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Conceptual Ecological Modelling of Shallow Sublittoral Mixed 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) which represent shallow sublittoral mixed sediment habitats in the UK. CEMs are diagrammatic representations of the influences and processes which occur within an ecosystem. They can be used to identify critical aspects of an ecosystem which 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 unimpacted state of the environment free from anthropogenic pressures.

The project scope included the Marine Strategy Framework Directive (MSFD) predominant habitat type 'shallow sublittoral mixed sediment'. This definition includes those habitats which fall into the EUNIS Level 4 classifications A5.43 Infralittoral Mixed Sediments and A5.44 Circalittoral Mixed Sediments, along with their constituent Level 5 biotopes which are relevant to UK waters. A species list of characterising fauna to be included within the scope of the models was identified using an iterative process to refine the full list of species found within the relevant Level 5 biotopes.

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

A model hierarchy was developed based on groups of fauna with similar species traits which aligned with previous sensitivity studies of ecological groups. A general model was produced to indicate the high level drivers, inputs, biological assemblages, ecosystem processes and outputs which occur in shallow sublittoral mixed sediment habitats. In addition to this, five detailed sub-models were produced. Each focussed on a particular functional group of fauna within the habitat: 'temporary or permanently attached epifauna', 'mobile epifauna, scavengers and predators', 'suspension and deposit feeding fauna', 'temporary or permanently attached surface dwelling or shallowly buried larger bivalves' and 'small mobile epifauna and tube dwelling crustaceans'. Each sub-model is accompanied by an associated confidence model which 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 within the models as a whole is generally high, reflecting the level of information gathered during the literature review.

Important drivers which 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, seabed mobility, suspended sediments, water chemistry and temperature and recruitment define and

influence the biological assemblages. In addition, the habitat sediment type plays an important factor in shaping the biology of the habitat.

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

Features within the models which are most useful for monitoring habitat status and change due to natural variation have been identified using the information gathered during the literature review, through interpretation of the models and through the application of expert judgement. Features within the models which may be useful for monitoring to identify anthropogenic causes of change within the ecosystem have also been identified. Physical and biological features of the ecosystem have mostly been identified as potential indicators to monitor natural variation, whilst physical features and output processes have predominantly been identified as most likely to indicate change due to anthropogenic pressures.

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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 tools for identifying the state of marine biodiversity and habitats. When a change in state occurs, these tools allow users to identify possible manageable causes.

An indicator is a measurable factor that can be either qualified or quantified, which may be used to monitor the status of an ecosystem (e.g. Noon & McKelvey 2006). Indicators can be related to any aspect of the marine environment, are typically straightforward to monitor, and allow the robust assessment of status and enable change within marine ecosystems to be identified. Indicators may include species, communities, habitats, or other biological properties, as well as physical or chemical properties of the environment.

It is well known that 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 current knowledge about the links in marine ecosystems to be drawn together in a diagrammatic way to highlight the ecological aspects of marine ecosystems that are important for monitoring (e.g. Gross 2003; Manley *et al* 2000; Maddox *et al* 1999). CEMs have been utilised for various purposes, including to facilitate understanding of the processes which occur in sensitive ecosystems (e.g. Wingard & Lorenz 2014) and to examine the role of invasive species in restored ecosystems (Doren *et al* 2009).

This project is focused on producing a series of CEMs for the marine habitat 'Shallow Sublittoral Mixed Sediments', following development of CEMs for the habitats 'Shallow Sublittoral Coarse Sediment' (Alexander *et al* 2014), 'Shallow Sublittoral Mud' (Coates *et al* 2015) and 'Sublittoral Rock' (Alexander *et al* 2015). It is envisioned that CEMs will be produced for a selection of habitat types defined under the UK Marine Biodiversity Monitoring R&D Programme (UKMBMP). The models produced under this project will demonstrate the ecological components and processes which occur across spatial and temporal scales within non-anthropogenic impacted ecosystems (control models). These, which along with stressor models designed to show the interactions within impacted habitats (outside the scope of this project), will form the basis of a robust method of indicator selection.

1.1 Habitat Background

The Marine Strategy Framework Directive (MSFD) predominant habitat type 'Shallow Sublittoral Mixed Sediment' is found within UK waters and has the potential to support a range of biodiversity. Sublittoral mixed sediment habitats are found in a range of environments, both inshore and offshore, in generally small-scale patches compared to other broadscale habitats. The habitat is characterised by mixed heterogeneous sediments, including muddy gravelly sands and also mosaics of cobbles and pebbles embedded in or lying upon sand, gravel or mud (EUNIS 2012; Connor *et al* 2004).

This project uses the UK Marine Habitat Classification (Connor *et al* 2004), as translated in EUNIS (European Nature Information System[1]), to provide a structure to the study. The shallow sublittoral mixed sediment habitat covers two biological zones at EUNIS Level 4: infralittoral (defined as those areas between the mean low water line and the maximum depth at which 1% light attenuation reaches the seabed) mixed sediments and circalittoral (defined as the zone between which 1% light attenuation reaches the seabed and the bottom of the wave base, 50-70m depth) mixed sediments (McBreen *et al* 2011; Cochrane *et al* 2010). The modelled distribution of EUNIS Level 4 biotopes which represent infralittoral and circalittoral mixed sediment habitats in the vicinity of the UK is shown in Figure 1.

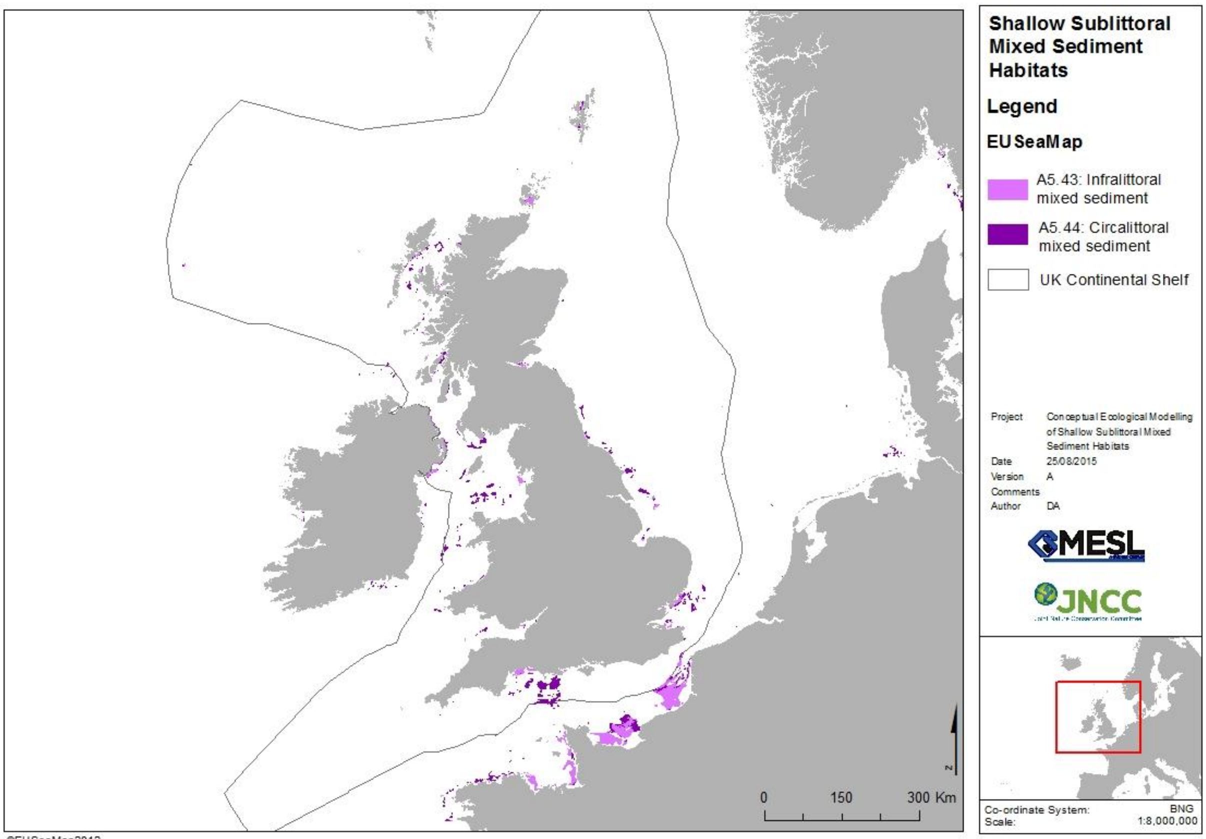

Figure 1. The modelled distribution of shallow sublittoral mixed sediment habitats around the UK, split by infralittoral and circalittoral zones. Data is taken from the EUSeaMap broad-scale modelled habitat mapping project[2]. Grey line represents the UK continental shelf boundary.

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

A5.43 (SS.SMX.Imx) - Infralittoral Mixed Sediment:

- **A5.431** (SS.SMX.IMx.CreAsAn) - *Crepidula fornicata* with ascidians and anemones on infralittoral coarse mixed sediment
- **A5.432** (SS.SMX.IMx.SpavSpAn) - *Sabella pavonina* with sponges and anemones on infralittoral mixed sediment
- **A5.433** (SS.SMX.IMx.VsenAsquAps) - *Venerupis senegalensis*, *Amphipholis squamata* and *Apseudes latreilli* in infralittoral mixed sediment
- **A5.434** (SS.SMX.IMx.Lim) - *Limaria hians* beds in tide-swept sublittoral muddy mixed sediment

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

- **A5.435** (SS.SMX.IMx.Ost) - *Ostrea edulis* beds on shallow sublittoral muddy mixed sediment

A5.44 (SS.SMX.CMx) - Circalittoral Mixed Sediments:

- **A5.441** (SS.SMX.CMx.ClloMx) - *Cerianthus lloydii* and other burrowing anemones in circalittoral muddy mixed sediment
- **A5.442** (SS.SMX.CMx.ClloModHo) - Sparse *Modiolus modiolus*, dense *Cerianthus lloydii* and burrowing holothurians on sheltered circalittoral stones and mixed sediment
- **A5.443** (SS.SMX.CMx.MysThyMx) - *Mysella bidentata* and *Thyasira* spp. in circalittoral muddy mixed sediment
- **A5.444** (SS.SMX.CMx.FluHyd) - *Flustra foliacea* and *Hydrallmania falcata* on tide-swept circalittoral mixed sediment
- **A5.445** (SS.SMX.CMx.OphMx) - *Ophiothrix fragilis* and/or *Ophiocomina nigra* brittlestar beds on sublittoral mixed sediment

1.2 Project Aims

The aim of this project is to produce a series of Conceptual Ecological Models (CEMs) to demonstrate the ecological links, drivers and ecosystem functions which occur in shallow sublittoral mixed sediment habitats. The models reflect the non-impacted state of the ecosystem (exclusive of anthropogenic influence) and will act as control models indicative of the natural state and 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 mixed sediment habitats, along with associated confidence and knowledge gap analyses.
2. Create a hierarchical set of control models to represent shallow sublittoral mixed sediment habitats and relevant subsystems.
3. Produce a list of key ecological aspects of the habitat which would be most useful for monitoring habitat status and change due to natural variation.
4. Describe how the driving influences and output processes of the habitat are likely to respond to pressures and identify those which may be useful for monitoring to identify anthropogenic causes of change.

2 Literature Review

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

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

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

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

2.1 Species Selection

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

An initial review of all taxa associated with the project biotopes yielded a list of 143 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 (adapted from the methodology developed in Alexander *et al* 2014 and Tillin & Tyler-Walters 2014):

- **Title species**: Fauna named in biotope title, e.g. *Cerianthus lloydii, Ophiothrix fragilis etc.*
- **Description species**: Species identified as particularly characterising in the biotope descriptive text but not included within the biotope title.

In some biotopes a faunal group is named in the title as opposed to a specific species. Alexander *et al* (2014) also selected example taxa from the full species list to represent groups named in the biotope titles. In this project the following species were selected:

- *Leptopentacta elongata* to represent burrowing holothurians
- *Urticina felina* to represent anemones
- *Amphilectus fucorum* to represent sponges

Alternative methods of reducing the list, e.g. grouping fauna by major taxonomic group or using a higher taxonomic classification, were ruled out due to the potential loss of critical

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

information on relevant ecosystem processes and/or functions, and the likelihood that species level information is required for effective results. The methodology used was modified from that presented in Alexander *et al* (2014) due to the differing complexity of biotopes between sediment habitats.

The Excel Add-In TREx (Taxonomic Routines for Excel) was used to check taxonomic information (spelling and name changes) about the species selected. TREx was also used to identify any species of conservation importance or alien species to the UK, which was followed up by a manual check. The results of this indicated that three species (*Crepidula fornicata*, *Monocorophium sextonae* and *Styela clava*) are regarded as alien species in the UK, and three species are listed under conservation designations; *Echinus esculentus* is listed as 'near threatened' on the IUCN Red List[5], *Ostrea edulis* is OSPAR listed and is a priority species under the UK Post-2010 Biodiversity Framework, and *Phymatolithon calcareum* is listed under Annex II of the EC Habitats Directive and is a priority species under the UK Post-2010 Biodiversity Framework.

Expert judgement was applied to the list of species to remove certain taxonomically similar taxa which are likely to perform very similar ecosystem functions, or those which were likely to have limited spatial distribution. A rationale for the species excluded and included in the project is presented as part of Worksheet 3b (Sublittoral Mixed Sediment CEM Literature Review and Ancillary Information Spreadsheet) which accompanies this report.

Species listed under conservation designations were automatically included in the final species list for the project with the exception of *Phymatolithon calcareum*. *Phymatolithon calcareum,* otherwise known as maerl, is a coralline red algae which has the ability to form large beds which may support a diverse array of taxa. However, for the biotopes under consideration as part of this project, *Phymatolithon calcareum* forms a minor part of only biotope A5.443 (*Mysella bidentata* and *Thyasira* spp. in circalittoral muddy mixed sediment), and is specifically listed as not occurring in maerl bed form. This species was therefore excluded from the project species list, as it was thought not to be wholly representative of shallow sublittoral mixed sediment habitats. Its inclusion in the project species list also has the potential to skew the models as the surrounding literature is likely to solely focus on maerl beds, and their ecological function.

A revised list of 56 benthic species to be considered within the immediate scope of the project was taken forward for review in the literature, as shown in the accompanying 'Species Selection' worksheet and in Appendix 1.

