presented in Appendix 3). Changes to the main driving influences may also create an altered state of the habitat, possibly creating a beneficial situation for the settlement of non-native species that could endanger the natural diversity (De Mesel. 2013).		
Recruitment	Recruitment is a key biological factor that affects fauna related to shallow sublittoral mud habitats at a local scale. Despite the likely high natural variability of recruitment as a process (driven by supply of propagules and feedback loops), it is thought that this factor would be beneficial to monitor given its large influence over benthic faunal composition. Defining species to specifically monitor cannot be stated without further literature evidence, although some studies do exist which could be used to address this (e.g. Hiscock. 2005).	Medium (largely informed by expert judgement)	All

8 Monitoring components to identify anthropogenic causes of change

Table 8 presents key driving influences and output processes of the shallow sublittoral mud habitat which are likely to be sensitive to anthropogenic pressures operating on the ecosystem, and as such may be useful for monitoring to identify anthropogenic causes of change in the environment. Definitions of each of the pressures, along with relevant benchmarks (from Tillin. 2010), are presented in Appendix 15. It should be noted that no consideration has been given to the monitoring methodology or practicality of including these features in a monitoring programme at this stage. No consideration of the biological assemblages and their response to pressures has been undertaken in this project as sensitivity assessments of sedimentary habitat ecological groups has been completed as part of Tillin and Tyler-Walters. 2014.

The assessment presented in Table 8 is very simplistic and does not consider the potential degree of sensitivity of each model component, nor the potential rate of recovery and how sensitivity might be influenced by the extent and magnitude of the pressure. The presented information provides a good starting point for selecting indicators to identify anthropogenic cause of change but the literature reviewed to inform this assessment is limited.

The factors included in Table 8 are based on a combination of literature evidence and expert judgement. A short rationale is presented for each potential monitoring feature and confidence has been assigned based on the protocols presented in Sections 2.5 and 4.2. There may be other factors that are useful for monitoring to determine habitat status and change due to anthropogenic pressures; however those presented are the key components identified by this project.

Table 8. Key driving influences and output processes of shallow sublittoral mud habitats that are likely to be sensitive to pressures and may be useful for monitoring to identify anthropogenic causes of change. Descriptions of each of the pressures and associated benchmarks are presented in Appendix 15.

Pressure	Model Component	Rationale	Confidence
Habitat Structure changes / Physical damage (e.g. beam trawling, dredging) - surface abrasion and sub-surface abrasion	Suspended Sediment and seabed mobility	Surface and sub-surface abrasion will enhance fine suspended sediments and seabed mobility in sublittoral mud habitats (Kenny and Rees. 1994).	High
	Light attenuation	The increased suspended sediments caused by physical abrasion and extraction will have a direct effect on the light attenuation in the water column (Devlin. 2008), decreasing the light available for primary production.	Medium
	Sediment stability	Surface and sub-surface abrasion will destroy upper parts of infaunal burrows and tubes (Hughes. 1998b), which can lead to a local decrease in the sediment stability of sublittoral mud habitats (Ciutat. 2007, 2006).	Medium
	Habitat Provision	Removal of bioengineering species will decrease their habitat provision to other fauna as they are essential for the survival of lower parts of the food web (Braeckman. 2011).	Medium
	Supply of propagules	Physical disturbances to the seabed will destruct reef structures and burrows and impact the settlement and survival rate of propagules (Dannheim. 2014; Neal and Avant, 2008).	Medium
	Biogeochemical cycling	Oxygen cycling in the sublittoral mud habitats may decrease if a significant amount of bioturbating and bioengineering fauna are removed during surface and sub-surface abrasion (Volkenborn and Reise 2006).	Medium (largely informed by expert judgement)
Removal of target species	Bioturbation and Biodeposition	The mollusc *Cerastoderma edule* and crustacean *Nephrops norvegicus* are commercially fished in certain areas around the UK (Hughes. 1998b; MarLin. 2006; Sabatini and Hill. 2008), the removal of these species has the potential to reduce bioturbation and biodeoposition rates in the sublittoral mud habitat resulting in disruptions to all local and global ecosystem functions.	Medium (informed by expert judgement and literature evidence)

