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Conceptual Ecological Modelling of Shallow Sublittoral Coarse Sediment 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 Coarse Sediment Habitat in the UK. CEMs are diagrammatic representations of the influences and processes that occur within an ecosystem. They can be used to identify critical aspects of an ecosystem that may be taken forward 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 state of the environment free from adverse anthropogenic impacts and pressures.

It is intended that the models produced by this project will be used to inform indicator selection for the monitoring of this habitat in UK waters. CEMs may eventually be produced for all habitat types defined under the UK Marine Biodiversity Monitoring Research and Development Programme (UKMBMP), which along with stressor models, which are designed to show the interactions within impacted habitats, would form the basis of a robust method for indicator selection. This project has developed the first series of CEMs within this programme and will inform the future potential roll out to all other habitats.

The project scope included the Marine Strategy Framework Directive (MSFD) predominant habitat type 'Shallow sublittoral coarse sediments'. This definition includes those habitats that fall into the EUNIS Level 4 classification A5.13 Infralittoral Coarse Sediment and A5.14 Circalittoral Coarse Sediment, along with their constituent Level 5 biotopes that 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 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 coarse sediment habitat. All information gathered during the literature review was entered into a data logging pro-forma spreadsheet, which accompanies this report (Appendix 14). 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. One general control model was produced that indicated the high-level drivers, inputs, biological assemblages, ecosystem processes and outputs that occur in shallow sublittoral coarse sediment habitats. In addition to this, four detailed sub-models were produced, which each focussed on a particular functional group of fauna within the habitat: epibenthic fauna, sedimentary tube-building fauna, infauna, and interstitial fauna. 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 whilst 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 in 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 faunal recruitment, define and influence the food sources consumed by the biological assemblages of the habitat, and the nature of 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 factors include secondary production, bioturbation, biodeposition, supply of propagules and bioengineering; these in turn influence nutrient and biogeochemical cycling, supply of food resources, sediment stability and habitat provision as ecosystem functions at the local scale. The export of biodiversity and organic matter, biodiversity enhancement, habitat stability and biotope maintenance 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 that may be useful for monitoring in order 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. These features are presented as preliminary lists and further consideration would be required to select appropriate aspects for monitoring in the field.

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1 Introduction

In order to manage the marine environment effectively, it is necessary for decision makers to have access to suitable methods for characterising the state (the 'well-being') of marine biodiversity and habitats at a variety of geographical scales. Then, where a deterioration (an 'unfavourable' change) in state occurs and is detected by such methods, it is possible to infer possible causes for the change – natural or anthropogenic – which then determine the best type of corrective management measures that might be introduced, if considered necessary. All methods rely on the use of single or combined *indicators* that are used as a proxy for the actual ecological status.

An indicator is a factor that may be used to monitor the likely status of an ecosystem (e.g. Noon & McKelvey 2006). Indicators can be related to a variety of aspects of the marine biological environment, but the most appropriate ones are typically straightforward to monitor, and provide crucial information about aspects of the target habitat, which may otherwise be hard to assess in its totality. Indicators may include species' numbers, variety, and assemblage characteristics as well as variety of habitat type and other physical or chemical properties, such as the energy of the water environment, light attenuation or nutrient levels.

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

It is well known that the process of determining indicator selection is no easy task (e.g. Noon & 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 contemporary knowledge about the links in marine ecosystems to be drawn together in a diagrammatic way, which can highlight the ecological aspects of marine ecosystems that are important for monitoring (e.g. Maddox *et al* 1999; Manley *et al* 2000; Gross 2003).

This project is focussed on producing a series of CEMs for the marine habitat 'Shallow Sublittoral Coarse Sediment'. It is intended that the models produced by this project will be used to inform indicator selection for the monitoring of this habitat type in UK waters. CEMs may eventually be produced for all habitat types defined under the UK Marine Biodiversity Monitoring Research and Development Programme (UKMBMP). The project has developed the first series of CEMs within this programme and will inform the potential future roll out to all other habitats. The models produced under this project will demonstrate the ecological components and processes that occur across spatial and temporal scales within ecosystems that have not been subject to anthropogenic impacts (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] www.ices.dk/community/groups/Pages/ACOM.aspx

1.1 Habitat Background

The EU Marine Strategy Framework Directive (MSFD[2]) predominant habitat type 'Shallow Sublittoral Coarse Sediments' is common within UK waters and has the potential to support a wide range of biodiversity. Sublittoral coarse sediment habitats are found in a range of environmental conditions and are characterised as containing both coarse sands and gravels (Connor *et al* 2004).

This project makes use of biotope classifications to provide a structure to the study. The sublittoral coarse sediment habitat covers two biological zones at EUNIS Level 4 (see Connor *et al* 2004): infralittoral coarse sediment, defined as those areas between the mean low water line and the maximum depth at which 1% light attenuation reaches the seabed; and circalittoral coarse sediment, defined as the zone between which 1% light attenuation reaches the seabed and the bottom of the wave base (approximately 50-70m depth) (Cochrane *et al* 2010; McBreen *et al* 2010). The distribution of EUNIS Level 4 biotopes which represent infralittoral and circalittoral coarse sediment habitats in the UK is shown in Figure 1.

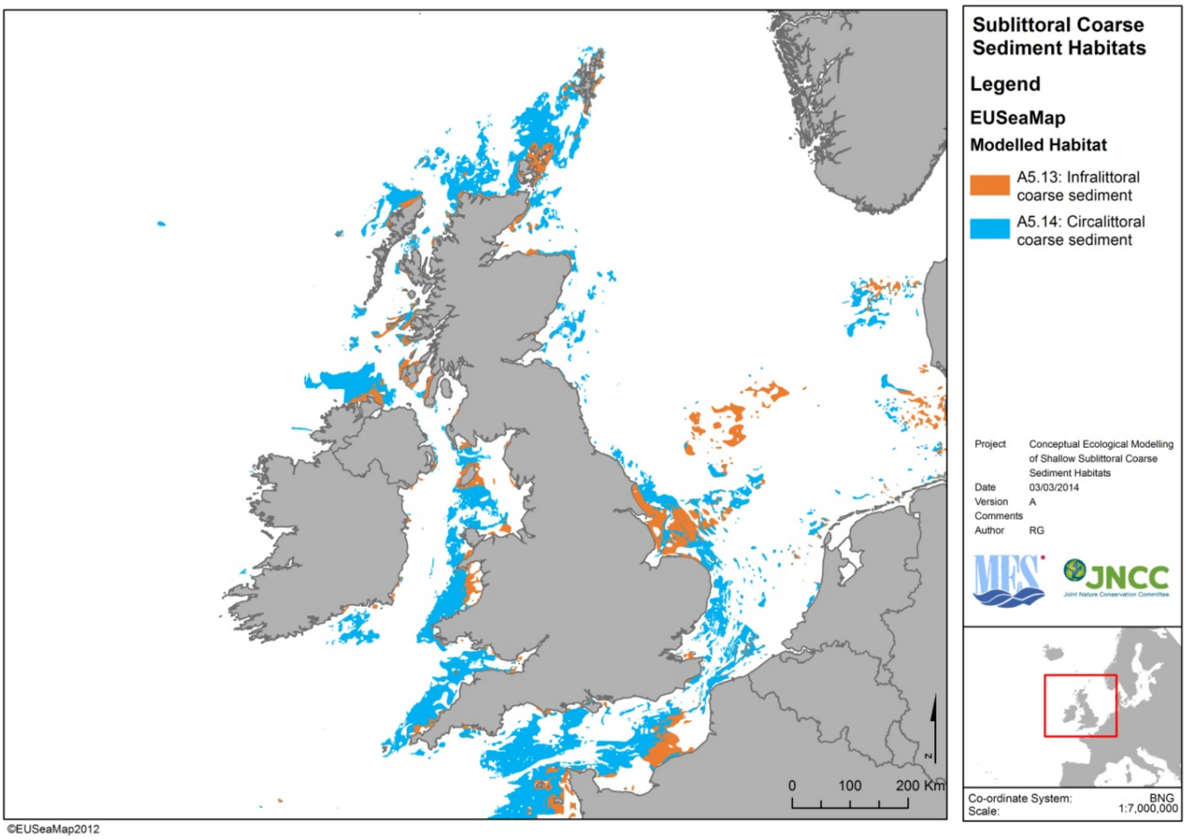

Figure 1. The distribution of shallow sublittoral coarse sediment habitats around the UK, split by infralittoral and circalittoral zones. Data is taken from the EUSeaMap broad-scale modelled habitat mapping project (Cameron & Askew 2011).