2.2 Species Traits Selection

Species traits are an essential consideration within the CEM, impacting the ecosystem functions and feedback loops within the habitat. A comprehensive list of biological traits was collated from the MarLIN Biological Traits Information Catalogue (BIOTIC) database (MarLIN 2006) and further supplemented with other traits considered to be important by the project team for informing the models. This resulted in a list of 47 species traits which was further refined based on other comparable studies (e.g. Bolam *et al* 2014; Tillin & Tyler-Walters 2014; Van der Linden *et al* 2012) and through expert opinion to give a manageable list of 23 relevant traits for inclusion in the project. The list of 23 traits is shown in the data logging spreadsheet (Worksheet 4, Trait Selection), including a short justification for the inclusion of each trait.

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

2.3 Literature Gathering

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

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

A 'grey literature' search (i.e. non peer-reviewed literature, such as articles, theses, technical reports, agency publications *etc*.) was also undertaken following the same process as that for peer-reviewed information. The grey literature search was conducted using the Google and Google Scholar search engines and Government agency websites (such as JNCC, Natural England, Cefas, MarLIN, *etc*.).

Sources relating to information from the UK were prioritised. 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 below.

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

- *Apseudes latreillii*is now known as *Apseudopsis latreillii*
- *Corophium sextonae* is now known as *Monocorophium sextonae*
- *Esperiopsis fucorum* is now known as *Amphilectus fucorum*
- *Mysella bidentata* is now known as *Kurtiella bidentata*
- *Pomatoceros triqueter* is now known as *Spirobranchus triqueter*
- *Venerupis senegalensis* is now known as *Venerupis corrugata*
- *Philine aperta* in the UK is now known as *Philine quadripartita*

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 revised to reflect the most up to date nomenclature, thus some species names used in this project may differ to those listed in the biotope descriptions.

2.4 Data Logging Pro-forma

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

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

- **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).
- **Full species List**: Full list of species present in the constituent shallow sublittoral mixed sediment biotopes, including a description of whether any of the species is listed under any conservation designation and whether the species listed are known by any other names.
- **Species Selection**: A representation of the process followed to identify species from the full list which should be included in the project scope, as described in Section 2.1. A rationale for species exclusion is provided.
- **Trait Selection**: Species traits identified for inclusion in the project, as described in Section 2.2.
- **Faunal Traits Matrix**: Trait information for each of the selected species. Data was entered in such a way with one row in the spreadsheet representing information gathered from one particular source per taxon, thus there are multiple lines per characterising taxon. The reference code of each source is included at the end of each row.
- **Faunal Traits Summary**: Summary of the level of information gathered for each species, used to inform the gap analysis.
- **Interactions Matrix**: Information collated on relevant environmental drivers, ecosystem functions and ecosystem processes relevant to the project habitat. Information on relevant interactions was built up by reviewing the referenced information to establish a list of topics for research. Each piece of information contains metadata on the focus aspect (the model level the information informs), the specific model component the information relates to (temperature, bioturbation, *etc*.), and the final model links that the information will inform. Details on the source limitations (used to inform confidence), as well as the direction and magnitude of the interaction (based on expert opinion and the referenced information) are also included.
- **Reference Summary**: Source information, full reference, abstract, summary of relevant material extracted and source confidence. Each reference was given a unique code used to identify the source throughout all sheets.
- **Confidence Assessment**: A representation of the confidence assessment used in the project, as described in Section 2.5.
- **Definitions**: Definitions of key project terms.

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

2.4.1 Magnitude and Direction of Influence

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

Table 1. Assessment of direction of interaction (Alexander *et al* 2014).

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

Table 2. Assessment of magnitude of interaction (Alexander *et al* 2014).

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

2.5 Literature Review Confidence Assessment

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

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

Confidence in the individual sources gathered as part of the literature feeds into confidence in the resulting models produced by this project. Confidence in the models and the methodology applied is described in Section 4.2.

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

Individual Source Confidence	Quality Requirement
High	Peer reviewed Or grey literature reports by established agencies
Medium	Does not fulfil 'high' confidence requirement but methods used to ascertain the influence of a parameter on the habitat / biotope are fully described in the literature to a suitable level of detail, and are considered fit for purpose Or expert opinion where feature described is a well known/obvious pathway

Low	Does not fulfil ‘medium’ requirement for level of detail and fitness for purpose but methods used to ascertain the influence of a parameter on the habitat/biotope are described Or no methods adopted and informed through expert judgement

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

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

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

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

3 Summary of Literature Review

Over 220 peer-reviewed and grey literature sources were reviewed as part of this project. The information gathered during the literature review is detailed and summarised in the accompanying data logging pro forma spreadsheet. Specific evidence on ecosystem interactions or species traits which inform the models is presented and discussed throughout Section 5.

The majority of biological traits information was obtained from peer-reviewed and grey literature (such as the MarLIN BIOTIC database) and from taxonomic identification books and keys. Information obtained from journals was predominantly research that had been carried out internationally from comparable temperate regions, but in most cases can still be applied to UK species. Larger faunal species such as *Asterias rubens*, *Abra alba*, *Ostrea edulis*, *Urticina felina* and *Amphiura filiformis* were well researched. Fewer sources were available for poorly studied or smaller species such as the cumacean *Eudorella truncatula*, *Apseudopsis latreillii* and *Calyptraea chinensis.*

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 mixed 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 identified sources relating to environmental drivers were overarching papers that did not relate to a specific location or range. Preference was given to sources describing ecosystem function in shallow sublittoral mixed 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 the constituent parts of the mixed sediment biotopes; e.g. muddy sandy gravel), using comparable taxa likely to perform the same functions, and from comparable global locations. This has been reflected in the 'limitations in evidence' column in the data logging spreadsheet (worksheet 'Interactions Matrix') 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 literature review undertaken as part of this project is intended to be an iterative process, and was designed so that it can easily be updated in the future.

3.1 Knowledge Gap Assessment

Overall a high level of information has been gathered to date in order to inform the project as part of the literature review. 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 feeding method, mobility/movement and size are complete for all taxa covered by the project. Less information was sourced for more complex aspects such as species connectivity to other habitats/species, physiographic preference and whether a taxon is likely to have a naturally highly variable population. In some cases, expert opinion has been used to infill trait information, as indicated in the 'Faunal Traits Summary' tab. Expert opinion carries a lower confidence score (see Table 3a).

Information gathered on the ecosystem interactions which occur in sublittoral mixed sediment habitats were divided into seven levels: 1) Regional to global drivers, 2) Water column processes, 3) Local processes at the seabed, 4) Habitat and biological assemblage, 5) Output processes, 6) Local ecosystem functions and 7) Regional to Global Ecosystem Functions. The information is incorporated into the confidence assessments associated with each of the models produced by this project.
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 informed by expert judgement.

4 Model Development

4.1 Model Design

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

4.1.1 Model Hierarchy

General Model

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

Sub-Models

The sub-models will show a greater level of detail around specific ecological aspects of the shallow sublittoral mixed sediment habitat and aim to inform the selection of monitoring aspects at a meaningful ecological scale.

Functional groups of the shallow sublittoral mixed sediment habitat were identified for the key characterising species selected for each habitat type. The identification of these groups drew heavily upon the ecological groups described by Tillin and Tyler-Walters (2014). Tillin and Tyler-Walters described ten ecological groups based upon the characterising species of 33 sublittoral sedimentary biotopes. The ecological groups were distinguished by using both biological traits and habitat preferences, supported by ordination and clustering analyses. In some instances, expert judgement was applied where analyses did not place species into discrete clusters.

Two ecological groups described by Tillin and Tyler-Walters (2014) were not included as part of the sub-models as no key characterising species from the sublittoral mixed sediment habitat biotopes belonged to these groups: ‘Predatory polychaetes’ and ‘Burrowing hard bodied species’.

Based on the study carried out by Tillin and Tyler-Walters (2014), eight of the ten ecological groups were used to categorise the selected species into broad functional groups of the sublittoral mixed sediment habitat. These will represented be represented in 5 sub-models, as indicated in Figure 2. The ecological groups that have been attributed to each sub model are shown in Table 4.

Ecological group 8 (Echinoderms, split into sub-groups 8a-8d) forms a separate group in the study by Tillin and Tyler-Walters, however for the purposes of this study echinoderm species have been placed in each of the relevant other ecological groups. This is due to the diverse nature of the Echinodermata, the differing ecosystem input and output processes that affect the range of species considered by the project, and the large amount of information which would need to be presented if all echinoderms were shown in a separate model.

The group ‘very small to small, short lived (<2 years) free-living species defined on size and feeding type’ defined by Tillin and Tyler-Walters (2014) has been adapted to include a broader range of species for the study and to minimise the number of models produced. Sub-model 5 is thus referred to as ‘Small, Short-lived Crustaceans and Interface Suspension/Deposit Feeding Fauna’, which the original ecological groups form a part of at the major functional group level.

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.

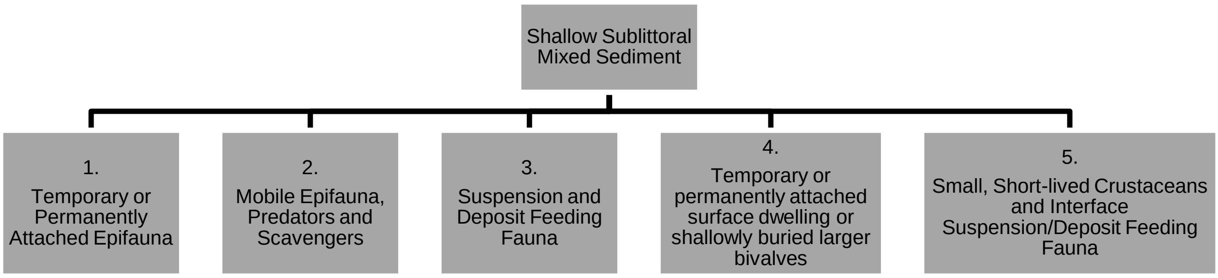

Figure 2. Shallow sublittoral mixed sediment habitat CEM hierarchy. The top level of the flowchart represents the general control model, with the five sub-models each documenting a specific functional group within this habitat.

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

Ecological Groups described by Tillin and Tyler-Walters (2014)	CEM Sub-Model
Group 1: Temporary or permanently attached epifauna, including sub-groups 1(b) Erect, shorter lived epifaunal species, 1(c) Soft bodied or flexible epifaunal species and 1(d) Small epifaunal species with robust, hard or protected bodies.	1. Temporary or Permanently Attached Epifauna
Group 3: Mobile epifauna, mobile predators and scavengers	2. Mobile Epifauna, Predators and Scavengers
Group 4: Infaunal very small to medium sized suspension and/or deposit feeding bivalves	3. Suspension and Deposit Feeding Fauna
Group 5: Small-medium suspension and/or deposit feeding polychaetes	
Group 10: Burrowing soft bodied species	
Group 2: Temporary or permanently attached surface dwelling or shallowly buried larger bivalves	4. Temporary or Permanently Attached Surface Dwelling or Shallowly Buried Larger Bivalves
Group 7. Very small to small, short lived (<2 years) free-living species defined on size and feeding type	5. Small, Short-lived Crustaceans and Interface Suspension/Deposit Feeding Fauna
Group 8(c). Free living interface suspension/deposit feeders	

Following the approach developed by Alexander *et al* (2014), the ecological groups which have been allocated to each sub-model (Table 4) will be investigated and presented separately by introducing different subdivisions into the sub-model relating to either feeding activity or taxonomic classification (Appendix 3).

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

4.1.2 Model Levels

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

Driving Influences:

- **1. Regional to Global Drivers** – high level influencing inputs to the habitat which drive processes and shape the habitat at a large-scale, e.g. water currents, climate etc. These are largely physical drivers which impact on the water column profile.
- **2. Water Column Processes –** processes and inputs within the water column which 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 which directly influence the characterising fauna of the habitat, e.g. food resources, recruitment *etc*.

Defining Habitat:

- **4. Habitat and Biological Assemblage** – the characterising fauna and sediment type(s) which typifies the habitat. For the sub-models, fauna are 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, please see Appendix 3.

Outputs:

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

4.1.3 Model Components

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

Table 5. Descriptions of the components which form various levels of the models. Note that for the general model some parameters have been grouped together to facilitate presentation and to summarise the key processes which occur within the habitat. Also note that not all parameters may be shown on all models due to the variability of the fauna represented.

ECOSYSTEM DRIVERS	
1. Regional to Global Drivers	
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
Geology	Underlying rock or substratum
Propagule Supply	Supply of larvae, spores and/or regenerative body fragments
2. Water Column Processes	
Water Chemistry & Temperature	The chemical and physical characteristics and composition of the water column. This parameter is inclusive of salinity, nutrients, chemicals in the water column and water temperature. Dissolved oxygen is included in this parameter.
Primary Production	The production of new organic substances through photosynthesis
Light Attenuation	The penetration of light in the water column
Suspended Sediment	Particles of sediment which have become elevated from the seabed and kept suspended by turbulence within the water column
3. Local Processes/Inputs at the Seabed	
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
- Living fauna	Live prey items such as bivalves, polychaetes or small fish
- Macro/micro algae	Plants and algae attached to the seabed
- Carrion	Dead and decaying animal flesh
- Bacteria & micro-organisms	Microbial and micro-organisms (e.g. bacteria, diatoms and protozoa)
Seabed Mobility	Movement of sediment on the seabed
Recruitment	The process by which juvenile organisms join the adult population. Combines settlement and early mortality
4. Habitat and Biological Assemblage	
Temporary or permanently attached epifauna	Erect, soft-bodied or flexible epifauna together with robust epifaunal crusts
Mobile Epifauna, Predators and scavengers	Mobile scavenging and predatory crustaceans, echinoderms and gastropods
Suspension and deposit feeding fauna	Suspension and deposit feeding fauna which includes burrowing or tube-dwelling soft-bodies species, polychaetes and bivalves, in addition to surface dwelling polychaetes
Attached surface dwelling or shallowly buried bivalves	Larger bivalves either permanently or temporarily attached to the seabed or shallowly buried
small, short-lived crustaceans and interface suspension/deposit feeding fauna	Small, short-lived, free-living (inhabit the sediment surface and are unattached to the seabed) fauna, crustaceans which dwell in semi-permanent tube structures, and mobile echinoderms and gastropods.