	Nutrient and biogeochemical cycling	Reduction of large numbers of targeted species will likely reduce the amount of nutrients deposited in the sediment and reduce the oxygen penetration into deeper layers of the sublittoral mud (Jones. 2000). In the absence of bioturbating activities, oxygen can only penetrate a few millimetres into muddy sediments through physical diffusion (Diaz and Rosenberg. 1995)	Medium (informed by expert judgement and literature evidence)
	Supply of propagules	The extraction of targeted species can result in a reduction in the supply of propagules, which will influence spawning stock biomass.	Medium (largely informed by expert judgement)
Siltation rate changes, including smothering (depth of vertical sediment overburden)	Suspended Sediment	An increase in siltation is likely to be preceded by increased suspended sediments in the water column (Devlin. 2008; Last . 2011).	Medium
	Light attenuation	If the siltation is prolonged, the increased suspended sediments will affect light attenuation (Devlin. 2008).	Medium (informed by expert judgement and literature evidence)
	Primary Production	During the process of siltation, particles are likely to become suspended, at least for a short period of time. During this time primary production will be reduced as a result of the suspended particles preventing light attenuating to lower depths (Munn. 2004; Jones. 2000).	Medium
	Nutrient cycling	Nutrient cycling has the potential to be reduced as faunal communities are affected by smothering. Once the faunal community has become re-established nutrient cycling will potentially return to pre-event levels.	Medium (largely informed by expert judgement)
Physical change (to another seabed type) e.g. installation of wind farms	Water currents	The physical change of the mud habitat due to the installation of infrastructures can modify local water movements around the structure (Vanhellemont and Ruddick. 2014).	High
	Habitat Provision	The physical change of the seabed due to the installation of new infrastructures has the potential to create new habitats and enhance colonisation (De Mesel. 2013). The structures may also create a refuge habitat for juvenile fish species with enhanced food availability (Derweduwen. 2012; Reubens. 2013).	High
	Sediment type	The changing water currents around installed infrastructures can in their turn affect the sedimentological characteristics of the seabed (Airoldi. 2005; Coates. 2014).	Medium

	Bioturbation	Change of sediment type to an artificial structure will limit the bioturbation potential to areas of the sediment which infaunal species can inhabit altering the structure of the sediment on a small scale.	Medium (largely informed by expert judgement)
Organic enrichment	Water chemistry and temperature	Organic enrichment from anthropogenic sources can have a large effect on water chemistry (Levinton. 2001; Lalli and Parsens. 2006). Direct loading of nutrients, organic matter and minerals will likely have large effects on benthic and epibenthic communities, and will alter ecosystem functions in a significant way (Munn. 2004).	High
	Primary Production	Organic enrichment of the natural environment is also likely to influence primary production (Hiscock. 2006). Nutrients are known to be a limiting factor in primary production and an increased input could lead to phytoplankton blooms (e.g. Lalli and Parsens. 2006). This will increase food availability in the short-term but is also coupled with increased microbial activity which can lead to hypoxia in a negative feedback loop (Munn. 2004).	High

9 Examining the effects of different pressures on the system using Bayesian Belief Network Models – an introduction and case study

Bayesian Belief Networks (BBNs) can help predict outcomes of different management scenarios, particularly when data is sparse or uncertain. The conceptual ecological models of shallow sublittoral mud habitats connect different components of the ecosystem, and associated processes and functions that lend themselves to modelling by Bayesian Belief Networks (BBNs).

Essentially a BBN is a formalised set of rules that indicates the probability of any 'node' in the system being in one of a number of fixed states. In practice, the node is any component box in the model (e.g. predatory polychaetes, bioturbation or biodiversity enhancement). In this case study, the fixed states the node can be in are either *increasing* or *decreasing.* These values are informed from the magnitude of influence in the diagrammatic models (Appendix 4–14).