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

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[2] http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2008:164:0019:0040:EN:PDF [Accessed May 2014]

A5.13 (SS.SCS.ICS): Infralittoral coarse sediment:

- **A5.131** (SS.SCS.ICS.SSh): Sparse fauna on highly mobile sublittoral shingle (cobbles and pebbles)
- **A5.132** (SS.SCS.ICS.HchrEdw): *Halcampa chrysanthellum* and *Edwardsia timida* on sublittoral clean stone gravel
- **A5.133** (SS.SCS.ICS.MoeVen): *Moerella* spp. with venerid bivalves in infralittoral gravelly sand
- **A5.134** (SS.SCS.ICS.HeloMsim): *Hesionura elongata* and *Microphthalmus similis* with other interstitial polychaetes in infralittoral mobile coarse sand
- **A5.135** (SS.SCS.ICS.Glap): *Glycera lapidum* in impoverished infralittoral mobile gravel and sand
- **A5.136** (SS.SCS.ICS.CumCset): Cumaceans and *Chaetozone setosa* in infralittoral gravelly sand
- **A5.137** (SS.SCS.ICS.SLan): Dense *Lanice conchilega* and other polychaetes in tide-swept infralittoral sand and mixed gravelly sand

A5.14 (SS.SCS.CCS): Circalittoral coarse sediment:

- **A5.141** (SS.SCS.CCS.PomB): *Pomatoceros triqueter* with barnacles and bryozoan crusts on unstable circalittoral cobbles and pebbles
- **A5.142** (SS.SCS.CCS.MedLumVen): *Mediomastus fragilis*, *Lumbrineris* spp. and venerid bivalves in circalittoral coarse sand or gravel
- **A5.143** (SS.SCS.CCS.Pkef): *Protodorvillea kefersteini* and other polychaetes in impoverished circalittoral mixed gravelly sand
- **A5.144** (SS.SCS.CCS.Nmix): *Neopentadactyla mixta* in circalittoral shell gravel or coarse sand
- **A5.145** (SS.SCS.CCS.Blan): *Branchiostoma lanceolatum* in circalittoral coarse sand with shell gravel

Some EUNIS level 5 biotopes have been excluded from the habitat definition as they are not relevant to the UK.

1.2 Project Aims and Approach

1.2.1 Project Aims

The aim of this project is to produce a series of Conceptual Ecological Models (CEMs) to demonstrate the ecological links, drivers and ecosystem functions that occur in shallow sublittoral coarse sediment habitats. The models require a 'benchmark' condition against which comparisons can be made. The non impacted state of the ecosystem (exclusive of anthropogenic influence) is used to produce control models indicative of the natural state and natural variability of the environment.

The specific project objectives are as follows:

1. Collate and review available information on the environmental and ecological aspects of shallow sublittoral coarse sediment habitats, along with associated confidence and knowledge gap analyses
2. Create a hierarchical set of control models to represent shallow sublittoral coarse sediment habitats and relevant subsystems
3. Produce a preliminary list of key ecological aspects of the habitat that would be most useful for monitoring habitat status and change due to natural variation

4. Produce a preliminary list of key ecological aspects of the habitat that are likely to be sensitive to pressures and may be useful for monitoring to identify anthropogenic causes of change.

1.2.2 Literature Review Approach

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

- Environmental drivers of the habitat and its constituent 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 distribution and 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 scales at which these functions occur.

In order to conduct the literature review effectively, 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 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 fauna and ecosystem are able to provide ecosystem functions.

Species Trait – a biological characteristic of a certain taxa relating to their life history, interactions or environmental preference.

Habitat/Biotope Composition – The physical, chemical and biological characteristics of the environment that support a particular ecological community. The biotopes included within the scope of this project (i.e. those contained within shallow sublittoral coarse sediments) 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[3] (Connor *et al* 2004) and the European Environment Agency European Nature Information System (EEA EUNIS) Habitat Type Classification[4].

1.2.3 Species Selection

Aside from the differentiation between light attenuation in the infralittoral and circalittoral biological zones, the large-scale environmental drivers for each biotope are broadly similar.

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

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 131 species (Connor *et al* 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:

i. **Title species**: Fauna named in biotope title, e.g. *Halcampa chrysanthellum, Glycera lapidum,* etc.
ii. **Title group species**: Example taxa identified from the full species list to represent those groups named in the biotope titles, e.g. *Dosinia lupinus* to represent venerid bivalves, *Iphinoe trispinosa* to represent cumaceans, etc. Representative species were chosen as those that typically represented the group, based on expert judgement.
iii. **Description species**: Species identified as particularly characterising in the biotope descriptive text but not included within the biotope title.
iv. **Description example taxa**: Example taxa identified from the full species list to represent those groups named in the biotope descriptive text, e.g. *Ampelisca spinipes* to represent amphipods, *Scoloplos armiger* to represent interstitial polychaetes, etc. Representative species were chosen as those that typically represented the group, based on expert judgement.

Alternative methods of reducing the list, e.g. grouping fauna by major groups or using a higher taxonomic classification, were ruled out due to the potential loss of critical details and the likelihood that species-level information would still be required for effective results.

The Excel Add-In TREx (Taxonomic Routines for Excel)[5] 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 131 identified species were of conservation importance or alien species to the UK (through a link to the World Register of Marine Species[6]). This check resulted in one species, *Echinus esculentus*, being added to the selection list.

A revised list of 41 benthic species to be considered within the immediate scope of the project was taken forward for review in the literature, as shown in Appendix 1 and the 'Species Selection' worksheet of Appendix 14. Turbellaria as a Class were initially included in the list of species to be researched in the project; however were removed following a lack of evidence for species traits and interactions.

1.2.4 Species Traits Selection

Species traits are an essential consideration within the model, impacting on the ecosystem functions and feedback influences within the habitat. A comprehensive list of species traits were 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. A list of 45 species traits was refined based on other comparable studies (e.g. Van der Linden *et al* 2012; Bolam *et al* 2014) and through expert opinion to give a manageable list of relevant traits for inclusion in the project. A revised list of 19 traits is shown in the 'Traits Selection' worksheet in Appendix 14, including a short justification for the inclusion of each trait.

[5] Taxonomic Routines for Excel, species name checking software available: http://unicomarine.mw1.vm.bytemark.co.uk/page/marine-biological-software
[6] http://www.marinespecies.org/ [Accessed May 2014]

1.2.5 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 coarse sediment 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 levels of the final models. This information was initially identified using peer-reviewed papers (e.g. Jones *et al* 2000) and was supplemented with information from other sources as the review progressed.

Using the above approach, literature sources were gathered and summarised to inform production of the final models and the final project outputs. A preference was given to peer-reviewed journal articles as sources of information, as these were likely to be the most reliable. Multiple electronic databases (e.g. Science Direct, Web of Knowledge, Wiley Online Library) were searched using a list of key words (included in Appendix 2). The use of keywords ensured that all databases were thoroughly interrogated, and allowed a systematic approach to the literature review.

A 'grey literature' search (i.e. that which has not been peer-reviewed, such as articles, theses, technical reports, agency publications etc.) was 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 the section below.

Taxonomic checking 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[7] indicated that several taxa have changed nomenclature. These are listed below:

- *Sertularia argentea* is a synonym of *Sertularia cupressina* var. *argentea*
- *Caulleriella zetlandica* may be called *Chaetozone zetlandica* in the literature
- *Pomatoceros triqueter* is now known as *Spirobranchus triqueter*
- *Anaitides maculata* is now known as *Phyllodoce maculata*
- The UK species of *Moerella* are now known as *Tellina*, although *Moerella* is still a recognised genus for other species outside of the UK, as is *Angulus*
- *Alcyonidium diaphanum* may have been known as *Alcyonidium gelatinosum* pre-2001 (Porter *et al* 2001).

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 *et al* 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 the habitat is defined by.

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

1.2.6 Data Logging Pro Forma

Information collated during the literature review was entered into a data logging spreadsheet for ease of reference (Appendix 14), 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. The information logged was divided into the following sections (worksheets):

- **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.
- **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 *et al* 2004).
- **Faunal Traits Matrix**: Trait information for each of the selected species. Data were entered in such a way so that one row in the spreadsheet represents 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 parameter 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.

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.

1.2.7 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 for the direction and magnitude of influence between components to be described. 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 as output processes from the ecosystem, and as driving factors on the biological components of the habitat could be both positive and negative.

Table 1. Assessment of direction of interaction.

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.

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.

1.2.8 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 utilises 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 (i.e. a source with a high-quality score and a medium applicability score would have an overall confidence of medium etc.). Confidence classifications were entered into the relevant column in the Reference Summary worksheet in Appendix 14 for each source.

Table 3a. Confidence assessment of quality for individual evidence sources.

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.

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.

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

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 2.2.

1.3 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. Specific evidence on ecosystem interactions or species traits that inform the models is presented and discussed throughout Section 3.

The majority of biological traits information was obtained from peer-reviewed grey literature (such as the MarLIN BIOTIC database; MarLIN 2006) 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 the UK species. During the literature review, it became apparent that information was more readily available for larger, common species, but less so for rare and smaller interstitial species. Larger epifaunal species such as *Urticina felina*, *Pagurus bernhardus* and *Ophiura albida* were well researched, as were many of the tube dwelling polychaete worms such as *Sabellaria spinulosa, Lanice conchilega* and *Spiophanes bombyx.* Fewer sources were available for species such as *Edwardsia timida* and smaller interstitial species such as *Protodrilus* sp. and *Microphthalmus similis.*

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 coarse sediment 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 sources identified, 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 coarse sediment 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 coarse sediment, sublittoral sand etc.), using comparable taxa likely to have the same functions, and from comparable global locations. This has been reflected in the 'Limitations in evidence' column in the 'Interactions Matrix' worksheet (Appendix 14) 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 two taxa, *Edwardsia timida and Echinus esculentus,* are of conservation importance (listed as a priority species for conservation under the UK Post 2010 Biodiversity Framework and as 'Near Threatened' on the IUCN Red List[8] respectively).

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.

1.3.1 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' tab in the accompanying spreadsheet indicates the degree of evidence that has been sourced for species trait information. The majority of faunal traits have a high level of information recorded. Information on basic traits, such as mobility type and size for example, 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, species status as a key prey item and whether a taxon is likely to have a naturally highly variable population.