ECOSYSTEM OUTPUTS	
5. Output Processes	
Secondary Production	Creation of biomass as a direct result of consumption
Bioengineering	Faunal modification of the natural habitat, e.g. tube building, boring organisms, algal canopy *etc*.
Bioturbation	Sediment re-working by marine fauna
Hydrodynamic Flow	Changes to water flow/movement as a result of organism activity
Biodeposition	The process by which organisms either deposit material onto the seabed, e.g. through the capture of particulate matter in the water column through filter feeding or the production of faeces/pseudo-faeces
Supply of Propagules	The production and transportation of larvae, spores or body fragments capable of regeneration
6. Local Ecosystem Functions	
Nutrient Cycling	Cycling of organic and inorganic nutrients that involves processing into a different chemical form
Biogeochemical Cycling	The cycling of organic carbon and nitrogen into different chemical forms
Food Resources	The provision of food resources for other organisms
Population Control	Control of lower trophic level organism population through predation
Sediment Stability	Cohesion of sediments into a stable form more resistant to disturbance
Habitat Provision	Provision of living space for other organisms through surface attachment of increased habitat complexity
Microbial Activity Enhancement	Enhanced growth and activity of microbial organisms (e.g. bacteria, diatoms and protozoa) within the sediment
7. Regional to Global Ecosystem Functions	
Export of Biodiversity	Export of biodiversity, including propagules, outside of the habitat
Export of Organic Matter	Export of organic material outside of the habitat, such as food sources etc.
Biodiversity Enhancement	Enhancements in biodiversity within the habitat resulting from increased sediment stability and habitat provision
Biotope Stability	Stability of the habitat through the habitat provision and increased sediment stability (including carbon sequestration)

4.1.4 Model Interactions

The models produced for this project follow the methodology and approach adopted in Alexander *et al* (2014). Each model component listed above is linked to one or more other components at either the same model level or a different level, using an arrow that is formatted according to the type of interaction.

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

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

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

In order to differentiate between driving factors 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.

4.1.5 Natural Variability

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

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

In common with Alexander *et al* (2014), natural variability is assigned a score of 1-3 where 1 represents low variability (small circle symbol on models), 2 medium variability (medium circle symbol on models) and 3 high variability (large circle symbol on models). 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. As each of the sub-models is a component of the same broad-scale habitat the main physical environmental drivers and water column processes which affect each model are highly similar. Food sources are a major source of input variation in the models, and are defined by the functional group being addressed. The fauna/flora covered in each model characterises the output processes, and in turn the ecosystem functions at the local to global scales.

4.2 Model Confidence

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

The combined confidence for the interactions from multiple sources is scored in accordance with the protocol presented in Table 6 and is based on the combined confidence methodology developed in Alexander *et al* (2014). 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 (Alexander *et al* 2014).

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

Table 6. Combined confidence assessment of relationship between CEM components (Alexander *et al* 2014).

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 6. No associated confidence model has been produced for the general model due to the difficulties of presenting conflicting confidence assessments for several functional groups summarised into one model.

4.3 Model Limitations

The conceptual models developed for this project have been created for the specific habitats and selected species identified only. As a result, not every existing link within the ecosystem is presented; links are shown if they are regarded as potentially important for habitat monitoring purposes. Supporting evidence exists or expert opinion can sufficiently inform these links. Some minor links and those with no substantial evidence (below low confidence) are not presented.

Models presented in this report are based only upon the selected species (Appendix 1 & Worksheet 3b in the accompanying spreadsheet). Other species (and functional groups) may be present within the relevant habitat biotopes which are subject to alternative influences and produce different ecosystem functions.

Changes in nomenclature and taxonomic classification have occurred since the biotope classifications were published (as detailed in Section 2.3). The models presented utilise the currently accepted scientific names for all species, thus species names may differ from those presented in the biotope descriptions (Connor *et al* 2004).

Confidence in the models is influenced by the extent of the literature review, time and budgetary constraints of the project.

5 Model Results

The completed models can be found in Appendices 4-9. 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 which accompanies this report for details of the physical parameters which define the habitat and each constituent biotope.

For each sub-model, the biological assemblage is described, followed by the ecosystem drivers and ecosystem functions. The biological assemblage is the defining element of each sub-model and explains the variation between sub-models. Ecosystem drivers and functions are described in a logical and pragmatic way, so that those which are linked are defined in turn, rather than described by model level.

Each sub-model can be interpreted independently. The magnitude of links in the models can be assessed between models. Information presented under each model heading is tied to the confidence assessments presented in Section 6 and the confidence models presented in Appendices 9-12. References for the information discussed are shown where literature sources have been found to back up the statements being made.

5.1 General Control Model and Common Model Components

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

The general model provides information on the large scale environmental drivers which affect the ecosystem, all of which are common to each sub-model. The output processes and resulting ecosystem functions at both the local and regional/global scale have been summarised in the general model to some extent for the purposes of presentation.

General information common to all the sub-models is discussed in the context of this section, and is not repeated under each specific sub-model heading, unless there is specific variance or a feature of interest which is particularly relevant to that model (such as local processes/inputs at the seabed, food sources, *etc*.).

5.1.1 Ecosystem drivers

Regional to Global Drivers

The majority of ecosystem drivers defined for the shallow sublittoral mixed sediment habitat relate to the physical environment in the general model, especially at the regional to global scale. Several of the drivers are critical in defining the nature of the habitat itself (such as depth), whereas others are crucial in shaping the subsequent faunal complement and resulting output processes (such as water currents). All of the regional to global drivers detailed below are of high relevance to infralittoral habitats and all but wave exposure are of high relevance to circalittoral habitats.

- **Depth** is a key defining factor of the shallow sublittoral mixed sediment biotopes being considered in this project, through separation of infralittoral and circalittoral biotopes and its influence on other critical drivers (Basford *et al* 1990; Cusson &

Bourget 2005; Eriksson & Bergstrom 2005; Bolam *et al* 2010). Increasing depth has a negative influence on key water column processes, significantly affecting light attenuation (Devlin *et al* 2008), temperature (Munn 2004) and sediment oxygen uptake (Middelburg & Soetaert 2004). Depth is therefore one of the major defining factors of the shallow sublittoral mixed sediment habitat, with a high relevance in both the circalittoral and infralittoral zones (Basford *et al* 1990).

- **Wave exposure**, driven by water depth, also has a major influence on the habitat (Connor *et al* 2004; Brown *et al* 2002a). 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 (Masselink & Hughes 2003; Brown *et al* 2002a). Wave exposure is a crucial factor defined in the biotope classifications (see 'Habitat Characterisation' spreadsheet for biotope-specific details) and varies for shallow sublittoral mixed sediment habitats from 'exposed' to 'extremely sheltered' (Connor *et al* 2004). The greater the wave exposure, the greater the physical stresses in the environment, and therefore organisms are likely to need a greater degree of adaptation to thrive there. Increased wave exposure also generally enhances the resuspension and sorting of sediments, increasing the concentration of suspended sediment in the water column and affecting the seabed mobility (Masselink & Hughes 2003; Brown *et al* 2002a). Wave exposure can also have an influence on the water column chemistry, temperature and dissolved oxygen availability by increasing mixing activity (Brown 2002b; Diaz & Rosenberg 1995). A moderate natural variability is defined for wave exposure, based on meteorological conditions including seasonal variation, cyclical fluctuations and the frequency of extreme events. For example, severe autumn storms can increase the impact of wave exposure, mixing of the water column and breakdown of summer thermoclines in deeper waters (Diaz & Rosenberg 1995).

- **Water currents** are defined to include both current mediated flow and tides (Reiss *et al* 2009). Currents provide a mechanism for transport of particulate matter, sediments, and components of the water chemistry and temperature profile, as well as supplying energy to the seabed (Hiscock *et al* 2004), affecting seabed mobility (Brown *et al* 2002a). The transport mechanism supplies food resources for filter feeding organisms, propagules and influences water column chemistry and temperature through mixing (Hiscock *et al* 2004; Biles *et al* 2003; Chamberlain *et al* 2001). Water circulation distributes dissolved oxygen in the water column and transfers oxygen from the surface to the seabed (Diaz & Rosenberg 1995). Bottom water currents interact with the sediment topography, creating a pressure driven advective pore water flow which transports dissolved oxygen and particulate matter through the interstitial spaces of mixed sediments (Ehrenhauss & Huettel 2004). These pore water flows enhance the nutrient efflux, oxygen penetration and consumption in mixed sediments. Although water currents do vary naturally in magnitude and direction through the seasons and annually (both tidal and non-tidal flows), natural variability is low in comparison to other components.

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

- **Propagule supply** is a major driver at the regional to global scale, and the only biological regional to global ecosystem driver. Connectivity between 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 composition of the biological assemblages. In turn this recruitment is driven by propagules from reproductively active organisms in this habitat or from other habitats, completing the feedback loop. It is also likely that the supply of propagules acts as a source of food and nutrients for some species. Propagule supply has high natural variability as it is dependent on a large number of different physical and biological factors. Temperature is an important environmental factor affecting the planktonic larval duration and development (Brennand *et al* 2010), while water currents mainly facilitate the distribution of larvae (Hiscock *et al* 2004; Qian 1999). Not all impacting factors relating to propagule supply have been shown on the models in an effort to minimise unnecessary complexity (see Siegel *et al* 2008 for a review).

- **Geology** is an environmental driver at the regional to global scale as it forms the physical basis of the benthic habitat. The morphology of the seabed together with the physical properties of bed rock and post-glacial drift material have an influence on sediment type, deposition and suspended sediment levels in the shallow sublittoral mixed sediment habitat. Of particular importance in the mixed sediment habitat are likely to be external (allocthonous) sediments transported and deposited from other habitats.

Water Column Processes

At the second model level (water column processes), four components link the regional/ global drivers to local inputs at the seabed. All of the water column processes detailed below are of high relevance to infralittoral habitats and suspended sediments and water chemistry and temperature are of high relevance to circalittoral habitats.

- **Primary production** by phytoplankton is a crucial base to the biological aspects of the habitat, and a key driver of prey sources (Hiscock *et al* 2006). The shallow infralittoral zone is where primary production predominantly occurs (Jones *et al* 2000). Primary production is a nutrient (water chemistry) and light dependent process (Devlin *et al* 2009; Hiscock *et al* 2006). As the top of the circalittoral zone is defined as receiving 1% light attenuation (Connor *et al* 2004) primary production is very low within this zone (Lalli & Parsons 2006). Water chemistry (nutrients) and temperature also influences primary production, as necessary factors for photosynthesis (Hiscock *et al* 2006; Lalli & Parsons 2006; Hily 1991).

- **Water chemistry and temperature** are large components which incorporate several features grouped together for ease of presentation. Properties include salinity, temperature, nutrients and dissolved organic material, along with dissolved oxygen. These may be influenced by many regional to global drivers; however wave exposure, depth, water currents, climate and primary production are shown on the model as particularly important due to direct influences on marine fauna (e.g. Dutertre *et al* 2012; Brown *et al* 2002b). Dissolved oxygen is an important feature of marine habitats and an integral part of water chemistry. However is not shown as a separate entity on the models for ease of presentation. Dissolved oxygen is not thought to be as important in mixed sediment substrates as it would be for muddy or sandy habitat, where the potential presence of anoxic conditions is a major driving force affecting benthic fauna.

Photosynthesis is the most important source of dissolved oxygen in the marine environment, while wave and wind exposure facilitate the uptake of dissolved oxygen from the atmosphere and mixing into the water column (Brown *et al* 2002b). In addition to primary production, water chemistry and temperature link to biological components such as food sources and the biological assemblage of the habitat, based on the need of organisms for dissolved components in the water column (nutrients, calcium carbonate *etc*.) and specific temperature requirements (Bolam *et al* 2010; Cusson & Bourget 2005). A feedback loop from nutrient and biogeochemical cycling (local ecosystem functions) to water chemistry signifies the re-supply of organic chemicals to the water column (Libes 1992). Water chemistry, temperature and dissolved oxygen have a moderate natural variability, based on environmental drivers and the potential for seasonal and long term changes.

- **Light attenuation** is another important factor of the shallow sublittoral mixed sediment habitat, driven principally by depth and suspended sediments in the water column (Devlin *et al* 2009; Masselink & Hughes 2003; Brown *et al* 2002a). Light attenuation links to primary production (as described above) as well as directly to the fauna and flora of the habitat.

- **Suspended sediments** are mainly influenced by wave exposure, water currents and to a lesser degree geology (Brown *et al* 2002b). Suspended sediments can directly affect light attenuation through increased turbidity of the water column, as well as some benthic species which require a supply of suspended sediments in order to build their protective tubes (this link is not shown on the general model and is explored further in sub-model 3). An increased suspension of fine sediments can influence suspension feeding infauna by clogging the filter-feeding mechanisms (Bilotta & Brazier 2008; Rhoads & Young 1970).

Local Processes and Inputs at the Seabed

Local processes and inputs at the seabed directly structure the physical and biological character of the habitat at a local scale.

- **Food sources** are a key driving factor for biological communities. Due to the diverse nature of fauna which inhabit shallow sublittoral mixed sediment habitats, there are a considerable number of specific food resources which need to be considered in the models.

  Phytoplankton are a significant source of food resources, and as primary producers, are significantly influenced by water chemistry and temperature (including nutrient availability) and light attenuation (e.g. Hiscock *et al* 2006; Lalli & Parsons 2006; Jones *et al* 2000; Hily 1991). 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 (Lalli & Parsons 2006; Jones *et al* 2000; Hily 1991; Eppley 1972). Phytoplankton is likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make this food source 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 2000) although it will also be influenced by other factors including reproduction of benthic and epibenthic fauna (producing propagules and larvae in the water column), particulate organic matter (POM) and water chemistry and temperature (dissolved oxygen in particular) (Lalli & Parsons 2006; Levinton 2001; Nybakken 2001). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006). As POM is derived from organic sources, including plankton, it is an important food source in both the infralittoral and circalittoral zones (MarLIN 2006; Lalli & Parsons 2006; Nybakken 2001).

Other important food sources in the models include POM, detritus, living prey and carrion. Detritus and POM in the marine environment is influenced by a number of factors, including the abundance of marine organisms and microbial activity (Lalli & Parsons 2006; Nybakken 2001; Brown *et al* 2002a).