A BBN is driven by two factors. Firstly the *prior* belief about whether a node or compartment is *increasing* or *decreasing* (e.g. there is a 0.9 probability of the population sizes of predatory polychaetes *increasing*; there is a 0.7 probability of biotope stability *decreasing*). The prior knowledge of changes is driven by considering different pressures on the system. For example, Table 8 provides a range of potential pressures, such as removal of target species. In this situation, it would be possible to examine the effects on the system of *Nephrops norvegicus* removal by changing the prior belief about the population to 0.9 that it will decrease (meaning 0.1 probability that it would increase). The exact figures used would depend on the certainty of the change. For example, targeted removal of *Nephrops norvegicus* may not result in a population decline, if recruitment were good, and the harvest was limited in size, so a probability of 0.9 may be suitable here. Different pressures would act on different components of the system, and some potential scenarios are described below. If nothing is known in advance about the fate of a node, its prior value can be left at 0.5 for both *increasing* and *decreasing*, meaning it is equally likely to increase or decrease.

The second factor in constructing a BBN is the probabilities of the interaction terms between nodes or compartments. In this study, these interaction probabilities were taken directly from the Burrowing Fauna sub-model (sub-model 2), from the Habitat and Biological Assemblage (level 4) through to the Regional and global ecosystem functions (level 7). Positive interactions between compartments meant that the probability of the target node *increasing*, $P(X_i)$ in the equation below, would increase if the causative node was itself *increasing* [$P(Y_i)$], but would decrease if the causative node was *decreasing* [$P(Y_d)$]. The network is parameterised using the assumption $P(Y_i) = 1$, or that the causative node is definitely *increasing*, and if this is the case, then the probability of the target node *increasing* is determined as either 0.95, 0.8 or 0.65. The value is taken directly from the magnitude of effect indicated in the burrowing fauna sub-model, with 0.95 representing large magnitude of effect, 0.8 moderate and 0.65 small. The few negative interactions displayed in the sub-model were of moderate size, hence the probability of the target node *increasing*, given the causative node was definitely *increasing* [$P(Y_i) = 1$] was taken as 0.2 (or the probability of the target node *decreasing* was 0.8).

Since in practice, the causative node does not have a probability of *increasing* or *decreasing* of exactly 1, the effect of each causative node (given its actual probability) on the target node is given by the following Bayesian equation:

$$P(X_i|Y)=[P(X_i|Y_i)*\ P(Y_i)\ +\ P(X_i|Y_d)*\ P(Y_d)]$$

where X is the component or node under consideration, and Y are the interacting components or nodes, subscripts i and d indicate *increasing* or *decreasing* respectively for the species. These values are calculated for each interacting component to create the *posterior* probabilities for each compartment.

Advances in methods for BBNs allow for cyclical interactions in the network (e.g. feedback and reciprocal interactions such as competition between species (Stafford and Williams. 2014; Stafford. 2014). Using networks modified from these studies, we examined a range of scenarios for the Burrowing Fauna sub-model (sub-model 2), from the Habitat and Biological Assemblage (level 4) through to the Regional and global ecosystem functions (level 7) respectively:

1) Targeted *Nephrops norvegicus* fishing – this involved setting the prior belief of *N. norvegicus decreasing* to 0.9 (and of *increasing* to 0.1).
2) Non-targeted fishing e.g. trawling for *N. norvegicus* - this involved setting the prior belief of *N. norvegicus decreasing* to 0.9 and all other fauna *decreasing* to 0.8 (*increasing* to 0.2). The prior belief of sediment stability *decreasing* was also set to 0.8 (and of *increasing* set to 0.2).
3) Ocean acidification (affecting hard shelled organisms). All hard-bodied species probability of *decreasing* set to 0.7 (0.3 of *increasing*).
4) Habitat destruction (physical loss of habitat) - Habitat destruction and biotope stability priors of *decreasing* set to 0.8 (0.2 *increasing*).

All other prior values were set as 0.5 for *decreasing* and *increasing* (i.e. both equally likely). The outputs of these simulations are shown in Table 9.

The results indicate the power of a BBN to identify changes occurring through a number of interconnected nodes, and indicate the direction and probability of the change occurring. For example, simply targeting *Nephrops norvegicus* and directly altering no other parameters causes 14 of the 20 nodes to show decreases with a probability of > 0.65, and one node to show an increase with probability > 0.65. Hence the power of the BBN approach is to quantify possible scenarios over a whole range of ecosystem measures and functions. In practice, this means that it may be possible, for example, to monitor ecological communities, and use this information to predict the effects of change on ecosystem functions (for example, a decline in *N. norvegicus* will lead to a decline in a range of processes and functions, as demonstrated in Table 9). Since it is easier to monitor population sizes of species than many of these other components, such models may provide a useful tool to indicate ecosystem health and function in the future, as well as a predictive tool for assessing the effects of anthropogenic activities.