Information gathered on the ecosystem interactions that occur in sublittoral coarse sediment habitats has been incorporated into the confidence assessments associated with each of the models produced by this project, as described in Section 2.2. 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 determine interactions between ecosystem components (see Section 2.2). Expert judgement carries a lower confidence score (see Table 5) 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 4). 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 3.

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

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 *et al* 2007), or are based on comparable species. Generally, few gaps in the literature were identified, and none which could not be addressed through expert judgement (see Section 4 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.

2 Model Development

2.1 Model Design

The Conceptual Ecological Models (CEMs) developed for shallow sublittoral coarse sediment habitats are designed to represent both an overarching general model for this habitat, as well as additional 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 indicate consistent presentation of parameters, interactions and temporal/spatial scales. In addition, a method was developed to address and represent the common overlapping species and characteristics between different biotopes in the models, using faunal groups.

2.1.1 Model Hierarchy

General Model

A general sublittoral coarse sediment 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 coarse sediment habitat as a whole.

Sub-Models

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

Species from the habitat as a whole were grouped together according to their general biological traits in order to identify functional groups. Groups of fauna were selected that occupy a similar position within the shallow sublittoral coarse sediment habitat, are influenced by similar drivers, and perform similar ecosystem functions. 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 functional groups were predominantly based on the environmental position of the species present in the habitat but also take into account the feeding type and principal prey resources from information gathered during the literature review (see Appendix 14). Four functional groups of species were identified, each of which form the basis to a sub-model, as identified in Figure 2. 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.

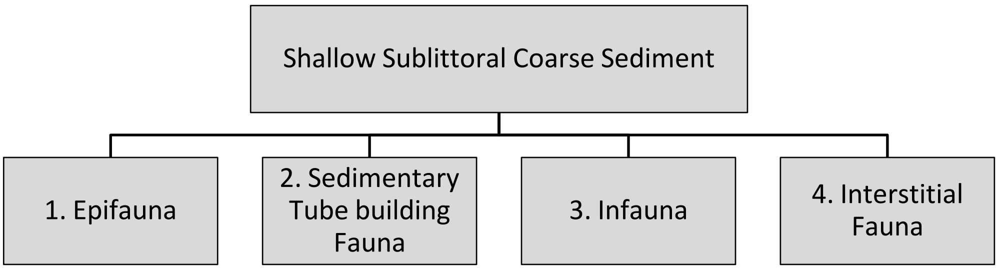

Figure 2. Shallow sublittoral coarse sediment habitat CEM hierarchy. The top level of the flowchart represents the general control model, with the four sub-models each documenting a specific functional group within this habitat.

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 function within the habitats. 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.

2.1.2 Model Levels

Each model is broken down into several component layers that 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 have an 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 relate to 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 that typifies the habitat. For the sub-models, fauna are broken down 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; 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 that 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.

2.1.3 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 4.

Table 4. Descriptions of the components that 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 that occur within the habitat.

DRIVING INFLUENCES	
1. Regional to Global Drivers	
Propagule Supply	Supply of larvae, spores and/or 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. This parameter is inclusive of dissolved oxygen, salinity, nutrients, in the water column and water temperature
3. Local Processes/Inputs at the Seabed	
Recruitment	The process by which juvenile organisms join the adult population. Combines settlement and 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
- Microbes	Microorganisms such as bacteria, diatoms and protozoa
Seabed Mobility	Movement of sediment on the seabed

DRIVING INFLUENCES contd	
4. Habitat and Biological Assemblage	
Epibenthic Fauna	Fauna that live on the surface of the seabed
Sedimentary Tube Building Fauna	Fauna that construct and live in tubes made from sedimentary material on the surface of the seabed
Infauna	Fauna that burrow or live within the sediment
Interstitial Fauna	Fauna that inhabit the space between sediment particles
OUTPUTS	
5. Output Processes	
Supply of Propagules	The production and transportation of larvae, spores or body fragments capable of regeneration
Bioengineering	Faunal modification of the natural habitat, e.g. tube building, burrow creation etc.
Biodeposition	The process by which filter feeding organisms capture particulate matter from the water column and deposit into the sediments
Secondary Production	Amount of biomass created as a direct result of consumption
Bioturbation	Sediment re-working by marine fauna
6. Local Ecosystem Functions	
Nutrient Cycling	Cycling of organic and inorganic nutrients that involves processing into a different chemical form
Food Resources	The growth of prey items as a food resource for other organisms
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
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 Maintenance	Maintenance of the habitat through sustained production and sediment stability
Carbon Sequestration	Capture and storage of carbon within the ecosystem

2.1.4 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, this 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.

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 3. 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 2. 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. 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 which 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.

2.1.5 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-section of fauna being addressed. The fauna covered in each model characterise the output processes, and in turn the ecosystem functions at the local to global scales.

2.2 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 1.2.8. 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 5. 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 determined 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 5. 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 4. 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.

2.3 Model Limitations

It is important to note that as these models are conceptual designs they have been produced for the specific habitats and selected species only. As a result, not every link present within the ecosystem is presented. Only those links that are regarded as 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 identified as important for characterising the biota of the selected biotopes. Other species (and functional groups) may be present within the relevant 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 1.2.3. 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 1.2.5). For the sake of continuity and 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 *et al* 2004).

Confidence in the models is influenced by the extent of the literature review, and time and budgetary constraints of the project. This is further discussed in Section 4.

3 Model Results

Each of the models produced is described and discussed over the following sections of this report. The models produced stand as an accompaniment to this report and are also included in Appendices 4-8. 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' spreadsheet that accompanies this report for details of the physical parameters that define the habitat and each constituent biotope.

The text supporting each sub-model is presented in such a way that 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 text does not necessarily support the model structure outlined in Table 4. Ecosystem drivers and functions are described in a logical and pragmatic way, so that those that are linked are defined in turn, rather than described by model level.

It should be noted that information presented under each model heading is tied to the confidence assessments presented in Section 4. References for the information discussed are shown where literature sources have been found to back up the statements being made.

3.1 General Control Model and Common Model Components

The general control model indicates the processes, interactions, influences and links that occur in shallow sublittoral coarse sediments as a whole. Information in the model is not split by biotope, nor by functional group (although these are included as individual components), since the model is intended to give an overview of the habitat, with the sub-models used to give an in-depth view of specific aspects of the habitat.

As such, 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. 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 that is particularly relevant to that model (such as local processes/inputs at the seabed, food sources, recruitment, etc.).

3.1.1 Ecosystem Drivers

The majority of ecosystem drivers defined for the general model relate to the physical environment, 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 a key defining factor of the biotopes being considered in this project and exerts influence on other critical drivers (Basford *et al* 1990; Cusson & Bourget, 2005; Bolam *et al* 2010). By definition, shallow sublittoral coarse sediment habitats are those that extend down to the wave base (Connor *et al* 2004). Depth is a particularly relevant driving factor to those habitats in both the infralittoral and circalittoral zones, influencing the limit of impact from light attenuation and wave exposure.

Wave exposure is a crucial factor defined in the biotope classifications (see 'Habitat Characterisation' worksheet in Appendix 14 for biotope-specific details) and varies from 'very exposed' to 'extremely sheltered' (Connor *et al* 2004). The limit of wave exposure is defined as the wave base, the maximum depth to which wave energy causes motion in the water column (Connor *et al* 2004). The effects of wave disturbance are far more prominent in shallower waters, i.e. the infralittoral zone (Brown *et al* 2002a; Masselink & Hughes, 2003). The greater the wave exposure, the greater the likelihood of enhanced suspended sediment concentrations and increased seabed mobility (Brown *et al* 2002a; Masselink & Hughes, 2003). Wave exposure is also likely to have an influence on water-column chemistry and oxygen availability due to mixing. Wave exposure is defined as having moderate natural variability, based on current meteorological conditions including seasonal variation, cyclical fluctuations and the frequency of extreme events.

Water currents are defined to include both current mediated flow and tides (Reiss *et al* 2010). They provide a mechanism for transport of suspended sediment and components of the water chemistry and temperature profile, as well as supplying energy to the seabed. The transport mechanism supplies food resources for filter feeding organisms, propagules and influences water column chemistry and temperature through mixing (Chamberlain *et al* 2001; Biles *et al* 2003). 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. Whilst supply may be from similar or different habitats, this driver also forms part of a feedback loop, indicating the importance of recruitment, which is necessary for the maintained continuation of a healthy habitat. 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 potentially has high natural variability, and is likely to be influenced by a number of physical and biological factors, not all of which have been shown on the models in order to minimise unnecessary complexity.

Climate is an important driver in the ecosystem and in this context 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 light attenuation as well as water chemistry and temperature (Hiscock *et al* 2006). The current climate is described as having moderate natural variability, and takes account of seasonal variation, cyclical fluctuations and the frequency of extreme events.

Geology is listed as an environmental driver at the regional to global scale largely for its position as the physical basis of the benthic habitat. Geology likely has an influence on suspended sediments and sediment type, depending on the nature of the geology itself, as discussed below.