- **Seabed mobility** is a proxy for the extent the habitat is affected by natural physical disturbance. Environments with high seabed mobility are likely to be characterised by fauna tolerant to mobile sediments and sediment movement. Fauna which require more stable sediments, such as burrowing bivalves, some tube dwelling fauna and sessile epifauna are not likely to flourish in highly mobile environments due to the potential for smothering and feeding difficulties. Filter feeding fauna, which strain 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 (Lalli & Parsons 2006; Masselink & Hughes 2003; Nybakken 2001).

- **Sediment type** is one of the key drivers influencing infaunal communities at the habitat level (Cooper *et al* 2011; Middelburg & Soetaert 2004; Ellingsen 2002; Seiderer & Newell 1999; Basford *et al* 1990). Sediment grain size directly influences the biological assemblage as many functional ecological groups have specific niche sediment requirements. In muddier mixed sediment habitats deposit feeders attain higher densities in comparison to suspension feeders, as the resuspension of fine sediments is stressful for suspension feeders due to the clogging of filtering structures (Rhoads & Young 1970). The mineralisation of organic matter will decrease with decreasing grain size due to lower oxygen and organic matter penetration depths into the sediment (Coates *et al* 2014; Ehrenhauss & Huettel 2004). An important adaptation of the infauna is the ability to burrow into the substrate or to create tubes which facilitates the transportation of oxygen into deeper sediment layers, resulting in increased oxygenation of the sub-surface habitat (Nybakken 2001).

- **Sediment type** is influenced by multiple factors, including wave exposure, water currents, underlying geology, seabed mobility and to some extent the fauna itself (Brown *et al* 2002a). The underlying geology may be an important driver of sediment type, however many sediment deposits found in UK waters are likely to be the product of Pleistocene (or similar) drifts (Limpenny *et al* 2011; Tappin *et al* 2011). This is especially likely to be the case for mixed sediment habitats where multiple sediment types are found in one area. Surface sediments may therefore be unconsolidated and could be prone to movement or winnowing (Masselink & Hughes 2003). Should this occur on a large scale, the underlying geology may be vastly different to the surface sediments.

All of these factors combined influence the biological component of the habitat, either directly or indirectly, across varying scales.

5.1.2 Ecosystem Outputs

Output Processes

The output processes described in this section are those which are generic to shallow sublittoral mixed sediment habitats. As output processes and ecosystem functions are heavily influenced by the characterising fauna of each habitat, the sub-models should be referred to for specific interactions (and references) related to one particular functional group.

Output processes from shallow sublittoral mixed sediment habitats can be broadly split into four main categories: secondary production, sediment processing, habitat modification and supply of propagules. These are sometimes described as ecosystem services, but for the purpose of this project are described as processes, as this study is not focussed on the supply of services that have direct value to humans.

- **Secondary production** (defined as converting energy to/from lower to higher trophic levels) is a core process undertaken by all fauna as growth and consumption of other lower trophic level organisms occurs (Lalli & Parsons 2006). This is a key feature of the conceptual ecological models and a key output process which in turn drives important ecosystem functions at the local scale, such as provision of food resources and nutrient cycling (Lalli & Parsons 2006; Nybakken 2001), and leads indirectly to the export of organic matter and the export of biodiversity at the wider scale. This is a major influencing factor in increasing food and prey availability within the habitat.

- **Sediment processing** refers to biological reworking of sediments, and incorporates actions such as biodeposition and bioturbation which have been grouped together for presentation in the general model. Biodeposition is a prominent process occurring in the shallow sublittoral mixed sediment habitat and largely refers to the capture of particulate matter in the water column by filter feeders and the transfer of this material to the benthic habitat; however it also refers to the production of faeces and pseudo-faeces. Biodeposition therefore influences nutrient cycling, and impacts biogeochemical cycling. Wave exposure and water currents are likely to impact the dispersal of material amassed through biodeposition, especially so in hard substrata biotopes. This link has not however been indicated on the general model in order to facilitate presentation. Bioturbation is another prominent process in the shallow sublittoral mixed sediment habitat, in common with most other habitat types which contain at least some soft sediment substrates. Bioturbation is purely driven by faunal actions, and has the potential to influence biogeochemical cycling and have a negative effect on sediment stability, in addition to a positive effect of oxygenating sediments.

- **Habitat modification** is defined as the biological modification of the natural environment, through processes such as tube or reef building, or the creation of permanent burrows. Habitat modification may lead to increased sediment stability, the provision of habitat for other organisms and potentially enhanced microbial activity.

- **Supply of propagules** is the product of reproduction and transport by water currents, which feeds back to recruitment at the input level. The supply of propagules is imperative for the continuation of the habitat and is essential for the maintenance of the shallow sublittoral mixed sediment biotopes and any other habitats connected to them.

Local Ecosystem Functions

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 in shallow sublittoral mixed sediment habitats by the representative fauna through the uptake of nutrients, decay and secondary production (Mermillod-Blondin 2011; Norling *et al* 2007a). These cycles are heavily influenced by bioturbation and biodeposition (Mermillod-Blondin 2011; Norling *et al* 2007b; Kristensen 2000; Probert 1984) and are also undertaken in part by microbial activity, which may be enhanced in the tubes and burrows of certain taxa (Kristensen *et al* 2012; Mermillod-Blondin 2011). 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 into deeper sediment layers, encouraging chemical exchange within the sediments and increasing the rates of nutrient and biogeochemical cycling in sediments (Kristensen *et al* 2012).

- **Sediment stability** is likely to be affected by the output processes of sediment processing and habitat modification. Consolidation of sediments by fauna is achieved in several ways, such as tube building, compacting sediment, mucus lining when burrowing or through biodeposition (Woodin *et al* 2010; Ziervogel & Forster 2006; Probert 1984). It should be noted however that sediment processing also has the potential to negatively affect sediment stability through reworking activities which destabilise the sedimentary environment (Meadows *et al* 2012), and in addition is likely to lead to sediment re-suspension, especially in higher energy environments, feeding back to suspended sediments at the input level.

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

- **Production of food resources** is represented as an ecosystem function, influenced by secondary production. This occurs through the creation of biomass by direct predation of other fauna by organisms of higher trophic levels. Through the export of food resources from the habitat, this also has the potential to influence regional to global ecosystem functions, as indicated on the model.

- **Population control** is closely related to the provision of food resources as an ecosystem function. A function performed by predatory fauna, population control is an important factor in finely balanced sublittoral sediment habitats, and is important in maintaining biotope stability.

Regional to Global Ecosystem Functions

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

5.1.3 Connectivity to other habitats

Connectivity to other habitats is a key part of the marine ecosystem (Connor *et al* 2004), although it is difficult to represent within the conceptual models. Principally this is because connectivity varies at spatial and temporal scales which have not been elucidated, or are difficult to represent generically.

Other habitat types may be found in close proximity to shallow sublittoral mixed sediment habitats. As mixed sediment habitats comprise a range of different substrate types, any habitats containing similar substrates to the project biotopes (gravels, sands or muds) located nearby are likely to be intrinsically linked. In terms of ecosystem drivers, connectivity is important for certain aspects of the models such as supply of propagules, nutrient cycling, temperature and food resources. All components are likely to be affected to some degree by adjacent habitat types, depending on the spatial scales involved.

Connectivity to other habitats is also a factor to be considered at the ecosystem function level. Several of the identified regional to global ecosystem functions concern the export of matter or biodiversity from the shallow sublittoral mixed 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.

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

5.2 Sub-model 1. Temporary or Permanently Attached Epifauna

5.2.1 Biological assemblage

The attached epifauna sub-model contains those fauna which are, at least for some part of their life cycle, fixed to the seabed. The group is described in Tillin and Tyler-Walters (2014) and is further broken down into three ecological groups:

- Erect, shorter lived epifauna
    - Hydrozoans e.g. *Hydrallmania falcata, Nemertesia antennina*
- Soft-bodied or flexible epifauna
    - Bryozoans e.g. *Flustra foliacea*
    - Soft corals e.g. *Alcyonium digitatum*
    - Sponges e.g. *Halichondria bowerbanki*
    - Ascidians e.g. *Ascidiella aspersa, Styela clava*
    - Anemones e.g. *Urticina felina, Cerianthus lloydii*
- Robust epifauna
    - Crustaceans e.g. *Balanus crenatus*
    - Polychaetes e.g. *Spirobranchus triqueter*

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

The fauna which constitute this model are found in both the infralittoral and circalittoral zones, and are typically suspension feeders, straining food particles from the water column. Anemones are the main exception to this and may be either suspension feeders (*Cerianthus lloydii*) or predators (*Urticina felina*).

5.2.2 Ecosystem Drivers

Several key environmental drivers are likely to be of large influence to attached epifauna in addition to those described for the general model. Other features common to all models may still be of high influence to shallow sublittoral mixed sediment habitats, however have been discussed under the context of the general model to avoid repetition of descriptions.

- **Water currents** are regarded as crucial for the supply of food resources to attached epifauna. As sessile filter feeders, the fauna represented within this model are reliant on transport of food resources suspended within the water column. Active filter feeders are able to create their own water flow to ensure the passage of suspended food items past feeding mechanisms, however a supply of food sources within the water column is a necessary starting point.

- **Food sources** are an important driver for temporary or permanently attached epifauna. Predominant food types for attached epifauna mainly consist of plankton (both phytoplankton and zooplankton) and particulate organic matter (POM), although anemones also consume detritus and living fauna (Porter 2012; MarLIN 2006; Hayward *et al* 1996; Hily 1991; Hancock 1956).

- **Seabed mobility** is also a key factor which will likely influence epibenthic fauna. High seabed sediment mobility is likely to prevent widespread colonisation of the seabed by all but the most adapted fauna, and may prohibit the development of encrusting fauna which require stable sediments for attachment.

- **Propagule supply** is an important biological driver of the attached epifauna sub-model. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN 2006); this suggests that connectivity to other habitats nearby could be an important aspect of the recruitment process. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop. Near-bed current flows, together with active larval substratum selection affect the settlement of faunal larvae and form one of the main controlling factors in determining where this functional group can establish itself (Qian 1999).

Other physical factors which affect the distribution of organisms include wave exposure, depth and climate (e.g. Lalli & Parsons 2006; Nybakken 2001).

5.2.3 Ecosystem Outputs

Attached epifauna support several important ecosystem functions, notably secondary production, biodeposition, bioengineering and habitat provision.

- **Secondary production** is a key process occurring within the shallow sublittoral mixed 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 (Lalli & Parsons 2006; Nybakken 2001) and is a major influencing factor in increasing food and prey availability within the habitat. Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale.

- **Biodeposition** is another output process performed by the attached epifauna, resulting from the capture of food matter from the water column and the transfer of energy from the pelagic to the benthic environment (Nybakken 2001). Sponges, anemones and hydroids are noted as especially important in transferring energy from pelagic to benthic ecosystems (Daly *et al* 2008; Bell 2008; Levinton 2001; Gili *et al* 1997), although all filter feeders play some role in transferring energy to the benthos from the water column and releasing metabolites, waste, gametes, and offspring back into the water column (Levinton 2001). Biodeposition influences nutrient and biogeochemical cycling within the sediments (Kristensen *et al* 2012; Libes 1992) by contributing to the sediment organic matter content (Pillay & Branch 2011). These processes are linked to the export of organic matter at a wider scale and to water column chemistry via a feedback loop.

- **Bioengineering** is undertaken by species included within the attached epifauna sub-model. Principally this is through the growth of prominent features and large body sizes which impact the marine environment. Erect epifauna and soft-bodied or flexible epifauna are prominent bioengineers and their presence is likely to influence ecosystem functions. Significant ecosystem functions resulting from bioengineering include habitat provision, influence on biogeochemical cycling, influence on hydrodynamic flow and impacts on sediment stability (Porter 2012; Bell 2008). Sponges are noted as particularly prevalent bioengineers, potentially impacting near-bed hydrodynamic flow in dense upright sponge patches (Bell 2008), increasing sediment and habitat stability through the stabilisation and consolidation of sediments (Bell 2008) and providing habitat for other benthic organisms (Bell 2008; MarLIN 2006). Reduced hydrodynamic flow through bioengineering or the presence of large bodied attached epifaunal species is also likely to increase sediment stability though the lowering of bed shear stress (Friedrichs 2009).

- **Habitat provision** is a local ecosystem function performed by sponges, hydroids, bryozoans and other attached epibenthic fauna. These species have been shown to act as microhabitats for a range of other species and have been shown to increase bacterial biomass within the ecosystem (Bell 2008). Actiniaria are likewise noted to be providers of habitat to other organisms (Vader 1984). In turn, this can lead to increased habitat stability and biodiversity enhancement across larger spatial scales. These output processes and local ecosystem functions in turn can lead to increased habitat stability and biodiversity enhancement across larger spatial scales.

- **As a food resource**, ascidians and Actiniaria are of limited importance, although sponges are known to be consumed by a range of organisms including fish, molluscs, crustaceans and echinoderms (Bell 2008). Hydroids and bryozoans may also be consumed by some fauna, including opisthobranch molluscs.

- **Supply of propagules**, in common with other models, is a key output process. A large proportion of the attached epifauna relevant to this CEM have planktotrophic larvae (MarLIN 2006); this indicates that connectivity to other habitats is likely to be important. Supply of propagules as an output process links back to recruitment as an input feature, and also links to the export of biodiversity at the regional to global scale.

Attached epifauna provide four regional to global ecosystem functions which are based on the output processes and local ecosystem functions in the model; the export of organic matter, the export of biodiversity, biodiversity enhancement and increased biotope stability.

5.3 Sub-model 2. Mobile Epifauna, Predators and Scavengers

5.3.1 Biological assemblage

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

- Crustaceans e.g. *Cancer pagurus, Pagurus bernhardus, Necora puber*
- Echinoderms e.g. *Asterias rubens, Luidia ciliaris*
- Gastropods e.g. *Philine quadripartita, Buccinum undatum*

Scavenging and predatory fauna typically have a high degree of mobility and a large body size. They are regarded as important secondary producers and play a role in population control in the shallow sublittoral mixed sediment environment. Fauna from this group are found in both the infralittoral and circalittoral zones.

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

5.3.2 Ecosystem Drivers

Several key environmental drivers are likely to be of significant importance to mobile epifauna, predators and scavengers, in addition to those described for the general model. Other features common to all models may still be of high influence to shallow sublittoral mixed sediment habitats, however have been discussed under the context of the general model to avoid repetition of descriptions.