The formulation of BBNs from the diagrammatic models produced is a relatively straightforward process, simply accounting for strength and confidence of each interaction. The BBNs are also easy to use to investigate any number of scenarios – the accompanying spreadsheet (BBN Sublittoral Mud CEM – Version 1.0) allows for different scenarios to be easily tested, simply by manipulating the values of prior belief of change of any node which may be thought to be affected.

Table 9. Calculated (posterior) probability of a node of the network *increasing* (*decreasing* values calculated as 1 – *increasing*) given different possible scenarios. Numbers in red indicate probability of *decreasing* >0.65 (or of *increasing* <0.35), numbers in green indicate probability of *increasing* >0.65 (or *decreasing* <0.35). Numbers in black indicate no high level of probability of change in either direction. Scenarios 1–4 represent: 1. Targeted *N. norvegicus* fishing; 2. Non-targeted fishing; 3. Ocean acidification; 4. Habitat destruction, see main text for details of prior values assigned to these scenarios.

		Pred HB	Dep HB	Pred poly	Oth Poly	Oth infa	Sec prod	Bio turb	Bio dep	Prop sup	Bio eng	Nut cyc	Food	Bio geo	Sed Stab	Hab prov	Micro	Exp biod	Exp org	Biod Enh	Bio Stab
1	**Posterior increase**	**0.09**	**0.80**	0.42	0.46	0.42	**0.12**	**0.12**	**0.12**	**0.12**	**0.12**	**0.24**	**0.26**	**0.16**	0.50	**0.19**	**0.26**	**0.26**	0.40	**0.27**	**0.33**
2	**Posterior increase**	**0.09**	**0.30**	**0.18**	**0.27**	**0.18**	**0.10**	**0.10**	**0.10**	**0.10**	**0.14**	**0.25**	**0.27**	**0.19**	**0.21**	**0.24**	**0.28**	**0.27**	0.41	**0.30**	**0.33**
3	**Posterior increase**	**0.28**	0.36	0.46	0.48	0.46	**0.25**	**0.25**	**0.25**	**0.25**	**0.26**	**0.34**	0.35	**0.28**	0.50	**0.31**	0.35	0.35	0.44	0.36	0.40
4	**Posterior increase**	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	**0.20**	0.50	0.50	0.50	**0.21**	**0.10**

Key:

Pred HB= hard bodied predators. Dep HB = Hard bodied deposit feeders, Pred poly = Predatory Polychaetes, Oth poly = other polychates, Oth infa = Other infauna, Sec prod = secondary production, Bio turb = Bioturbation, Bio dep = Biodeposition, Prop sup = supply of propagules, Bio eng = Bioengineering, Nut cyc = nutrient cycling, Food = food resources, Bio geo = biogeochemical cycling, Sed stab = sediment stability, Hab prov = habitat provision, Micro = microbial activity, Exp biod = export of biodiversity, Exp org = export of organic matter, Biod enh = Biodiversity enhancement, Bio Stab = biotope stability.

10 Conclusions

This project and the present report have demonstrated the links and interactions that occur within shallow sublittoral mud habitats through a series of Conceptual Ecological Models (CEMs). The models themselves are well informed by the literature review, and thus confidence is generally high in the outputs. Expert judgement has been used to inform some interactions within the models, and confidence has been reduced in these instances. Should additional data be added to the project in the future, confidence could likely be improved.

The information presented in Tables 7 and 8 shows which components of the models may be useful for monitoring habitat status and change due to natural variation and anthropogenic pressure, respectively; and may be worth taking forward to inform indicator selection for this habitat type. Typically, local inputs to the habitat are those most likely to serve as features useful for monitoring change in the context of natural variation. Sediment type, water column chemistry and temperature, and light attenuation are likely to be key monitoring aspects of the shallow sublittoral mud physical and chemical environment. Tube-building and burrowing fauna may be worth monitoring to assess habitat status and change due to natural variation from a biological point of view. Further work will have to be undertaken to identify specific species that would be useful to monitor from within these groups to reflect natural variation in the biological communities.