At the water-column processes model level, several key components link environmental drivers to local inputs at the seabed. Primary production by phytoplankton and phytobenthos is a crucial base to the biological aspects of the habitat, and a key driver of prey sources (e.g. Hiscock *et al* 2006). Larger macrophytes are generally less common in sublittoral coarse sediment habitats due to the typically high sediment mobility often associated with the habitat. Some prey resources may be primary producers themselves (e.g. phytoplankton), and some influenced by primary production within the water column (e.g.

zooplankton, living prey etc.). Primary production predominantly occurs in the infralittoral zone, closest to the sea surface (e.g. Jones *et al* 2000). As the top of the circalittoral zone is defined as receiving 1% light attenuation (Connor *et al* 2004), primary production will be relatively non-existent within this zone (e.g. Lalli & Parsons 2006). Light attenuation itself is driven by depth, climate and suspended sediments in the water column (Brown *et al* 2002a; Masselink and Hughes 2003; Devlin *et al* 2008). In addition to light, primary production is also influenced by water chemistry (nutrients) and temperature as necessary factors for photosynthesis (Hily 1991; Hiscock *et al* 2006; Lalli & Parsons 2006).

Suspended sediments, which are likely to be heavily influenced by wave exposure, water currents and to a lesser degree geology, directly affect light attenuation through turbidity of the water column. Suspended sediments also directly influence some faunal species, especially those which build tubes using sediment particles captured from the water column (e.g. Pearce *et al* 2013). A feedback loop exists from seabed mobility to seabed sediments, indicating that a mobile seabed is likely to result in suspended sediment in the water column (Masselink & Hughes 2003).

Water chemistry and temperature is a large component that incorporates many aspects grouped together for ease of presentation. Properties include salinity, temperature, nutrients, dissolved organic material and dissolved oxygen. These may be influenced by many drivers; however wave exposure, water currents and climate are shown on the model as particularly important due to direct influences, such as climate on water temperature, water currents on e.g. nutrient transport, and wave exposure on dissolved oxygen mixing (e.g. Brown *et al* 2002b; Dutertre *et al* 2013). In addition to primary production, water chemistry and temperature links to biological components, such as food sources and the biological complement of the habitat, based on the need of organisms for dissolved chemicals in the water column (nutrients, calcium carbonate etc.) and specific temperature requirements (Cusson & Bourget 2005; Bolam *et al* 2010). A feedback loop from biogeochemical cycling as a local ecosystem function to water chemistry also exists, signifying the re-supply of organic chemistry to the water column (e.g. Libes 1992). Water chemistry and temperature is defined as having moderate variability, based on environmental drivers and potential for changes over the short and long term.

Local processes and inputs at the seabed are those that have a direct impact upon 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 sublittoral coarse sediment habitats, there are a considerable number of specific food resources that need to be considered in the models, and these are thus presented in detail within the distinct sub-models, rather than the general model.

Seabed mobility, a proxy for the extent to which the habitat is affected by natural physical disturbance, is another key driver. Environments with a high degree of seabed mobility are likely to be characterised by fauna tolerant of mobile sediments and sediment movement. Fauna that require stable sediments in which to live, 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 finding food. Fauna that are filter feeders 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 & Hughes 2003; Lalli & Parsons 2006).

All of these factors combined influence the biological component of the habitat, either directly or indirectly, across varying scales. In combination with this, sediment type is a major influencing factor on fauna at the habitat level (Basford *et al* 1990; Seiderer & Newell 1999; Ellingsen 2002; MESL 2007; Cooper *et al* 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 *et al* 2002a). Whilst underlying geology may be an important driver of sediment type, it is important to note that many coarse sediment deposits found in UK waters are likely to owe their origin to Pleistocene age deposits derived from glacial and fluvio-glacial activity (e.g. Limpenny *et al* 2011; Tappin *et al* 2011) which may rest on unrelated, older, geological formations. As a result, surface sediments may be unconsolidated and could be prone to movement or winnowing (Masselink & Hughes 2003). Should this occur on a large scale, revealing an underlying geology that may be vastly different to surface sediments.

Multiple studies indicate that sediment type is a key driver of biological communities. Highest faunal diversity and abundance is typically found in coarse sediment deposits that allow for a range of fauna to colonise several environmental niches (Seiderer and Newell 1999; Cooper *et al* 2011). Finer-grained sediments are typically less diverse and tend to contain a lower abundance of organisms, whereas coarse sediments are typically more diverse and support more abundant faunal assemblages due to increase in habitat complexity (Cooper *et al* 2011). Some functional groups have specific niche sediment requirements, such as sedentary epifauna, which require hard surfaces upon which to attach themselves, and interstitial fauna, which require relatively large sediment grain sizes in order for there to be sufficient spaces between particles for them to inhabit.

3.1.2 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 the shallow sublittoral coarse sediment habitat can be broadly split into four main categories: sediment processing, secondary production, habitat modification and supply of propagules. Sediment processing refers to biological reworking of sediments, and incorporates actions such as bioturbation and biodeposition. Secondary production (defined as converting energy to/from lower to higher trophic levels, not necessarily from primary producers) is a process undertaken by all fauna as growth and consumption of other lower trophic level organisms occurs (Lalli & Parsons 2006). Habitat modification is defined as the biological modification of the natural environment, through processes such as tube or reef building, or the digging of burrows. Supply of propagules, as previously discussed in Section 3.1.1, 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 the biotopes and are heavily influenced by sediment processing (Probert 1984; Kristensen 2000; Norling *et al* 2007; Mermillod-Blondin 2011). These occur in part by the representative fauna themselves through natural process (such as uptake of nutrients, decay etc.) and secondary production (Norling *et al* 2007; Mermillod-Blondin 2011). 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 *et al* 2012). Microbial activity leads to nitrogen and carbon fixation, which feeds back to water chemistry as an ecosystem input (Bertics *et al* 2010). Reworking of sediments through bioturbation allows oxygen to penetrate the sediments deeper, permits bio-mixing of the sediments, allows bioirrigation and encourages chemical exchange within the sediments, increasing the rates of nutrient and biogeochemical cycling (Kristensen *et al* 2012).

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

Habitat provision is the result of both bioengineering of the natural environment (building of tubes, digging of burrows etc.) and colonisation of species that are found within the biotope themselves by symbiotic or commensal organisms (Vader 1984; Pretterebner *et al* 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 *et al* 2012).

Regional to global scale ecosystem functions resulting from sublittoral coarse sediment habitats include carbon sequestration through living organisms, export of both organic matter and biodiversity through the supply of propagules and secondary production, and biotope maintenance and biodiversity enhancement through sediment stabilisation and habitat provision (e.g. Nybakken 2001; Lalli & Parsons 2006).

3.1.3 Connectivity to other Habitats

Connectivity to other habitats is a key part of the ecosystem although is difficult to represent within the conceptual models.

There are multiple habitat types around the UK that may be found in proximity to sublittoral coarse sediment habitats which do not exist in isolation and are all intrinsically linked. In terms of ecosystem drivers, connectivity is important for aspects of the models such as supply of propagules, water chemistry and temperature and food resources, although 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 shallow sublittoral coarse sediment 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. This is particularly important of mobile epibenthic species that may actively move between habitat types as part of their routine movements or during different times in their life history.

As such, it should be kept in mind that whilst the models presented as part of this project detail the ecological processes that occur in sublittoral coarse sediment habitats, the habitats should not be thought of as operating in isolation, and connectivity to other habitats is likely to be a key factor.

3.2 Sub-model 1. Epifauna

3.2.1 Biological Assemblage

The epifauna sub-model represents fauna that inhabit the surface of the seabed. The habitat and biological assemblage is split into two main groups in terms of biota; sedentary epifauna, which is either encrusting or attached to the seabed; and active epifauna which is free-moving. These groups are further split as follows:

Sedentary Epifauna
- Colonial hydroids and bryozoans, e.g. *Alcyonidium* sp., *Sertularia* sp.
- Actiniaria, e.g. *Urticina* sp.
- Encrusting epifauna, e.g. *Pomatoceros* sp., *Balanus crenatus*

Active Epifauna
- Bivalves, e.g. *Pecten maximus*
- Echinoids, e.g. *Echinus esculentus*
- Ophiurids, e.g. *Ophiura albida*
- Decapods, e.g. *Pagurus* sp., *Liocarcinus* spp.

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

Epifauna represents a highly diverse functional group, and this sub-model contains the largest number of sub-functional groups of all the sub-models. This is due to the highly diverse nature of differing feeding mechanisms that the epifauna exhibit and the number of different environmental niches occupied.

3.2.2 Ecosystem Drivers

Physical environmental drivers are likely to be of significant importance to epifauna, as detailed for the general control model. As a large proportion of epibenthic fauna are filter feeders straining food resources from the water column, water currents passing by the habitat are likely to be necessary for these species to flourish.

Seabed sediment mobility is also a key factor that will likely influence epibenthic fauna. A high mobility of seabed sediments is likely to prevent widespread colonisation of the seabed by all but the most adapted fauna, whereas an environment with very low seabed energy (and thus seabed mobility) may not supply adequate food resources to filter feeding fauna.

Sediment type is also likely to be a key driving factor for some species considered in the epifauna model (e.g. Basford *et al* 1990). Sedentary epibenthic fauna often require hard surfaces on which to attach themselves, the absence of which is likely to be prohibitive to colonisation. Sediment type is less relevant for active epifaunal species, although their distribution is likely to be indirectly linked to sediment type (e.g. Basford *et al* 1990).