- **Physical drivers** which influence species distribution include wave exposure, depth, water currents and climate (Aguera *et al* 2012; Lalli & Parsons 2006; Nybakken 2001).

- **Food sources** of scavengers and predatory epifauna include carrion and living fauna (Naylor 2011; MarLIN 2006; Evans *et al* 1996; Allen 1983). These sources of food can be the product of other functional groups found within the habitat, indicated by the feedback loop in the model. Detritus and macro/micro algae are also noted as food sources for some omnivorous species of crab (MarLIN 2006; Ingle 1996), especially *Necora puber* and *Liocarcinus depurator* in the absence of abundant prey items (Naylor 2011). Numerous factors affect the presence of detritus and macro/micro algae in the marine environment (e.g. Hiscock *et al* 2006; Lalli & Parsons 2006; Brown *et al* 2002a; Nybakken 2001; Jones *et al* 2000; Hily 1991). As these food sources are a minor part of the diet of predatory and scavenging fauna, all of the links for these influences are not shown on the model.

- **Seabed mobility** is likely to have a small driving impact on predators and scavenging fauna as most species are likely to be highly adaptable to physical disturbance given their greater mobility compared to other fauna which cannot reposition within, or on, sediments (Kaiser *et al* 1998).

- **Sediment type** is expected to have a smaller influence on this sub-model than other sub-models considered in this project as the species have a wide range of substratum preferences (Basford 1990). This however is highly variable between species and their distribution is likely to be indirectly linked to sediment type. For example, the hermit crab *Pagurus bernhardus* will appear in substrates ranging from large boulders to fine sand while the gastropod *Philine quadripartita* is limited to muddy mixed sediments (MarLIN 2006).

- **Propagule supply** is an important biological driver of predatory and scavenging fauna. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN 2006) suggesting that connectivity to other habitats nearby could be an important aspect of the recruitment process. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

5.3.3 Ecosystem Outputs

Several important ecosystem functions are performed by mobile epifauna, predators and scavengers.

- **Secondary production** is a key process occurring within the shallow sublittoral mixed 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 (Lalli & Parsons 2006; Nybakken 2001), 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.

- **Population control** is an ecosystem function performed as a consequence of secondary production, whereby predatory fauna act as top-down controllers of lower trophic level fauna (Nybakken 2001). This has the potential to negatively influence biodiversity enhancement within the mixed sediment biotopes, but also contributes towards biotope stability by maintaining population dynamics through balancing predator-prey relationships.

- **Biodeposition** is another key output process performed by predators and scavengers. Biodeposition (principally through the capture of prey resources from the water column and the production of faeces) modifies the nutrient and biogeochemical cycling of the sediments (Kristensen *et al* 2012; Libes 1992) by contributing to the sediment organic matter content (Pillay & Branch 2011). These processes are linked to the export of organic matter at a wider scale and to water column chemistry through a feedback loop.

- **Bioturbation** is a moderately important process performed by predatory and scavenging crabs in the shallow sublittoral mixed sediment habitat (Vopel 2003; Schratzberger & Warwick 1999; Ambrose 1993), mainly through ploughing activities related to their feeding behaviour or by physically burrowing. The bioturbation activity increases the potential for biogeochemical cycling and enables smaller organisms (e.g. nematodes) to penetrate to deeper layers of the sediment (Reise 2002; Schratzberger & Warwick 1999). However, excessive bioturbation can have a destabilising effect on the sediment (Ciutat *et al* 2006).

- **Habitat provision** is a minor ecosystem function afforded by some species within the shallow sublittoral mixed sediment habitat, principally by species such as the hermit crab *Pagurus bernhardus* and the whelk *Buccinum undatum*. These species offer additional habitat provision to symbionts and epibiota through their protective shells (Pretterebner *et al* 2012), enhancing the biodiversity at regional to global ecosystem levels.

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

Scavengers and predatory fauna provide four regional to global ecosystem functions which are based on the output processes and local ecosystem functions in the model; the export of organic matter, the export of biodiversity, biodiversity enhancement and increased biotope stability.

5.4 Sub-model 3. Suspension and Deposit Feeding Fauna

5.4.1 Biological assemblage

The suspension and deposit feeding fauna sub-model is a large group which represents fauna in the shallow sublittoral mixed sediment habitat that are deposit or suspension feeders or can switch between these two feeding methods. Species presented in this group are not permanently attached to the seabed (as those in sub-model 1), although some taxa may form tube structures for part of their adult life. The group is described in Tillin and Tyler-Walters (2014) and can be split into three main functional groups as follows:

- Burrowing soft-bodied species
  - Holothurians e.g. *Leptopentacta elongata*
- Infaunal suspension and/or deposit feeding bivalves
  - Burrowing bivalves e.g. *Abra alba, Kurtiella bidentata, Venerupis corrugata*
- Suspension and/or deposit feeding polychaetes
  - Burrowing or burrow dwelling polychaetes e.g. *Scoloplos armiger, Mediomastus fragilis*
  - Surface dwelling polychaetes e.g. *Prionospio fallax*
  - Tube building polychaetes e.g. *Lanice conchilega, Sabella pavonina*

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

Suspension or filter feeders separate particulate organic matter and plankton from the water column while deposit feeders will typically consume detritus and organic matter from the surrounding sediment.

This group also represents species that are mainly characterised by their bioengineering potential in the sediment. The fauna are typically positioned at the sediment-water interface, live within a burrow system, or construct robust tubes made from sediment particles.

5.4.2 Ecosystem Drivers

Several key environmental drivers are likely to be of significant importance to suspension and deposit feeding fauna. Other features common to all models may still be of high influence to shallow sublittoral mixed sediment habitats, however have been discussed under the context of the general model to avoid repetition of descriptions.

- **Food sources** are an important driver of suspension and deposit feeding fauna. The species represented within this model are either suspension feeders which capture plankton and particulate organic matter from the water column, or detritivores feeding on organic material contained in the seabed sediments (EUNIS 2014; Naylor 2011; MarLIN 2006; Mattson & Cedhagen 1989).

- **Physical environmental drivers** are likely to be of significant importance to suspension and deposit feeding fauna, as detailed for the general control model. Physical factors which affect the distribution of organisms include wave exposure, depth, water currents and climate (e.g. Lalli & Parsons 2006; Nybakken 2001). Water currents, as specified above, are particularly important for the supply of food resources.

- **Seabed mobility** is a large driver for this model. High levels of sediment mobility could 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. High seabed mobility may also disrupt the activity of burrowing fauna and prohibit the flow of water through burrows.

- **Suspended sediments** link directly to tube building fauna in the model, as some fauna acquire a degree of suspended sediment from the water column to construct their protective tubes. Conversely, some tube building fauna are known to select sediment particles from the seabed itself and do not rely on suspended particles (Noffke *et al* 2009). That said, suspended sediments are a factor in tube construction, as indicated by the link on the model. High concentrations of fine suspended sediments can however have a negative influence on the filter-feeding mechanisms of suspension feeding infauna (Bilotta & Brazier 2008; Rhoads & Young 1970).

- **Propagule supply** is an important biological driver of suspension and deposit feeding infauna. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN 2006) suggesting that connectivity to other habitats nearby could be an important aspect of the recruitment process. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop. Near-bed current flows can affect the settlement of larvae (especially larvae of tube building species). Water currents form an important factor in determining where this functional group can establish itself in a certain area together with the active larval substrate selection (Qian 1999). Relatively strong hydrodynamics can reduce larval settlement due to the erosion of larvae from the seabed (Coates *et al* 2013; Qian 1999).

5.4.3 Ecosystem Outputs

Secondary production, biodeposition, bioturbation and bioengineering are the major output processes performed by suspension and deposit feeding fauna in the shallow sublittoral mixed sediment habitat.

- **Secondary production** is an important output process performed by suspension and deposit feeding fauna, which consume primary producers and organic material, and in turn serve as an important food resource for multiple other organisms such as fish, crustaceans, molluscs and polychaetes (MarLIN 2006; Levinton 2001; Jones *et al* 2000; Francour 1997; Fauchald & Jumars 1979). Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale.

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

- **Bioturbation** is another key output process performed by the fauna represented in this sub-model, and indeed these species represent the greatest bioturbators considered in the shallow sublittoral mixed sediment habitat due to their position within the sediments and their burrowing activity. Each of the sub-functional groups represented in the model engage to some degree in bioturbation (Quieros *et al* 2013) either through the shallow burrowing and ploughing activities related to their feeding activity or through the physical construction of burrows and tubes. This reworking and overturning of the sediment leads to the bioirrigation of sediments, increasing the potential for nutrient and biogeochemical cycling (Kristensen *et al* 2012; Pillay & Branch 2011), which in its turn stimulates bacterial growth rates and microbial decomposition processes (Probert 1984). In turn, these processes can lead to increases in biodiversity enhancement and biotope maintenance across larger spatial scales. The active sediment reworking and bioturbation potential of tube-building polychaetes is limited as most species, once settled, live in fixed tubes restricting them to movements within their tubes (Quieros *et al* 2013). Both the building of tubes and body movements within them (e.g. feeding activity) enhance the biogeochemical fluxes in sublittoral mixed sediment habitats, transporting oxygen and organic matter to deeper sediment layers (Rigolet *et al* 2014; Braeckman *et al* 2010) and creating a feedback loop to water chemistry, temperature and dissolved oxygen. Bioturbation is linked with mainly positive ecosystem functions (Mermillod-Blondin *et al* 2011; Bertics *et al* 2010; Norling *et al* 2007a), however excessive bioturbation can destabilise sediments and increase the erosion potential by increasing the re-suspension of fine surficial sediments (Meadows *et al* 2012; Woodin *et al* 2010; Paterson & Black 1999).

- **Bioengineering** through the construction of (semi-) permanent burrows or sedimentary tubes is a major output processes in this sub-model, performed by tube building polychaetes and burrowing polychaetes and bivalves (MarLIN 2006; Levinton 2001). The complexity of burrows varies from species to species, but most burrows contain two entrances through which an influx of oxygen rich water is pumped into the burrow by the organism and an efflux of dissolved nutrients and prey filtered out (Reise 2002; Nybakken 2001). These micro-habitats within the sediments serve several functions above those directly benefiting the host organism, including the provision of a habitat for associated organisms, increasing sediment stability through the creation of compacted or mucus lined sediment tunnels which increase shear stress resistance of sediments and restrict lateral inflow of water in the burrows (Eca *et al* 2013; Grove *et al* 2000; Probert 1984). These stable environments can provide an extended and protected platform for biogeochemical cycling bacteria to colonise along the burrow walls (Eca *et al* 2013; Meadows *et al* 2012; Papaspyrou *et* *al* 2005; Munn 2004), allowing greater oxygen penetration into the seabed (Lalli & Parsons 2006; Levinton 2001; Nybakken 2001). 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 increased habitat stability, biotope maintenance and biodiversity enhancement across larger spatial scales.

- **Habitat provision** is a resulting ecosystem function which is influenced by habitat modification and creation of sedimentary tubes. The tubes enhance the habitat provision for other organisms increasing the colonisation of both macro- and meiofaunal species (Rigolet *et al* 2014; Eca *et al* 2013; Larson *et al* 2009; Bolam & Fernandes 2003; Zulkhe 2001; Grove *et al* 2000; Dobbs & Scholly 1986) and by providing a refuge to species which are otherwise highly susceptible to predation (Rigolet *et al* 2014; Larson *et al* 2009). Tube-building fauna create a positive feedback loop from bioengineering to recruitment by providing a settlement surface for larval and post-larval benthic organisms (Qian 1999) and by creating a favourable and sheltered environment for the larval settlement of many benthic species (Bolam & Fernandes 2003).

- **Microbial activity** is also enhanced by bioengineering as tube-builders create favourable conditions for microbes in and around their tubes (Passarelli *et al* 2012), increasing the biogeochemical cycling of nutrients and oxygen in the shallow sublittoral mixed sediment habitat (Meadows *et al* 2012). Microbes can then add sediment stability by increasing the adhesion between sediment particles (Probert 1984).

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

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

Suspension and deposit feeding fauna provide four regional to global ecosystem functions which are based on the output processes and local ecosystem functions in the model; the export of organic, the export of biodiversity, biodiversity enhancement and increased biotope stability.

5.5 Sub-model 4. Temporary or Permanently Attached Surface Dwelling or Shallowly Buried Larger Bivalves

5.5.1 Biological assemblage

The attached surface dwelling bivalves sub-model is distinct among the sub-models produced for this project in that it only comprises one major functional group.

The bivalves considered in this model include the king scallop *Pecten maximus*, the European oyster *Ostrea edulis*, the horse mussel *Modiolus modiolus* and the flame shell *Limaria hians*. These species may either exist as solitary individuals or as dense aggregations on the seabed (sometimes referred to as reefs) and produce a number of key output processes and ecosystem functions. Representatives of this group are generally attached to (or intrinsically linked to) the seabed, are principally suspension feeders and are found in a range of biotopes across both the infralittoral and circalittoral zones.

A full species list of the selected taxa which comprise this model, and a breakdown of the biotopes they represent are presented in Appendix 3.

5.5.2 Ecosystem Drivers

Attached surface dwelling or shallowly buried larger bivalves inhabit the surface sediments of the identified biotopes, and are thus subject to physical environmental drivers. Other features common to all models may still be of high influence to shallow sublittoral mixed sediment habitats, however have been discussed under the context of the general model to avoid repetition of descriptions.

- **Physical factors** which affect the distribution of organisms include wave exposure, depth, water currents, water chemistry and climate (e.g. Howarth *et al* 2015; Lalli & Parsons 2006; Lesser & Kruse 2004; Christophersen & Strand 2003; Chauvaud *et al* 2001; Nybakken 2001; Cano *et al* 1997; Pazos *et al* 1997). Water currents are deemed particularly important for the supply of food resources (MarLIN 2006; Trigg 1999; Pazos *et al* 1997).

- **Food sources** are an important driver of large bivalves. The species included in this model are typically suspension feeders which capture plankton, POM, detritus and bacteria and microorganisms from the water column.