In terms of aspects that may be useful for monitoring habitat status and change due to anthropogenic pressures, certain key driving influences (e.g. water currents, light attenuation, suspended sediments and water chemistry) have been identified as potentially sensitive to pressures. Output processes of the shallow sublittoral mud habitat, which have been identified as potentially useful monitoring aspects in relation to pressures, include bioturbation, habitat provision, nutrient cycling and biogeochemical cycling.

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12 List of Appendices

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In addition to the appendices listed, a spreadsheet containing ancillary electronic information supporting the literature review also accompanies this report, as referred to within the main report sections (Sublittoral Mud CEM Literature Review and Ancillary Information - Version 1.0). There is also a spreadsheet containing the information used to support the Bayesian Belief Network (BBN) sections of this report (BBN Sublittoral Mud CEM – Version 1.0).

Appendix 1 – List of Species Included in Project Scope

Please see accompanying data logging proforma for full species list and details of how this list was refined.

Abra alba
Abra nitida
Ampelisca tenuicornis
Ampharete lindstroemi
Amphiura filiformis
Aphelochaeta marioni
Arenicola marina
Brissopsis lyrifera
Callianassa subterranea
Calocaris macandreae
Capitella capitata
Carcinus maenas
Cerastoderma edule
Cirriformia tentaculata
Echinocardium cordatum
Echinus esculentus
Euclymene oerstedii
Galathowenia oculata
Goniada maculate
Hediste diversicolor
Labidoplax media
Lagis koreni
Leptosynapta bergensis
Macoma balthica
Magelona johnstoni
Malacoceros fuliginosus
Maxmuelleria lankesteri
Mediomastus fragilis
Melinna palmata
Microprotopus maculatus
Mya truncata
Mysella bidentata
Nephrops norvegicus
Nephtys hombergii
Nuculoma tenuis
Ocnus planci
Owenia fusiformis
Pagurus bernhardus
Phaxas pellucidus
Philine aperta
Pholoe inornata (sensu petersen)
Phoronis muelleri
Photis longicaudata
Polydora ciliata
Pygospio elegans
Rhodine gracilior
Sagartiogeton undatus
Scalibregma inflatum
Scoloplos armiger
Spiophanes bombyx
Thysanocardia procera
Tubificoides (pseudogaster)
Virgularia mirabilis

Appendix 2 – List of Keywords used as search terms

Amphipod
Annelida
Anoxia
Bacteria
Benthic
Biodeposition
Bioengineering
Biogeochemical process
Bioirrigation
Biological driver
Biotope
Bioturbation
Bivalve
Brittlestar
Burrowing
Circalitoral
Climate
Climate variation
Cohesive sediments
Crustacea
Currents
Deposit feeder
Depth
Diatoms
Dissolved oxygen
Echinodermata
Ecology
Ecosystem functioning
Ecosystem process
Ecosystem service
Environmental driver
Environmental position
Epifauna
Feeding method
Filter feeding
Fine sands
Food resource
Food web
Functional group
Geology
Grazer
Growth form
Habitat provision
Habitat stability
Holothuroidea
Hydrodynamic flow
Hypoxia
Infauna
Infralittoral
Interstitial
Lifespan
Light attenuation
Macrofauna
Marine
Meiofauna
Microalgae
Microbial activity
Mobility
Muddy sediments
Mud
Nitrogen flux
Nutrient cycling
Nutrient provision
Ocean acidification
Organic Carbon
Organic matter
Physical driver
Physiographic
Phytoplankton
Polychaete
POM
Predator
Prey
Primary production
Salinity
Sandy mud
Seabed energy
Seabed mobility
Seasonal variability
Secondary production
Sediment
Sediment dynamics
Sediment resuspension
Sediment stability
Sediment transport
Species trait
Sublittoral
Substratum
Subtidal
Suspension feeder
Suspension feeding
Temperature
Temporal variability
Tidal stress
Trophic level
Tube dwelling
Turbidity
Water chemistry
Water composition
Water flow
Wave energy

In addition to the search words used above, each of the selected species names were also searched for individually.