As with other models, propagule supply is an important biological driver, without which the biological assemblage could not exist. Several of the species covered in this model are known to have a planktonic larval stage (MarLIN 2006; MESL 2008) suggesting that connectivity to other habitats nearby could be an important consideration. These may include different subtidal and intertidal habitats and other areas of sublittoral coarse sediment. Recruitment into the adult population will drive the biological assemblage directly, which in turn will produce further propagules, completing the feedback loop.

The final key driver operating on epibenthic species is food resources. Due to the diverse nature of the epibenthos, multiple food sources are included in the model, reflecting various feeding strategies.

Plankton (both phytoplankton and zooplankton) and particulate organic matter (POM) are primary sources of food for colonial hydroids, Actiniaria, encrusting epifauna, bivalves and ophiurids (MarLIN 2006; MESL 2008; Saraiva *et al* 2011). Phytoplankton, as primary producers, are heavily influenced by water chemistry and temperature (including nutrient availability) and light attenuation (e.g. Hily 1991; Jones *et al* 2000; Lalli & Parsons 2006; Hiscock *et al* 2006). Light attenuation is however ascribed a small level of influence in the model due to the fact that other food sources are less influenced, at least directly, by light attenuation. Other food sources are likely to be less affected by light attenuation, at least directly. Other larger-scale drivers such as water currents and wave exposure (promoting water column mixing) will also influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley 1972; Hily 1991; Jones *et al* 2000; Lalli & Parsons 2006). Phytoplankton are generally more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make them 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 chemistry and temperature (dissolved oxygen in particular) (Levinton 2001; Nybakken 2001; Lalli & Parsons 2006;). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons, 2006). POM derived from organic sources including plankton is an important food source in both the infralittoral and circalittoral zones (Nybakken 2001; MarLIN 2006; Lalli & Parsons 2006).

Detritus, organic matter contained within seabed sediments or on the seabed, is an important food source for deposit feeding and scavenging fauna such as echinoids and decapods (MarLIN 2006). Detritus in the marine environment is influenced by a number of factors, including marine life (Brown *et al* 2000a; Nybakken 2001; Lalli & Parsons 2006) not all of which are indicated on the model for the sake of simplicity.

Phytobenthos, marine plants attached to the seabed, are likewise a source of food for echinoids such as the edible urchin *Echinus esculentus* (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 sediment 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 (the link is not shown on the model, since marine plants are not thought to be a key characterising biological component of the shallow sublittoral coarse habitat). Phytobenthos will only be present in the infralittoral zone where light attenuation is great enough to permit photosynthesis.

Carrion and living prey are key sources of food for decapods such as the hermit crabs *Pagurus* sp. and the swimming crabs *Liocarcinus* spp. (MarLIN 2006; Dauvin *et al* 2013). These sources of food are largely the product of other functional groups found within the habitat, indicated by the feedback loop in the model.

3.2.3 Ecosystem Outputs

The major and relatively unique output process performed by epifauna is biodeposition. This process is especially prevalent in the epifauna sub-model due to the environmental niche inhabited by epifauna at the seabed–water column continuum, and as a large number of the species covered by this model are filter feeders, they are capturing particulate matter from the water column (MarLIN 2006; MESL 2008). Ophurids, Actiniaria and hydroids are the greatest contributors to biodeposition and lay down large amounts of organic and sedimentary particles into the benthic sediments (Allen 1998; Gili *et al* 1998; Daly *et al* 2008; Dauvin *et al* 2013). This process is far more widely performed in this sub-model than any other due to the species composition. Biodeposition enhances organic deposits in the sediments and is a key stage in nutrient cycling, as excreted matter is laid down (Libes 1992). This also leads to the export of organic matter at a wider scale. A feedback loop is present from nutrient cycling as an ecosystem function to water column chemistry as a water column process/input.

Secondary production is a key process occurring within the shallow sublittoral coarse sediment habitat, whereby energy from lower trophic levels is converted to higher trophic levels through energy transfer (Lalli & Parsons 2006). This in turn provides ecosystem functions at the local scale by driving nutrient cycling (Nybakken 2001; Lalli & Parsons 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 through connectivity via propagule dispersal with other habitats. Food resources in the sublittoral coarse sediment habitat may be negatively affected by a high population of active predators such as decapods.

Another local ecosystem function performed directly by epifauna is the provision of habitat. Colonial hydroids and bryozoans, Actiniaria, encrusting epifauna, and, to a lesser extent, hermit crabs may all provide a habitat for other marine organisms to inhabit, colonise, or make use of (Vader 1984; Pretterebner *et al* 2012). This in turn contributes to the overall enhancement of biodiversity at wider scales.

Epibenthic fauna can be said to engage in bioengineering to a limited degree. Encrusting species such as calcareous-tubed *Pomatoceros* sp. and *Balanus crenatus* are technically habitat modifiers, although likely provide few benefits to other organisms in terms of ecosystem functions. Other larger fauna, such as decapods, may modify the surface sediments to some extent, although this is thought to be a relatively low magnitude process.

3.3 Sub-model 2. Sedimentary Tube Building Fauna

3.3.1 Biological Assemblage

The sedimentary tube building fauna sub-model represents those species in shallow sublittoral coarse sediment habitats that construct and live in either colonies or individual tubes made out of sediment particles. Two main functional groups have been identified within this collection of fauna:

- Gregarious Tube Building Fauna, e.g. *Ampelisca spinipes, Sabellaria spinulosa*
- Solitary Tube Building Fauna, e.g. *Sabella pavonina*, *Spiophanes bombyx*

A full species list of the selected taxa that constitute these groups, and a breakdown of the constituent biotopes they represent is presented in Appendix 3. The species represented by this group are distinct from other tube building or encrusting fauna covered by other models (such as *Pomatoceros* spp.) in that all the tubes made by these species are constructed from sedimentary sources, rather than from secreted (biogenic) calcareous material.

This model represents a moderate number of species, all characterised by their traits of bioengineering and habitat modification. The taxa that comprise this model are predominantly filter feeders, straining food particles and prey out of the water column. The drivers and inputs likely to affect both gregarious and solitary tube builders are similar in nature, and unlikely to vary between the differing living approaches adopted by the split functional groups. The output processes and ecosystem functions provided by each group are however quite different, a result of the scale and degree of habitat modification undertaken.

The Ross worm, *Sabellaria spinulosa*, is included within this model. *Sabellaria spinulosa* is noted for its ability to form complex biogenic reefs under the right conditions, although also exists as solitary individuals, clumps or thin veneers. Biogenic reefs formed by *Sabellaria* are listed under Annex I of the EU Habitats Directive[9] and identified as one of those habitats considered to be most in need of conservation at a European Level. It should however be noted that that protection is only afforded to the reef habitats, and not the species itself.

3.3.2 Ecosystem Drivers

As with other models, propagule supply is an important biological driver, without which the biological assemblage could not exist. Several of the species covered in this model are known to have a planktonic larval stage (MarLIN 2006; MESL 2008), suggesting that connectivity to other habitats nearby could be an important consideration. Recruitment into the adult population will drive the biological assemblage directly, which in turn will produce further propagules, completing the feedback loop.

Seabed sediment mobility is a key 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 *et al* 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, and gregarious tube builders in particular (Pearce *et al* 2013). Despite this, a degree of suspended sediment is likely to be required for tube growth by some fauna. Taxa that build sedimentary tubes, such as *Sabellaria spinulosa*, need a supply of sediments suspended in the water column to trap particles and form their protective tubes (Holt *et al* 1998; Levinton, 2001; Dubois *et al* 2002; Last *et al* 2011). Other fauna obtain the sediment used in tube construction from the seabed itself, and do not rely on suspended particles.

Physical disturbance resulting from wave exposure may also hinder tube building and may be a controlling factor in determining where this functional group is found. As tube building fauna are predominantly filter feeders, water currents are likely to be a necessity to some degree for supply of particulate food sources.

Primary food sources for tube building fauna are plankton within the water column (both phytoplankton and zooplankton) and POM (Fauchald & Jumars 1979; MarLIN 2006). Phytoplankton are heavily influenced by factors affecting primary production, such as light attenuation, climate, and water column chemistry and temperature, including nutrient content (Hily 1991; Jones *et al* 2000; Lalli & Parsons 2006; Hiscock *et al* 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; Jones *et al* 2000; Lalli & Parsons 2006). Phytoplankton are likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make them 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 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 & Parsons 2006;). Zooplankton are expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006). POM is an important food source in both the infralittoral and circalittoral zones (Nybakken 2001; Lalli & Parsons 2006; MarLIN 2006).

[9] http://eurlex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:NOT [Accessed May 2014]

3.3.3 Ecosystem Outputs

The output processes and ecosystem functions performed by sedimentary tube building fauna are well documented in the literature. The key output processes performed by sedimentary tube building fauna are bioengineering, biodeposition, secondary production and the supply of propagules.

Modification of the natural environment by these fauna as they construct their tubes is a key process, and one not performed in the same way by any other functional group in the sublittoral coarse sediment habitat. By trapping suspended sediment particles from the water column and secreting them into solid tube structures, several output processes and ecosystem functions are performed. The degree of bioengineering varies from species to species; solitary tube building fauna, such as *Spiophanes bombyx*, alter the natural habitat to a much lesser degree than a large aggregation of *Sabellaria spinulosa* individuals, which under the right conditions may form a dense biogenic reef structure (however, important monitoring aspects of these 'reefs' will be considered separately from shallow sublittoral coarse sediments).