- **Seabed mobility** is a large driver for this model. High levels of sediment mobility will likely disrupt surface dwelling bivalves which require relatively stable environments to prosper, especially those which are not able to re-adjust after a disturbance (*Ostrea edulis, Modiolus modiolus* and, to a lesser extent, *Limaria hians*). This is likely to be at least in part influenced by a feedback loop from the sediment stabilising ecosystem function performed by the bivalves themselves. Suspended sediment concentration is also likely to be an influencing factor on the fauna represented in this model. Elevated levels of fine sediments in the water column are known to potentially clog the filter-feeding mechanisms of suspension feeding fauna (Bilotta & Brazier 2008; Rhoads & Young 1970), and deposition may lead to smothering of organisms. Finally, sediment type may be a crucial factor in defining the benthic assemblage, as several species included in this sub-model are likely to need coarse substrate on the seabed to which to attach their byssus threads.

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

5.5.3 Ecosystem Outputs

Temporary or permanently attached surface dwelling or shallowly buried larger bivalves support several important ecosystem functions, notably secondary production, biodeposition and bioengineering.

- **Secondary production** is a key process occurring within the shallow sublittoral mixed 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 (Lalli & Parsons 2006; Nybakken 2001), and is a major influencing factor in increasing food and prey availability within the habitat. Through filter feeding, bivalves have been shown to have a top-down control on the abundance of suspended food resources in the water column (plankton and POM), which may affect food resources for other organisms (Meadows 2012; Saravia 2011; Gosling 2003).

  Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale.

- **Biodeposition** is performed by filter feeding bivalves, which trap particulate matter from the water column and deposit this onto the seabed via the production of faeces or pseudo-faeces (Saravia 2011). This facilitates the transfer of energy from the pelagic to the benthic environment (Nybakken 2001), therefore transferring energy to the benthos from the water column and releasing metabolites, waste, gametes, and offspring back into the water column (Daly *et al* 2008; Levinton 2001). This process contributes to nutrient and biogeochemical cycling in the habitat (Navarro 1997; Korringa 1946). Aggregations of *Ostrea edulis*, *Modiolus modiolus* and *Limaria hians* are noted as particularly important in influencing nitrogen and biogeochemical cycles (Trigg 1999; Navarro 1997; Dame 1985; Korringa 1946).

- **Bioengineering** is another considerable output process performed by the fauna represented in this sub-model. Attached bivalves such as *Ostrea edulis, Modiolus modiolus and Limaria hians* can form large aggregations which modify the natural habitat and lead to numerous ecosystem functions, principally habitat provision.

- **Sediment stability** is increased by the binding of individuals and sediment by byssus threads, sediments are consolidated and stability is increased (Meadows 2012; Trigg 2011; Friedrichs 2009; Hall-Spencer 2000; Trigg 1999). This in turn leads to potential biodiversity enhancement within the habitat and biotope stability at the wider scale by providing increased habitat complexity and stability, which other fauna may colonise (Thurstan *et al* 2013; Trigg 1999, 2011; Korringa 1946). *Limaria hians* and *Ostrea edulis* in particular are noted to have a positive effect on habitat structure and habitat complexity (Thurstan *et al* 2013; Hall-Spencer & Moore 2000), influences on nutrient and biogeochemical cycling, current flow and sediment deposition (Lenihan 1999).

- **Habitat provision** is a key function of attached bivalves, providing shelter and a potential food supply to other organisms (Thurstan *et al* 2013). The presence of a single attached bivalve individual has been shown to increase species richness and biomass in the local habitat (Norling & Kautsky 2008). Habitat provision is also afforded through the shells of individual organisms, providing a settlement space for other organisms and algae (Smyth & Roberts 2010; Ross 1965; Korringa 1946).

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

Attached surface dwelling or larger bivalves provide four regional to global ecosystem functions which are based on the output processes and local ecosystem functions in the model; the export of organic matter through nutrient cycling; the export of biodiversity through secondary production and the supply of propagules; biodiversity enhancement through habitat provision and increased sediment stability; and increased biotope stability through the provision of habitat and increased sediment stability.

5.6 Sub-model 5. Small, Short-Lived Crustaceans and Interface Suspension/Deposit Feeding Fauna

5.6.1 Biological assemblage

The small, short-lived crustaceans and interface suspension/deposit feeding fauna sub-model represents those species which live on the surface of the sediment, are not attached to the seabed (with the exception of amphipod tubes), and are classed as non-predatory. The ecological group is described in Tillin and Tyler-Walters (2014) and has been split into two main functional groups:

- Small short-lived crustaceans
    - Cumaceans e.g. *Eudorella truncatula*
    - Amphipods e.g. *Maera grossimana*
    - Tube-dwelling amphipods e.g. *Ampelisca tenuicornis, Monocorophium sextonae*
    - Tanaids e.g. *Apseudopsis latreillii*
- Mobile surface dwelling suspension/deposit feeders
    - Urchins e.g. *Psammechinus miliaris, Echinus esculentus*
    - Brittlestars e.g. *Amphipholis squamata, Ophiothrix fragilis*
    - Gastropods e.g. *Crepidula fornicata, Calyptraea chinensis*

A full species list of the selected taxa which constitute these functional groups, and a breakdown of the biotopes they represent are presented in Appendix 3. The fauna in this model are found in a range of biotopes across both the infralittoral and circalittoral zones and are generally characterised by their mobile nature.

5.6.2 Ecosystem Drivers

Physical environmental drivers are likely to be of significant importance to short-lived crustaceans and interface suspension/deposit feeding fauna, as detailed for the general control model. Other features common to all models may still be of high influence to shallow sublittoral mixed sediment habitats, however have been discussed under the context of the general model to avoid repetition of descriptions.

- **Physical factors** which affect the distribution of organisms include wave exposure, depth, water chemistry, water currents and climate (e.g. Lalli & Parsons 2006; Nybakken 2001; Corbera & Cardell 1995; McGee & Targett 1989).

- **Supply of food resources** is a principal driving factor for small mobile fauna. Primary food sources for short-lived crustaceans and interface suspension/deposit feeding fauna mainly consist of particulate organic matter and detritus. Fauna are typically detritivores or grazers, although some fauna are suspension feeders, and others feed upon macro/microalgae or small living prey in the water column (MarLIN 2006). Numerous factors affect the availability of food resources, including water currents primary production, water chemistry and temperature (Hiscock *et al* 2006; Lalli & Parsons 2006; Jones *et al* 2000; Hily 1991). Macro/microalgae is likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make this food source of limited importance at the top of the circalittoral zone (Hily 1991).

- **Seabed mobility** is likely to have a small driving impact on small mobile fauna as most species are likely to be highly adaptable to physical disturbance given their greater mobility compared to other fauna which cannot reposition within, or on, sediments (Kaiser *et al* 1998). Tube-dwelling amphipods however are likely to be heavily influenced by seabed mobility, and likely require stable sediments in which to construct their tubes.

- **Sediment type** is expected to have a moderate influence on this sub-model as the species have a wide range of substratum preferences (Basford 1990); however this is highly variable between species and their distribution is likely to be indirectly linked to sediment type. Tube dwelling amphipods are likely to require specific sediment types in order to form their protective semi-permanent tubes.

- **Propagule supply** is an important biological driver of small, mobile fauna and tube dwelling crustaceans. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN 2006) suggesting that connectivity to other habitats nearby could be an important aspect of the recruitment process. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

5.6.3 Ecosystem Outputs

Small short-lived crustaceans and interface suspension/deposit feeding fauna support several important ecosystem functions, notably secondary production, biodeposition, bioturbation, bioengineering and habitat provision.

- **Secondary production** is an important function performed by small crustaceans and interface dwelling fauna which consume primary producers and organic material, and in turn serving as an important food resource for many other organisms such as fish, crustaceans, molluscs and polychaetes (MarLIN 2006; Levinton 2001; Jones *et al* 2000; Francour 1997; Corbera & Cardell 1995). Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale. As some organisms serve as a food source within this model, a feedback loop exists from food resources up to the local processes level (MarLIN 2006; Pechenik *et al* 2001, 2004; Jones *et al* 2000).

- **Biodeposition** is likely to be an important process as part of this sub-model through the activity of suspension feeders (brittlestars and amphipods) which strain food particles from the water column and subsequently excrete waste material (Rigolet *et al* 2014; Dauvin 2013; Levinton 2001; Nybakken 2001; Hughes 1998; Davoult & Gounin 1995). Other species which are regarded as deposit feeders or grazers are also likely to be important through the production of faeces and pseudo-faeces. The non-native *Crepidula fornicata* in particular is noted as an important biodepositer (Wallentinus & Nyberg 2007). Biodeposition modifies the nutrient and biogeochemical cycling of the sediments (Kristensen *et al* 2012; Libes 1992) by contributing to the sediment organic matter content (Pillay & Branch 2011; Martin *et al* 2006). These processes are linked to the export of organic matter at a wider scale and to water column chemistry through a feedback loop.

- **Bioturbation** is an output process of the small crustaceans and interface suspension/deposit feeding fauna sub-model which occurs through the physical shallow burrowing and ploughing activities which are related to the feeding activity of the fauna. Bioturbation by the species represented in this model is unlikely to compare to the levels of bioturbation exhibited by burrowing fauna, however their surficial modification activities are likely to contribute to this as an output process (Grant 1981). Bioturbation leads to the bioirrigation of sediments, increasing the potential for nutrient and biogeochemical cycling (Kristensen *et al* 2012; Pillay & Branch 2011), which in its turn stimulates bacterial growth rates and microbial decomposition processes (Probert 1984). In turn, these processes can lead to increases in biodiversity enhancement and biotope maintenance across larger spatial scales. Bioturbation is linked with mainly positive ecosystem functions (Mermillod-Blondin *et al* 2011; Bertics *et al* 2010; Norling *et al* 2007b), however excessive bioturbation can destabilise sediments and increase the erosion potential by increasing the re-suspension of fine surficial sediments (Meadows *et al* 2012; Woodin *et al* 2010; Paterson & Black 1999).

- **Bioengineering** is another output process. The fauna represented in this model include amphipods that will modify the habitat through the construction of semi-permanent burrows or sedimentary tubes (MarLIN 2006; Levinton 2001). The amphipod *Ampelisca tenuicornis* constructs mats which enable them to form dense aggregations. Through construction of these mats, amphipods will enhance the habitat provision for other organisms (Rigolet *et al* 2014) and aid sediment stability (Probert 1984). Burrow dwellers and tube-builders also create favourable conditions for the microbial activity in the surrounding environment (Passarelli *et al* 2012), increasing the biogeochemical cycling of nutrients and oxygen in the sediment (Meadows *et al* 2012).

- **Habitat provision**, whilst enhanced through bioengineering of some species represented in this sub-model, is also shown to be negatively influenced through the presence of other benthic species. High abundances of the invasive gastropod *Crepidula fornicata* have been shown to have a negative effect on the abundance of native species, particularly epibenthic taxa (Le Pape *et al* 2004; Vallet *et al* 2001; de Montaudouin *et al* 1999). This is linked to the dense aggregations that *Crepidula fornicata* can form, reducing habitat availability for other taxa, and reducing the proportion of soft substrate in the habitat (Vallet *et al* 2004). This reduction in habitat availability is likely to have knock-on effects on the enhancement of biodiversity and biotope stability.

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

Small, short-lived crustaceans and interface suspension/deposit feeding fauna provide four regional to global ecosystem functions which are based on the output processes and local ecosystem functions in the model; export of biodiversity through the supply of propagules and secondary production, export of organic matter through food resources and nutrient cycling, and biodiversity enhancement and biotope stability through the enhanced stabilisation of the sediment and habitat provision.

6 Confidence Assessment

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

In general, a high level of literature has been sourced to inform the models, thus confidence is relatively good 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 mixed sediment habitats in the future, the models can easily be updated.

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

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

Confidence was largely dependent on how well a particular functional group and its ecosystem functions had been studied. For example, macroalgae and attached fauna have a generally high confidence reflecting the large amount of literature and research that has been carried out on the related species and their importance within the ecosystem.

7 Monitoring habitat status and change due to natural variation

Using the information gathered during the literature review and presented in the models, the CEM components of shallow sublittoral mixed sediment habitats which are most useful for monitoring habitat status in the context of natural variation in the environment have been identified. Identification of these components will allow monitoring programmes to take account of how the habitat is varying naturally, so that any changes detected can be put within this context. These components have been identified through an assessment of interactions within the models and are presented in Table 7. Habitat components presented in Table 7 have been further refined into sub-components to indicate specific features of the shallow sublittoral mixed sediment habitat which could indicate status change due to natural variation.

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

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

The information presented in Table 7 is based 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 5.1.5). It must be recognised that the relative natural variability of components of biological assemblages is widely unknown, thus expert judgement has been applied. It is suggested that further research on the natural variability of model components may be useful to further inform indicator selection for monitoring purposes.

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

Table 7. Key components of shallow sublittoral mixed sediment habitats which would be most useful for monitoring habitat status and change due to natural variation.