Bioengineering and modification of the habitat through the construction of tubes has several associated ecosystem functions. These include provision of habitat for other organisms to colonise (Dubois *et al* 2002; Pearce *et al* 2007, 2013; Meadows *et al* 2012), increased sediment stability through cohesion and trapping of sediment particles (Kirtley & Tanner 1968; Pandolfi *et al* 1998; Van Hoey *et al* 2008; Woodin 2010), which feeds back to seabed mobility, and the provision of a platform from which enhanced biogeochemical cycling can occur through microbial activity within the tubes themselves (Van Hoey *et al* 2008; Mermillod-Blondin *et al* 2011). Bioturbation is likely to be limited for the majority of species that form this functional group due to the relatively fixed mobility of species within their tubes (Queirós *et al* 2013). Bioengineering is in some cases noted to have a negative feedback to water currents at a local scale, reducing current flow through increased seabed rugosity disrupting flow patterns and shear stress at the seabed (e.g. Holt *et al* 1998). The degree of this interaction will obviously be variable depending on whether solitary or gregarious organisms are being considered. It should be noted that not all output process are considered positive; it has been suggested that a low density of solitary tube building fauna may have a negative impact on sediment stability through point destabilisation of sediments (Eckman *et al* 1981; Probert 1984). Other studies have also indicated that the tubes of invertebrates may reduce the mobility of other benthic burrowing fauna, reducing ecosystem function, abundance and diversity (Brenchley 1982).

Biodeposition is another key process performed by both functional groups covered by this sub-model. This involves the trapping of sediment particles and POM from the water column and transport to the seabed. Biodeposition enhances organic deposits in the sediments and is a key stage in nutrient and biogeochemical cycling, as excreted matter is laid down (Libes 1992). This is linked to the export of organic matter at a wider scale and to water column chemistry and temperature via a feedback loop.

Sedimentary tube building fauna are important secondary producers, consuming primary producers and particulate matter. In turn, some tube building fauna are noted prey items for species belonging to higher trophic levels, such as crustaceans and fish (Taylor 1962; Pearce *et al* 2008, 2013). Food processing through secondary production contributes to nutrient cycling within the ecosystem, and the dispersal of adults, juveniles and propagules exports biodiversity from the habitat to other areas.

Sedimentary tube building fauna provide four main regional to global ecosystem functions based on the output processes and local ecosystem functions of the fauna; export of biodiversity through the supply of propagules and secondary production, export of organic matter through food resources, and biodiversity enhancement and biotope stability through increased sediment stabilisation and habitat provision.

3.4 Sub-model 3. Infauna

3.4.1 Biological Assemblage

The infauna model represents the largest group of fauna considered in the sublittoral coarse sediment sub-models. Benthic infauna are those taxa that live within the sediments, either freely burrowing or those that inhabit a semi-permanent fixed burrow. This group of species is highly diverse, characterised mainly by polychaete worms and bivalve molluscs. Fauna are subdivided into a number of different groupings relating mainly to either feeding type or specific environmental niche as follows:

Predatory Infauna

- Predatory Infauna, e.g. *Anaitides maculata, Protodorvillea kefersteini*

Non-Predatory Infauna

- Burrowing Bivalves, e.g. *Dosinia lupinus*
- Other Burrowing Fauna, e.g. *Caulleriella zetlandica*, *Bathyporeia pelagica*
- Burrow-Dwelling Fauna, e.g. *Scoloplos armiger*, *Travisia forbseii*

A full species list of the selected taxa that constitute these groups, and a breakdown of the constituent biotopes they represent, is presented in Appendix 3.

Predatory infauna are those that actively hunt living infaunal or interstitial prey within the sediments or at the sediment surface. Non-predatory fauna are divided into those which freely burrow through sediments (further split into bivalves and other non-bivalves) and those which dwell in a burrow permanently. Those species that are not active predators are either deposit feeders, typically consuming detritus and organic matter contained within the sediments, or filter feeders, separating particulate matter from the water column or from water pumped through burrows.

3.4.2 Ecosystem Drivers

As with other models, propagule supply is an important biological driver, without which the biological assemblage could not exist. Several of the species covered in 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, which in turn will produce further propagules, completing the feedback loop.

Driving influences directly acting on infauna include seabed mobility, water chemistry and temperature (e.g. Nybakken 2001; Lalli & Parsons 2006), sediment type (Basford *et al* 1990; Seiderer and Newell, 1999; Ellingsen 2002; MESL 2007; Cooper *et al* 2011) and food sources. Larger spatial scale environmental drivers will also affect benthic infauna, although to a lesser degree than for those functional groups which inhabit the sediment surface, such as sedimentary tube building fauna and epifauna. Living within the sediments provides some degree of protection to the infauna from the environmental conditions, and evidence suggests that strong tidal flow within a habitat favours the prevalence of infauna and burrowers (Dutertre *et al* 2013).

The primary food source of predatory polychaetes is other benthic infauna, interstitial fauna, and in some case epibenthic fauna (Fauchald & Jumars 1979; MarLIN 2006). Living prey is likely to comprise other fauna represented in the model, which is indicated by the feedback loop from food resources as a local ecosystem function in the model.

POM and plankton (both phytoplankton and zooplankton) form the primary prey source for those species that are filter feeders, such as bivalves and some burrow dwelling fauna (Nybakken 2001; Levinton 2001; Rota *et al* 2009; Saraiva *et al* 2011; Conchological Society 2013). 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; Jones *et al* 2000; Hiscock *et al* 2006; Lalli & Parsons 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; Jones *et al* 2000; Lalli & Parsons 2006). Phytoplankton are likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make them 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 will also be influence by other factors, including reproduction of benthic and epibenthic fauna (producing propagules and larvae in the water column), POM and water chemistry and temperature (dissolved oxygen in particular) (Levinton 2001; Nybakken 2001; Lalli & Parsons 2006). Zooplankton are expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006). Particulate matter derived from organic sources is a major food source in both the infralittoral and circalittoral zones (Nybakken 2001; Lalli & Parsons 2006; MarLIN 2006).

Other fauna that freely burrow through the sediments are deposit feeders, thus organically derived detritus is the main source of their food intake (Fauchald & Jumars 1979; Telford *et al* 1983; Nybakken 2001; Budd & Curtis 2007; Rota *et al* 2009).

3.4.3 Ecosystem Outputs

Alongside secondary production and the supply of propagules for recruitment, the major local output processes performed by benthic infauna are bioturbation and biodeposition. Each of the functional groups represented in the infaunal model engage in bioturbation to some degree (Queirós *et al* 2013). This reworking and overturning of the sediment is a particularly key process undertaken by those fauna that are most active, such as predators, and those fauna that freely burrow through sediments (Mermillod-Blondin *et al* 2011; Queirós *et al* 2013). Bioturbation leads to bioirrigation of sediments, increases the potential for nutrient and biogeochemical cycling, and is an important process in habitat maintenance (Probert 1984; Hiscock *et al* 2006; Norling *et al* 2007; Bertics *et al* 2010; Kristensen *et al* 2012; Queirós *et al* 2013). Bioturbation is linked with mainly positive ecosystem functions (Norling *et al* 2007; Bertics *et al* 2010; Mermillod-Blondin *et al* 2011), however evidence does exist that shows that excessive bioturbation can lead to a destabilising effect on sediments, increasing erosion potential (Woodin *et al* 2010; Meadows *et al* 2012).

Biodeposition is another key output process performed by filter feeding benthic infauna, such as burrowing bivalves, other burrowing fauna, and burrow dwelling fauna that pump seawater through their burrows in order to feed (Norkko *et al* 2001). Particulate matter is strained from the water column by the fauna and subsequently laid down into sediments through the excretion of waste material (Levinton 2001; Nybakken 2001).

Some benthic infauna engage in bioengineering through the construction of semi-permanent burrows in the sediment (e.g. Levinton 2001; MarLIN 2006). The complexity of these burrows varies from species to species, but many contain two entrances through which seawater can be pumped by the organism, and then particulate matter and prey filtered out (Nybakken 2001). Other burrows may include chambers or branches. These micro-habitats within the sediments serve several functions above those directly benefiting the host organism, including the provision of a habitat for other commensal organisms, increases in 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 (Munn 2004; Meadows *et al* 2012), and allowing greater oxygen penetration of the seabed, reducing anoxia (Levinton 2001; Nybakken 2001; Lalli & Parsons 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 *et al* 2011). In turn, this can lead to increases habitat stability, biotope maintenance and biodiversity enhancement across larger spatial scales.

Benthic infauna are important secondary producers (involved in the transfer of energy from one trophic level to another), consuming other infauna, primary producers and organic material, and in turn serving as an important food resource for multiple other organisms (Fauchald & Jumars 1979; Levinton 2001; MarLIN 2006; Nybakken 2011). Secondary production also serves to cycle nutrients in the ecosystem, and contributes to an overall export of biodiversity from the habitat at the regional to global scale, especially given the position of benthic infauna at the base of many marine food webs (Libes 1992; Lalli & Parsons 2006).

The supply of propagules is another key output process. A large proportion of benthic infauna have planktotrophic larvae (MarLIN 2006), or are at least broadcast spawners, indicating that connectivity to other habitats is likely to be important, as are water currents at the driver level. 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.

3.5 Sub-model 4. Interstitial Fauna

3.5.1 Biological Assemblage

The interstitial fauna sub-model represents fauna that inhabit the space between sediment particles on the seabed. Interstitial fauna represent a relatively small functional group in the shallow sublittoral coarse sediment habitat, although occupy an environmental niche not covered by other taxa.

Just three species form the basis of this model; *Protodrilus* spp., *Hesionura elongata* and *Microphthalmus similis*, all of which represent the biotope A5.134 (*Hesionura elongata* and *Microphthalmus similis* with other interstitial polychaetes in infralittoral mobile coarse sand). Interstitial fauna are typically very small bodied, allowing them to move freely between sediment grains. Species may be either deposit feeders or active predators. Largely due to their size, environmental position and role in the environment, the fauna represented by this model do not perform a large number of ecosystem functions compared to other functional groups represented in other models.

This functional group is poorly researched by the scientific community and there is not a wealth of supporting literature available with which to inform the model. As such, a large amount of the information presented in the model and discussed over the following sections is based on expert judgement.

3.5.2 Ecosystem Drivers

The major factor driving the presence of interstitial fauna is likely to be sediment type (Nybakken 2001). Sediment type is intrinsically linked to faunal abundance and diversity (Basford *et al* 1990; Seiderer & Newell 1999; Cooper *et al* 2011), and this is thought to be particularly relevant to interstitial fauna, which require sediments of a certain grain size (large enough to enable fauna to inhabit the voids between grains) to provide their niche habitat (Nybakken 2001).

Physical drivers that shape the habitat are also likely to be important, none more so than seabed sediment mobility. High-energy environments, where there is a large degree of sediment movement, are likely to be prohibitive to substantial interstitial fauna colonisation due to sediment movement and the potential for the gaps in the sediment to be disturbed (Nybakken 2001). Other driving factors that are related to water column provision may still be significant driving forces, but are less likely to have a direct impact on interstitial fauna, due to the relative protection afforded by living within and between sediment grains.

As with other models, propagule supply is an important biological driver, without which the biological assemblage could not exist. Interstitial fauna are thought to be restrictive in their distribution of larvae, with some species keeping propagules within the sediments (Nybakken 2001). Interstitial fauna are not typically as fecund as infaunal taxa (Nybakken 2001). Recruitment into the adult population will drive the biological assemblage directly, which in turn will produce further propagules, completing the feedback loop.

Food sources are limited for interstitial fauna, which are split by main feeding method of the species present: active predators or deposit feeding detritivores. Those species which are predators, such as *Hesionura elongata*, are known to feed on other interstitial fauna and various infaunal invertebrate species (MarLIN 2006; MESL 2008). *Microphthalmus similis* and *Protodrilus* spp. are detritivores, feeding on deposits of organic matter, in addition to diatoms and microbes within the sediments (Gray 1967; Fauchald & Jumars 1979).

Each of these food sources are likely to be affected by multiple drivers of their own, including the conditions necessary for primary production, physical drivers and water column chemistry and temperature being the key influences.

3.5.3 Ecosystem Outputs

The ecosystem functions of interstitial fauna are limited compared to other functional groups assessed within this study, likely influenced by the restricted environmental niche the fauna inhabit and the relatively low diversity of species represented by the group.

The main output processes performed by interstitial fauna are the albeit limited supply of propagules and secondary production. The supply of propagules feeds back to recruitment as an input and ultimately aids in biotope maintenance. This in turn can lead to the export of biodiversity from the ecosystem through larval supply to adjacent habitats where conditions allow.

Interstitial fauna are important secondary producers in the ecosystem (Nybakken 2001) and serve as an important food source for other interstitial species, infaunal species, and higher level consumers (MarLIN 2006). Interstitial fauna are thought to be prolific secondary producers compared in infauna due to their small size, higher metabolic activity, and high turnover rate (Nybakken 2001). This leads to the provision of significant energy to higher trophic levels and ultimately to the export of organic matter and biodiversity at a regional to global scale.

In terms of ecosystem functions at the local scale, interstitial fauna are known to have a positive effect on sediment stability, whereby those fauna that excrete mucus have the ability to trap sediment grains (Probert 1984; Meadows *et al* 2012). In turn, this has the potential to contribute to the maintenance and stability of the biotope, and to potentially enhance the biodiversity of the biotope at a wider scale by providing a stable habitat for other fauna to colonise.

Another ecosystem function performed by interstitial fauna is likely to be nutrient cycling, through uptake of nutrients and organic matter, and subsequent natural processes, such as excretion or decay (Libes 1992). This in turn feeds back to water chemistry inputs to the habitat. Those interstitial fauna that excrete mucus are known to stimulate bacterial decay with their metabolic secretions (Nybakken 2001). It may be possible that interstitial organisms are important for regulating ecosystem functions (e.g. regulation of biogeochemical processes) however evidence is lacking to fully support this hypothesis, thus the links are not shown in the model.

Bioturbation is a potential output process, as well as the associated ecosystem functions that accompany this, however due to the small size of the species represented by this group, and the fact that sediment is not typically reworked as it would be for benthic infauna, this has not been included in the model.

4 Confidence Assessment

A discussion of the confidence models produced for each sub-model is presented over the following section. The confidence models form an accompaniment to this report and are also included in Appendices 9-12. The confidence models replicate the components and layout of each of the sub-models described in Section 2 (although no confidence model exists for the general model). 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 colour coded and weighted to indicate strength of confidence supporting the links. As detailed in Section 2.2, 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 5.

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 coarse sediment habitats in the future, the confidence models can be easily updated.

Typically, local processes and inputs at the seabed are well informed by the literature review for all models. Expert judgement has been used to a larger degree on some models than others, reflective of the level of information available regarding particular functional groups. Local ecosystem function and regional/global ecosystem functions links are largely informed by expert opinion in places for all models, owing to the level of literature available.

4.1 Sub-model 1. Epifauna

The epifauna sub-model has a high overall associated confidence compared to other models. The majority of driving inputs (Levels 1 to 3) are well informed by the literature review, with most links showing at least medium confidence. Links between food sources and the fauna are particularly well informed and show high confidence. Exceptions to this are links relating to water chemistry and temperature and feedback loops operating on driving factors, which are largely informed by expert judgement, although there is a high degree of certainty to this, confidence is shown as medium for most links.

Links between the fauna and output processes are well informed in many cases, although some gaps in the literature review are apparent when the model reaches local ecosystem functions, and low confidence expert judgement is used to inform some of the influences. All of the links leading to regional to global ecosystem functions are informed by expert judgement.

4.2 Sub-model 2. Sedimentary Tube Building Fauna

Confidence in the sedimentary tube building fauna sub-model is generally high. As with other models, the main environmental drivers at all scales are reasonably well informed by the literature review. Some gaps exist in the literature review regarding links relating to water column processes that have been filled in using expert judgement.

High confidence links are shown between the fauna and the key output processes, such as bioengineering and biodeposition. Confidence is less for links that are less well described, or those that feed into the wider ecosystem functions at a regional/global scale, where expert judgement is relied upon.

Confidence in this model strongly reflects the focus of research undertaken on sedimentary tube building fauna. Many of the studies which look at this functional group focus on the specific biology and resulting ecosystem services of the species themselves, or the relationship between the organisms and human activity, rather than assessing wider ecosystem function, and benefits to the natural environment.

4.3 Sub-model 3. Infauna

Confidence in the infauna model is generally high, reflective of the amount of literature dedicated to infaunal research, and the specific ecosystem functions they perform. Links throughout the model are generally high or medium confidence, especially for Levels 1 to 5, and most are informed by the literature review.

Some degree of expert judgement has been used to inform environmental drivers at the top levels of the model, and as with other models, the regional to global ecosystem functions. Links relating to food sources or between those factors that influence the fauna directly are generally supported by high confidence evidence.

4.4 Sub-model 4. Interstitial Fauna

The interstitial fauna model, which contains the least components, has relatively high confidence for the main environmental drivers. As with other models, links to and from food sources are mostly high confidence, although there are some lower confidence links informed by expert opinion surrounding water column chemistry and temperature.

The output processes and ecosystem functions for interstitial fauna are relatively poorly informed by the literature review and as such show low confidence expert judgement for many of the links. Overall this is likely due to the low level of research undertaken regarding interstitial fauna.

5 Monitoring habitat status and change due to natural variation

Using the information gathered during the literature review and presented in the models, a preliminary list of the features of shallow sublittoral coarse sediment habitats that may be useful for monitoring habitat status in the context of natural variation in the environment have been identified. Identification of these aspects will allow monitoring to take account of how the habitat type is varying naturally, so that any changes detected can be put within this context. These features have been identified through interrogation of the model components and their interactions and are presented in Table 6. 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.

Habitat components have been selected to fulfil this role which have a large magnitude of effect on the structure and functioning of the habitat, a generally low level of natural variability, and those which operate at relevant spatial and temporal scales to reflect change in the habitat.

A short rationale is presented for each potential monitoring feature in Table 6. Confidence in the model components has been assigned based on the protocols presented in Sections 1.2.8 and 2.2.

The information presented in Table 6 is based to a large degree on expert judgement, and relies on the levels of natural variability assigned to each factor as part of the model formation (see Section 2.1.5). It must be recognised that the relative natural variability of components of biological assemblages is widely unknown, thus expert judgement which takes into account current understanding has been applied.

There may be other factors that are useful for monitoring to determine habitat change due to natural variation, however those presented are considered the key components identified by this project. Further work would be required to select appropriate aspects from this list to monitor in the field.