Habitat Component	Habitat Sub-Component	Rationale	Confidence	Relevant Models
Seabed Mobility /Sediment Stability	Sediment consolidation	Seabed mobility has a strong influence over the benthic biological assemblage (Lalli & Parsons 2006; Masselink & Hughes 2003; Nybakken 2001) and is driven by other higher level factors which are subject to considerable seasonal variation. Increases in the mobility of the mobile fine sediments are likely to have considerable knock on effects on the fauna of the relevant biotopes, and ultimately several ecosystem functions which could reduce ecosystem outputs at local and wider scales. Sediment stability is a product of the ecological component of the shallow sublittoral mixed sediment habitat, influenced principally by bioengineering and bioturbation (Mermillod-Blondin *et al* 2011; Pillay & Branch 2011; Bertics *et al* 2010). Sediment stability is likely to have	High (supported by large amount of literature evidence)	All

		some degree of natural variation. An increase in bioengineering is likely to consolidate seabed sediments and increase stability e.g. (Pillay & Branch 2011). An increase in bioturbation is likely to reduce sediment stability (e.g. Norling *et al* 2007a). Sediment stability is thought to be a useful indicator to measure natural variation in the ecosystem through variations in these interrelated factors. Sediment stability has the potential to affect several other model components, including ecosystem functions at the regional/global scale, further indicating the usefulness of this component as an indicator for monitoring.		
Attached Epifauna	Abundance and diversity of attached epifauna	Attached epifauna are a key part of shallow sublittoral mixed sediment, and include erect epifauna, soft bodied or flexible epifauna, epifaunal crusts and attached surface dwelling or shallowly buried bivalves. The presence of these species is linked to suitable substrate to which the fauna can attach themselves, where this is sediment of a particular size or hard benthic features (e.g. Qian 1999). These fauna can therefore be considered unique to habitats which contain suitable substrates, such as shallow sublittoral mixed sediment biotopes. Natural variability in attached epifauna over time is likely to be relatively low in an unimpacted environment provided the driving influences remain unperturbed. At the output level, attached epifauna are major contributors to bioengineering and biodeposition (e.g. Thurstan *et al* 2013; Porter 2012; Saravia 2011; Bell 2008). Attached epifauna are therefore thought to be a good indicator group to represent natural variability, as variability in the main driving forces will be represented in the high level of output functions the group provides.	High (supported by large amount of literature evidence)	Sub-models 1 & 4
Burrow Dwelling Fauna	Abundance and diversity of burrow dwelling fauna	Burrow dwelling fauna play an important role in the shallow sublittoral mixed sediment habitat. They contribute to several output processes and ecosystem functions at varying scales. Burrowing fauna are influenced by a high number of driving factors, including seabed mobility, sediment type and other physical drivers (e.g. Lalli & Parsons 2006; Nybakken 2001). At the output level burrowing fauna are major contributors to bioturbation, bioengineering and biodeposition (e.g. Kristensen *et al* 2012; Pillay & Branch 2011; Quieros *et al* 2013; Reise 2002). Burrowing fauna are thought to be a good indicator group to represent natural variability, as variability in the main driving forces will be represented in the high level of output functions the group provides.	High (supported by large amount of literature evidence)	Sub-model 3
Bioengineering	Seabed rugosity	Bioengineering is performed by several ecological groups represented within the models (e.g. tube building polychaetes and crustaceans, temporary or permanently attached surface dwelling bivalves *etc*.). As an output process, bioengineering is predominantly influenced by the faunal assemblage of the habitat, thus variability in the	High (supported by large amount of literature evidence)	All

		drivers affecting the biology of the habitat is likely to affect bioengineering. As an output process, modification of the natural environment by fauna provides several key functions, namely habitat provision, increased sediment stability and ultimately biotope stability (e.g. Meadows *et al* 2012; Porter 2012; Friedrichs 2009; Dobbs & Scholly 1986). Bioengineering is thought to be a good indicator to assess natural variation within the shallow sublittoral mixed sediment habitat.		
Sediment Type	Sediment particle size distribution	Natural variation in sediment composition over time is likely to be relatively low, although it is known to occur (e.g. from studies of reference areas in proximity to aggregate extraction sites, e.g. Cooper *et al* 2011). Changes in sediment type would be particularly affected by changes in current flows and wave energy. Any alteration to sediment particle-size distribution may have a large impact on benthic fauna (Cooper *et al* 2011; Seiderer & Newell 1999; Basford *et al* 1990), 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 (in particular SM 3, SM 4 & SM 5)
Benthic Infauna (in particular burrowing soft bodied species & suspension /deposit feeding polychaetes)	Abundance and diversity of benthic infauna	Benthic infauna is a crucial part of the shallow sublittoral mixed sediment habitat; these species are influenced by numerous factors and perform several key functions within the habitat (MarLIN 2006). Infauna are considered to be useful 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. It may be pragmatic to select specific species from within the main functional group that could serve as indicators for specific habitats (those species listed in model/biotope matrix presented in Appendix 3).	Medium (informed by both expert judgement and literature evidence)	All (in particular SM 3 & SM 4)
Recruitment	Planktonic larvae production	Recruitment is a key biological factor which affects fauna related to shallow sublittoral mixed sediment habitats at a local scale. Despite the likely high natural variability of recruitment as a process (driven by supply of propagules and feedback loops), it is thought that this factor would be beneficial to monitor given its large influence over benthic faunal composition. In particular it is thought that monitoring of species which produce planktonic larvae would be the most susceptible to natural variation. Defining species to specifically monitor cannot be stated without further literature	Medium (largely informed by expert judgement)	All

		evidence, although some studies do exist which could be used to address this (e.g. Hiscock *et al* 2006).		

8 Monitoring components to identify anthropogenic causes of change

Table 8 presents key driving influences and output processes of the shallow sublittoral mixed 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 15. It should be noted that no consideration has been given to the monitoring methodology or practicality of including these features in a monitoring programme at this stage. No consideration of the biological assemblages and their response to pressures has been undertaken in this project as sensitivity assessments of sedimentary habitat ecological groups has been completed as part of Tillin and Tyler-Walters (2014).

The assessment presented in Table 8 is very simplistic and does not consider the potential degree of sensitivity of each model component, nor the potential rate of recovery and how sensitivity might be influenced by the extent and magnitude of the pressure. The presented information provides a good starting point for selecting indicators to identify anthropogenic cause of change but the literature reviewed to inform this assessment is limited. It is also expected that a stressor model for shallow sublittoral mixed sediment habitats will be produced by JNCC following a detailed sensitivity assessment of the ecological groups of the habitat type.

The CEM components included in Table 8 are based on a combination of literature evidence and expert judgement. A short rationale is presented for each potential monitoring component and confidence has been assigned based on the protocols presented in Sections 2.5 and 5.2. There may be other factors which are useful for monitoring to determine habitat status change due to anthropogenic pressures; however those presented are the key components identified by this project.

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

Pressure	Model Component	Rationale	Confidence
Introduction or spread of non-indigenous species (NIS)	Habitat Provision	The shallow sublittoral mixed sediment habitat contains biotopes classified as containing the invasive gastropod *Crepidula fornicata*. This species is already established within this habitat and is negatively linked to the provision of habitat for other species (Le Pape *et al* 2004; Vallet *et al* 2001; de Montaudouin *et al* 1999). Monitoring the spread or proliferation of this invasive taxon would therefore be useful in assessing anthropogenic impacts on the shallow sublittoral mixed sediment habitat.	High

Removal of non-target species	Ecosystem functions	The removal of non-target species through fishing activity by-catch or damage will have knock-on effects on various ecosystem functions depending on the ecological groups affected. Principally this includes secondary production, biodeposition, bioturbation, bioengineering and supply of propagules as output processes, which in turn will affect food resources, nutrient and biogeochemical cycling, sediment stability and habitat provision at the local scale, and in turn will affect the export of biodiversity, the export of organic matter, biodiversity enhancement and biotope stability at the regional to global scale.	Medium
Removal of target species	Ecosystem functions	Several species included in the project scope are commercially fished in certain areas around the UK (MarLIN 2006) and directly removed from the ecosystem. Target species include *Cancer pagurus*, *Necora puber, Buccinum undatum, Ostrea edulis, Pecten maximus*, and to a lesser extent *Echinus esculentus*. The removal of these species may result in disruptions to output processes and ecosystem functions such as predatory control of other organisms (Nybakken 2001), bioengineering (Thurstan *et al* 2013; Hall-Spencer & Moore 2000) and biodeposition (Saravia 2011; Levinton 2001), as well as affecting the supply of propagules, in turn potentially influencing spawning stock biomass. However, Simberloff (1998) cautions that an indicator subject to single species management is no longer an indicator. This observation has substantial implications in marine systems, because some species that are readily observable are also harvested by humans to some degree and, therefore, make poor indicators (Zacharias & Roff 2001).	Medium
Physical damage or change to Habitat Structure	Suspended Sediment	Surface and sub-surface abrasion may enhance fine suspended sediments in shallow sublittoral mixed sediment habitats, particularly those with muddy or sandy sediment complements (Kenny & Rees 1994). Increased suspended sediment is likely to have a direct effect on light attenuation (Devlin 2008), reducing primary production by phytoplankton and thus reducing food sources. Additionally increased suspended sediment may lead to the clogging of filtering mechanisms of suspension feeders (Bilotta & Brazier 2008; Rhoads & Young 1970).	High

	Seabed Mobility /Sediment Stability	Physical damage to shallow sublittoral mixed sediment habitats, through surface and subsurface abrasion and habitat structure changes through the removal of substratum, have the potential to affect both seabed mobility and sediment stability through direct physical effects and indirect effect on fauna. Abrasion and physical impacts may destroy upper parts of infaunal burrows and tubes (Hughes 1998) which can lead to a local decrease in the sediment stability of sublittoral sedimentary habitats (Ciutat *et al* 2006, 2007). Biogenic structures such as tubes constructed by annelid worms, which act to bind sediment together, may also be destroyed by excessive abrasion. All fauna which influence sediment stability through bioengineering which occupy niche sedimentary habitats of a particular sediment size may be affected by habitat type change, although sediment stability may increase with a decrease in bioturbation activity.	High
	Habitat Provision	Damage to bioengineering species through physical disturbance will decrease their habitat provision to other fauna as they are essential for the survival of lower parts of the food web (Braeckman *et al* 2011).	Medium
	Supply of propagules	Physical disturbances which result in the removal or mortality of fauna are likely to disrupt the supply of propagules. Additional, sub-lethal impacts of habitat structure changes or physical damage to the habitat may impact the settlement and survival rate of propagules (Dannheim *et al* 2014; Neal & Avant 2008).	Medium
Changes in suspended solids (water clarity)	Light attenuation	Increased suspended sediments will reduce water clarity and light attenuation, potentially affecting primary production and resulting in secondary impacts to other organisms. An increase in suspended sediments may also negatively interact with filter feeding fauna by clogging feeding mechanisms (Bilotta & Brazier 2008). This may be tied to an increase in other pressures such as wave exposure.	High
Physical change (to another seabed type)	Habitat Provision	The physical change of the seabed due to the installation of new infrastructures has the potential to create new habitats and enhance colonisation (De Mesel *et al* 2013). The structures may also create a refuge habitat for juvenile fish species with enhanced food availability (Reubens *et al* 2013; Derweduwen *et al* 2012), which may in turn predate within the soft-sediment habitat. Shallow sublittoral mixed sediment habitat is likely to be lost as part of this impact; the habitat provision afforded by certain fauna (e.g. tube builders, burrowing fauna) will also likely be lost, and the species which colonise the new substrate may be dissimilar to the original habitat.	High

	Sediment type	The changing of the physical habitat to another seabed type is likely to principally affect sediment type, assuming that mixed sediment is lost from the habitat. This in turn will affect the faunal complement that the habitat will support, and all associated ecosystem output process at all scales. Should the replacement habitat contain substrates which are suitable for colonisation by benthic fauna, some of the output processes described in the models may develop in the future.	Medium
Organic and nutrient enrichment	Water chemistry and temperature	Organic and nutrient enrichment from anthropogenic sources can have a large effect on water chemistry (Lalli & Parsons 2006; Levinton 2001). Direct loading of nutrients, organic matter and minerals will likely have large effects on benthic and epibenthic communities, and will alter ecosystem functions in a significant way (Libes 1992).	High
	Primary Production	Organic and nutrient enrichment of the natural environment is also likely to influence primary production (Hiscock 2006). Nutrients are known to be a limiting factor in primary production and an increased input could lead to phytoplankton blooms (e.g. Lalli & 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 (informed by literature evidence)

9 Conclusions

This project has demonstrated the links and interactions which occur within shallow sublittoral mixed 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 7 and 8 shows which components of the models may be useful for monitoring habitat status and change due to natural variation and anthropogenic pressure respectively, and may be worth taking forward to inform indicator selection for this habitat type. Typically, local inputs to the habitat, the biological assemblage and ecosystem processes are those aspects of the models most likely to serve as features useful for monitoring change in the context of natural variation. Seabed mobility/stability, sediment type, recruitment and bioengineering are likely to be key monitoring aspects of the shallow sublittoral mixed sediment environment. In addition, benthic fauna and in particular attached epifauna and burrow dwelling fauna may be worth monitoring to assess habitat status and change due to natural variation from a biological point of view. Further work will have to be undertaken to identify specific species which would be useful to monitor from within these groups to reflect natural variation in the biological communities.

In terms of aspects of the habitat which may be useful for monitoring habitat status and change due to anthropogenic pressures, certain key driving influences at a variety of scales (e.g. suspended sediments, seabed mobility, supply of propagules, water chemistry and temperature) have been identified as potentially sensitive to pressures. Output processes of the shallow sublittoral mixed sediment habitat which have been identified as potentially useful monitoring aspects in relation to pressures include habitat provision, ecosystem functions related to the removal of commercially targeted and non-species, suspended sediments, seabed mobility, water chemistry and temperature and various other ecosystem processes connected to these features.

10 References

Agüera, A., Trommelen, M., Burrows, F., Jansen, J.M., Schellekens, T. & Smaal, A. 2012. Winter feeding activity of the common starfish (*Asterias rubens* L.): The role of temperature and shading.Journal of Sea Research. **72**, 106–112.

Alexander, D., Coates, D.A., Tillin, H. & Tyler-Walters, H. 2015. Conceptual Ecological Modelling of Sublittoral Rock Habitats to Inform Indicator Selection. Marine Ecological Surveys Ltd. *JNCC Report No. 560*. JNCC, Peterborough.

Alexander, D., Colcombe, A., Chambers, C. & Herbert, R.J.H. 2014. Conceptual Ecological Modelling of Shallow Sublittoral Coarse Sediment Habitats to Inform Indicator Selection. Marine Ecological Surveys Ltd. *JNCC Report No. 520*. JNCC, Peterborough. http://jncc.defra.gov.uk/page-6761

Allen, P.L. 1983. Feeding behaviour of *Asterias rubens* (L.) on soft bottom bivalves: A study in selective predation. Journal of Experimental Marine Biology and Ecology, 70, 79-90.

Ambrose, W.G. 1993. Effects of predation and disturbance by ophiuroids on soft-bottom community structure in Oslofjord: results of a mesocosm study. Marine Ecology Progress Series, **97**, 225-236.

Basford, D., Eleftheriou, A. & Raffaelli, D. 1990. The Infauna and Epifauna of the Northern North Sea. Netherlands Journal of Sea Research, **25 (1/2),** 165-173.

Bell, J. 2008. The functional roles of marine sponges. Estuarine, Coastal and Shelf Science. **79**, 341-353.

Bertics, V.J., Sohm, J.A., Treude, T., Chow, C.E.T., Capone, D.G., Fuhrman, J.A. & Ziebis, W. 2010. Burrowing deeper into benthic nitrogen cycling: the impact of bioturbation on nitrogen fixation coupled to sulphate reduction, Marine Ecological Progress Series, **409**, 1–15.