Table 6. A preliminary list of key ecological aspects of shallow sublittoral coarse sediment 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 at aggregate extraction sites). Any alteration to sediment particle size distribution is likely to have a potentially large impact on benthic fauna (e.g. Basford *et al* 1990; Seiderer & Newell 1999), 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
Recruitment	Recruitment is a key biological factor that affects fauna related to shallow sublittoral coarse sediment habitats at the local scale. Despite the likely high natural variability of recruitment as a process (driven by supply	Medium (largely informed by expert	All

	of propagules and feedback loops), it is thought that this factor would be beneficial to monitor as a key driving factor 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 *et al* 2005).	judgement)	
Water Chemistry and Temperature	Water chemistry and temperature is an influencing factor on fauna as well as primary production (and food sources), and as such is a key component in the habitat. 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, dissolved oxygen content and nutrient content of the water column are all potential key sub-components.	Medium (informed by expert judgement and literature evidence)	All
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.	High (largely informed by literature evidence)	All
Gregarious Sedimentary Tube Building Fauna	Gregarious tube building fauna form an important functional group within the shallow sublittoral coarse sediment habitat, producing numerous ecological functions not performed to the same degree by any other group (e.g. habitat provision and biodeposition). Some aggregations of tube building fauna are known to vary naturally over time (Limpenny *et al* 2010; Pearce *et al* 2013). Evidence shows that reef aggregations containing a higher number of live worms provide a greater output of associated ecosystem functions (Pearce *et al* 2013). A natural decrease in the abundance of the gregarious 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.	High (largely informed by literature evidence)	Sub-model 2
Benthic Infauna	Benthic infauna are a crucial part of the shallow sublittoral coarse sediment habitat; these species are influenced by numerous factors and perform several key functions within the habitat. Infauna are 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 themselves under a non-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. In reality, rather than assessing benthic fauna as a whole, it would 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).	Medium (informed by both expert judgement and literature evidence)	Sub-model 3

Based on expert judgement, it was considered that mobile epibenthic fauna as a group would be too naturally variable to function as a suitable monitoring aspect to identify habitat change due to natural variation. However, there may be merit in monitoring more stable sessile species, or even those mobile epibenthic species which are commonly targeted for commercial purposes.

6 Monitoring features to identify anthropogenic causes of change

Table 7 presents a preliminary list of key aspects of the shallow sublittoral coarse sediment 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 *et al* 2010), are presented in Appendix 13. 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.

The assessment presented in Table 7 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 7 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 1.2.8 and 2.2. Some pressures identified in Appendix 13 (such as the removal of non-target species) are not shown in Table 7 as no relevant features that would be useful for monitoring have been identified using the information gathered as part of the project literature review. There may be other factors that are useful for monitoring to determine habitat status change due to anthropogenic pressures; however those presented are the key components identified by this project. Further work would be required to select appropriate aspects from this list to monitor in the field.

Table 7. A preliminary list of key ecological aspects of shallow sublittoral coarse sediment 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 13.

Pressure	Model Component	Rationale	Confidence
Habitat Structure changes – surface abrasion and sub-surface abrasion	Sedimentary tube building fauna	Increases in suspended sediments and seabed mobility may result in removal of habitat provision, potential destruction of the biogenic reef structure and smothering caused by increased suspended particles (Kenny and Rees 1994; Dubois *et al* 2002; Pearce *et al* 2013).	High
	Sessile epifaunal species	Sessile epifaunal species are likely to be sensitive to surface and sub-surface abrasion through physical damage (e.g. Riley and Ballerstedt 2005; Jackson and Hiscock 2008). Mobile species are likely to be more robust to impacts due to avoidance behaviour.	High

Habitat structure changes – removal of substratum (extraction)	Sessile epifauna	Sessile epifauna (epiflora and epiphytes in particular) are likely to be sensitive to the removal of substratum via a loss of holdfasts (Jackson and Hiscock 2008).	High
	Sedimentary tube builders	Sedimentary tube building fauna (both solitary and gregarious) utilise seabed surface sediments in their habitat construction, and direct removal of these sediments is likely to result in la reduction or cessation of tube building activity, and loss of all the ecosystem functions provided by this stabilisation from tubes, at least in the short-term. Recovery is likely to be possible should the supply of propagules be intact and other environmental factors (such as remaining sediment type) be favourable (Hill *et al* 2011).	High
	Biological assemblages	Removal of substratum would lead to direct removal of the fauna contained within (Tillin *et al* 2011). This particularly concerns benthic infauna, interstitial fauna, and sedimentary tube building fauna (Desprez 2000). Recovery of the biological assemblages is possible assuming the subsurface deposits are similar in sediment grain size (Hill *et al* 2011), of a comparable depth, and there is a ready supply of propagules for recruitment.	High
Removal of target species	Epibenthic fauna/infauna	Molluscs such as *Pecten maximus* and *Spisula solida* and the echinoderm *Echinus esculentus* may be targeted for specific removal from the ecosystem (MarLIN 2006). This direct pressure may result in disruptions to output processes and ecosystem functions such as biodeposition and bioturbation, as well as affecting the supply of propagules, in turn potentially influencing spawning stock biomass.	High
Siltation rate changes, including smothering (depth of vertical sediment overburden)	Light attenuation	An increase in siltation is likely to be preceded by increased suspended sediments in the water column (Devlin *et al* 2008). If the change is prolonged, this has the potential to affect light attenuation, and ultimately primary production, resulting in potential secondary impacts to fauna (Jones 2000; Munn 2004).	Medium
	Sessile Epifauna	Sessile epifauna are likely to be affected by siltation rate changes due to their largely immobile nature (MESL 2008). Changes in siltation (and especially overburden) would affect feeding and food sources, and may lead to smothering of the organisms (Riley & Ballerstedt 2005; Jackson & Hiscock 2008). Some organisms may be adapted to recover from 'light' smothering (e,g, Last *et al* 2011).	High
	Infauna	Burrow-dwelling fauna and burrowing bivalves (especially those which are filter feeders) are likely to be sensitive to siltation rate changes and overburden via disruption of feeding (MESL 2008).	High

Physical change (to another seabed type)	Sediment type	Physical change (into another seabed type) will result in changes to sediment composition, thus this aspect is considered essential for monitoring. Sediment type has a large influence on biological communities (e.g. Basford *et al* 1990; Seiderer & Newell 1999) and is a defining feature of the coarse sediment habitat. Is it however not recommended that this aspect is monitored in isolation of the biological components, as other factors are known to influence biological community distribution (e.g. Bolam *et al* 2010).	High
	Benthic infauna and interstitial fauna	Benthic infauna and interstitial faunal communities are heavily influenced by sediment type (e.g. Basford *et al* 1990; Seiderer * Newell 1999). A permanent change in sediment composition would likely lead to large changes in community composition to species adapted to the new sediment type (Desprez 2000). If changes were severe, it is unlikely that the biotope would continue to exist in its recognised form and would alter i.e. to a new biotope classification. Should the environment be altered to a hard substrate from infrastructure installation, it is possible that complete loss of infauna would occur.	High
	Epibenthic fauna	Epibenthic faunal communities are strongly influenced by sediment type (e.g. Basford *et al* 1990); therefore a change in sediment particle size distribution would be expected to alter epifaunal community composition (Jackson & Hiscock 2008). This would affect both sedentary epifauna (by disrupting attachment sites) and active epifauna. Installation of infrastructure and hard surfaces would offer habitat for alternative species to colonise, potentially altering the biotope classification.	High
Organic enrichment	Water chemistry and temperature	Organic enrichment from anthropogenic sources has the potential to have a large effect on water chemistry (Levinton 2001; Lalli & Parsons 2006;). Direct loading of nutrients, organic matter and minerals is likely to have large effects on benthic and epibenthic communities, and will alter ecosystem functions in a significant way (Munn 2004). Organic enrichment of the natural environment is also likely to influence primary production (Hiscock *et al* 2006). Nutrients are known to be a limiting factor in primary production and an increased input could lead to phytoplankton blooms (e.g. Lalli & Parsons 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

7 Conclusions

This project has demonstrated the links and interactions that occur within shallow sublittoral coarse sediment 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 6 and 7 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 coarse sediment physical and chemical environment. Gregarious tube building fauna and benthic infauna may be worth monitoring to assess habitat status and change due to natural variation from a biological point of view. It is recommended that further work is undertaken to identify specific species that would be useful to monitor from within these groups.

In terms of aspects which may be useful for monitoring habitat status and change due to anthropogenic pressures, highest confidence is placed in the biological aspects of the habitat. Other localised input features have also been identified as potentially sensitive to pressures. Key biological components of the ecosystem identified as important for monitoring include sessile epifauna, sedimentary tube builders and infauna. Other functional groups may be important, albeit less so than those primarily identified. Physical and chemical components that have been identified as potentially useful monitoring aspects in relation to pressures include water chemistry and temperature, light attenuation and seabed mobility. As with the biological components identified as useful for monitoring change due to natural variation, it is recommended that further work is undertaken to identify specific species that would be useful to monitor from within these groups. The process used to select the monitoring aspects identified in Tables 6 and 7 was preliminary and future work to identify what is monitored in the field will need to take consideration of the specific monitoring objectives, relevant spatial and temporal scales, currently available methodologies and other practicalities specific to each monitoring activity.

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9 List of Appendices

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