Biles, C.L., Solan, M., Isaksson, I., Paterson, D.M., Emes, C. & Raffaelli, D.G. 2003. Flow modifies the effect of biodiversity on ecosystem functioning: an in situ study of estuarine sediments. *Journal of Experimental Marine Biology and Ecology* **285-286**: 165-177.

Bilotta, G.S. & Brazier, R.E. 2008. Understanding the influence of suspended solids on water quality and aquatic biota. Water Research, **42**, 2849-2861.

Bolam, S.G. & Fernandes, T.F. 2003. Dense aggregations of *Pygospio elegans* (Claparede): Effect on macrofaunal community structure and sediments. Journal of Sea Research. **49,** 171-185.

Bolam, S.G., Barrio-Frojan, C.R.S. & Eggleton, J.D. 2010, Macrofaunal Production along UK Continental Shelf. Journal of Sea Research**, 64,** 166–179.

Bolam, S.G., Coggan, R.C., Eggleton, J., Diesing, M. & Stephens, S. 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach, Journal of Sea Research**, 85**, 162–177.

Braeckman, U., Provoost, P., Gribsholt, B., Van Gansbeke, D., Middelburg, J.J., Soetaert, K., Vincx, M. & Vanaverbeke, J. 2010. Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. Marine Ecology Progress Series, **399**, 173-186.

Brown, E., Colling, A., Park, D., Phillips, J., Rothery, D. & Wright, J. 2002a. Waves, Tides and Shallow-Water Processes. Oxford: Butterworth-Heinemann.

Brown, E., Colling, A., Park, D., Phillips, J., Rothery, D. & Wright, J. 2002b. Seawater: It's Composition, Properties and Behaviour. Oxford: Butterworth-Heinemann.

Cano, J., Rosique, M.J. & Rocamora, J. 1997. Influence of environmental parameters on Reproduction of the European flat oyster (*Ostrea edulis* l.) in a coastal lagoon (Mar Menor, southeastern Spain). Journal of Molluscan Studies, **63**, 187-196.

Chamberlain, J., Fernandes, T.F., Read, P., Nickell, T.D. & Davies, I.M. 2001. Impacts of biodeposits from suspended mussel (*Mytilus edulis* L.) culture on the surrounding surficial sediments, ICES Journal of Marine Science**, 58,** 411–416.

Chauvaud, L., Donval, A., Thouzeau, G., Paulet, Y.M. & Nezan, E. 2001. Variations in food intake of *Pecten maximus* (L.) from the Bay of Brest (France): Influence of environmental factors and phytoplankton species composition. Life Sciences, **324**, 743-755.

Christophersen, G. & Strand, O. 2003. Effect of reduced salinity on the great scallop (*Pecten maximus*) spat at two rearing temperatures. Aquaculture, **215**, 79-92.

Ciutat, A., Widdows, J. & Pope, N.D. 2007. Effect of *Cerastoderma edule* density on near-bed hydrodynamics and stability of cohesive muddy sediments. Journal of Experimental Marine Biology and Ecology. **346**, 114-126.

Ciutat, A., Widdows, J. & Readman, J.W. 2006. Influence of cockle *Cerastoderma edule* bioturbation and tidal-current cycles on resuspension of sediment and polycyclic aromatic hydrocarbons. Marine Ecology Progress Series. **328**, 51-64.

Coates, D. 2014. The effects of offshore wind farms on macrobenthic communities in the North Sea. Chapter 5. PhD Thesis. Ghent University. 182 pp.

Coates, D., Deschutter, Y., Vincx. M. & Vanaverbeke, J. 2013. Macrobenthic enrichment around a gravity based foundation. In: Degraer, S. *et al* (Ed.). 2013. Environmental impacts of offshore wind farms in the Belgian part of the North Sea: Learning from the past to optimise future monitoring programmes, 141-151.

Coates, D.A., Alexander, D., Stafford, R. & Herbert, R.J.H. 2015. Conceptual Ecological Modelling of Shallow Sublittoral Mud Habitats to Inform Indicator Selection. Marine Ecological Surveys Ltd. *JNCC Report No: 557*. JNCC, Peterborough.

Cochrane, S.K.J., Connor, D.W., Nilsson, P., Mitchell, I., Reker, J., Franco, J., Valavanis, V., Moncheva, S., Ekebom, J., Nygaard, K., Serrão Santos, R., Narberhaus, I., Packeiser, T., van de Bund, W. & Cardoso, A.C. 2010. Marine Strategy Framework Directive Task Group 1 Report, Biological diversity. JRC Scientific and Technical Report.

Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B. 2004. The Marine Habitat Classification for Britain and Ireland Version 04.05. JNCC, Peterborough. ISBN 1 861 07561 8 (internet version) www.jncc.gov.uk/MarineHabitatClassification

Cooper, K.M., Curtis, M., Wan Hussin, W.M.R., Barrio Frojan, C.R.S., Defew, E.C., Nye, V. & Paterson, D.M. 2011. Implications of dredging induced changes in sediment particle size composition for the structure and function of marine benthic macrofaunal communities. Marine Pollution Bulletin*,* **62**, 2087–2094.

Corbera, J. & Cardell, M.J. 1995. Cumaceans as indicators of eutrophication on soft bottoms. Scientia Marina, **59** (Suppl. 1), 63-69.

Cusson, M. & Bourget, E. 2005. Global patterns of macroinvertebrate production in marine benthic habitats, Marine Ecology Progress Series, **297**, 1–14.

Daly, M., Chaudhuri, A., Gusmão, L. & Rodríguez, E., 2008. Phylogenetic relationships among sea anemones (Cnidaria: Anthozoa: *Actiniaria*), Molecular Phylogenetics and Evolution, **48 (1),** 292-301.

Dame, R.F., Wolaver, T.G. & Libes, S.M. 1985. The summer uptake and release of nitrogen by an intertidal oyster reef. Netherlands Journal of Sea Research, **19**, 265-268.

Dannheim, J., Brey, T., Schröder, A., Mintenbeck, K., Knust, R. & Arntz, W.E. 2014. Trophic look at soft-bottom communities - Short-term effects of trawling cessation on benthos. Journal of Sea Research, **85,** 18-28.

Dauvin, J.C., Mear, Y., Murat, A., Poizot, E., Lozach, S. & Beryouni, K. 2013. Interactions between aggregations and environmental factors explain spatio-temporal patterns of the brittle-star *Ophiothrix fragilis* in the eastern Bay of Seine. Estuarine, Coastal and Shelf Science, **131**, 171-181.

Davoult, D. & Gounin, F. 1995. Suspension-feeding Activity of a Dense *Ophiothrix fragilis* (Abildgaard) Population at the Water-Sediment Interface: Time Coupling of Food Availability and Feeding Behaviour of the Species. Estuarine, Coastal and Shelf Science, **41**, 567-577.

De Mesel, I., Kerckhof, F., Rumes, B., Norro, A., Houziaux, J.-S. & Degraer, S. 2013. Fouling community on the foundations of wind turbines and the surrounding scour protection, in: Degraer, S., Brabant, R. & Rumes, B. (Eds.). Environmental impacts of offshore windfarms in the Belgian Part of the North Sea: Learning from the past to optimise future monitoring programmes. Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Marine Ecology and Management Section, 123-137.

de Montaudouin, X., Audemard, C. & Labourg, P. 1999. Does the slipper limpet (*Crepidula fornicata*, L.) impair oyster growth and zoobenthos biodiversity? A revisited hypothesis. Journal of Experimental Marine Biology and Ecology, **235,** 105–124.

Derweduwen, J., Vandendriessche, S., Willems, T. & Hostens, K. 2012. The diet of demersal and semi-pelagic fish in the Thorntonbank wind farm: tracing changes using stomach analyses data, in: Degraer, S., Brabant, R. & Rumes, B. (Eds.). Offshore wind farms in the Belgian part of the North Sea. Heading for an understanding of environmental impacts. Royal Belgian Institute for Natural Sciences, Management Unit of the North Sea Mathematical models, 73-84.

Devlin, M.J., Barry, J., Mills, D.K., Gowen, R.J., Foden, J., Sivyer, D. & Tett, P. 2008. Relationship between suspended particulate material, light attenuation and Secchi depth in UK marine waters. Estuarine, Coastal and Shelf Science. **79**. 429-439.

Diaz, R.J. & Rosenberg, R. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna, Oceanography and Marine Biology: An Annual Review**, 33**, 245-303.

Dobbs, F.C. & Scholly, T.A. 1986. Sediment processing and selective feeding by *Pectinaria koreni* (Polychaeta: Pectinariidae). Marine Ecology Progress Series, **29**, 165-176.

Doren, R.F., Richards, J.H. & Volin, J.C. 2009. A conceptual ecological model to facilitate understanding the role of invasive species in large-scale ecosystem restoration. Ecological Indicators, 9, 150-160.

Dutertre, M., Hamon, D., Chevalier, C. & Ehrhold, A. 2012. The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management, ICES Journal of Marine Science, **70 (2**), 294-308.

Eca, G.F., Pedreira, R.M.A. & Hatje, V. 2013. Trace and major elements distribution and transfer within a benthic system: Polychaete *Chaetopterus variopedatus*, commensal crab *Polyonyx gibbesi*, worm tube, and sediments. Marine Pollution Bulletin, **74**, 32–41.

Ehrenhauss, S. & Huettel, M. 2004. Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments. Journal of Sea Research, **52**, 179-197.

Ellingsen, K.E. 2002. Soft sediment benthic biodiversity on the continental shelf in relation to environmental variability. *Marine Ecology Progress Series*, **232**, 15-27.

Eppley, R.W. 1972. Temperature and Phytoplankton growth in the sea. Fishery Bulletin, **70**, 1063-1085.

Eriksson, B.K. & Bergstrom, L. 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. Estuarine, Coastal and Shelf Science. **62,** 109–117.

Evans, P.L., Kaiser, M.J. & Hughes, R.N. 1996. Behaviour and energetics of whelks, *Buccinum undatum* (L.), feeding on animals killed by beam trawling. Journal of experimental Marine Biology and Ecology, **197**, 51-62.

Fauchald, K. & Jumars, P.A. 1979. The diet of worms: A study of Polychaete feeding guilds. Oceanographic Marine Biology Anniversary Review, **17**, 193-284.

Francour, P. 1997. Predation on holothurians: a literature review. Invertebrate Biology. **116 (1).** 52-60.

Friedrichs, M., Leipe, T., Peine, F. & Graf, G. 2009. Impact of macrozoobenthic structures on near-bed sediment fluxes. Journal of Marine Systems, **75**, 336-347.

Gili, J.M., Alva, V., Coma, R., Orejas, C., Pages, F., Ribes, M., Zabala, M., Arntz, W., Bouillon, J., Boero, F. & Hughes, R.G. 1997. The impact of small benthic passive suspension feeders in shallow marine ecosystems: the hydroids as an example. Zoologische Verhandelingen, **323**, 99-105.

Gosling, E. 2003. Bivalve Molluscs, Biology, Ecology and Culture. Fishing News Books, Oxford: Blackwell Publishing.

Grant, J. 1981. Factors affecting the occurrence of intertidal amphipods in reducing sediments. Journal of Experimental Marine Biology, **49**, 203-216.

Gross, J.E. 2003. Developing conceptual models for monitoring programmes. NPS Inventory and Monitoring Programme, USA
http://science.nature.nps.gov/im/monitor/docs/Conceptual_modelling.pdf

Grove, M., Finelli, C.M., Wethy, D.S. & Woodin, S.A. 2000. The effects of symbiotic crabs on the pumping activity and growth rates of *Chaetopterus variopedatus*. Journal of Experimental Marine Biology and Ecology, **246**, 31-52.

Hall-Spencer, J.M. & Moore, P.G. 2000. *Limaria hians* (Mollusca: Limacea): a neglected reef-forming keystone species. Aquatic Conservation: Marine and Freshwater Ecosystems, **10**, 267-277.

Hancock, D.A., Drinnan, R.E. & Harris, W.N. 1956. Notes on the biology of *Sertularia argentea*. Journal of Marine Biological Association of UK. **35,** 307-325.

Hayward, P.J., Nelson-Smith, T. & Shields, C. 1996. Seashore of Britain and Northern-Europe. Collins Pocket Guide. London: Harper Collins.

Hily, C. 1991. Is the activity of benthic suspension feeders factor controlling water quality in the Bay of Brest? Marine Ecology Progress Series, **69**, 179-188.

Hiscock, K., Marshall, C., Sewell, J. & Hawkins, S.J. 2006. The structure and functioning of marine ecosystems: an environmental protection and management perspective. English Nature Research Reports, No 699.

Hiscock, K., Southward, A., Tittley, I. & Hawkins, S. 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. Aquatic Conservation: Marine and Freshwater Ecosystems. **14.** 333-362.

Holt, T.J., Rees, E.I., Hawkins, S.J. & Seed, R. 1998. Biogenic Reefs (volume IX). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science (UK Marine SACs Project). 170 Pages.

Howarth, L.M., Roberts, C.M., Hawkins, J.P., Steadman, D.J. & Beukers-Stewart, B.D. 2015. Effects of ecosystem protection on scallop populations within a community-led temperate marine reserve. Marine Biology, **162**, 823-840.
http://www.fs.fed.us/rm/pubs/rmrs_p042/rmrs_p042_944_951.pdf

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

Ingle, R.W. 1996 Shallow-water Crabs. Synopses of the British Fauna. No. 25.

Jones, L.A., Hiscock, K. & Connor, D.W. 2000. Marine habitat reviews. A summary of ecological requirements and sensitivity characteristics for the conservation and management of marine SACs. JNCC, Peterborough (UK Marine SACs Project report).

Kaiser, M.J., Edwards, D.B., Armstrong, P.J., Radford, K., Lough, N.E.L., Flatt, R.P. & Jones, H.D. 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. ICES Journal of Marine Science, **55**, 353-361.

Kenny, A.J. & Rees, H.L. 1994. The effects of marine gravel extraction on the macrobenthos: early post-dredging recolonization. Marine Pollution Bulletin, **28**, 442-447.

Kirtley, D.W. & Tanner, W.F. 1968. Sabellariid worms: Builders of a major reef type. Journal of Sedimentary Research. **38(1)**, 73-78.

Korringa, P. 1946. The shell of *Ostrea edulis* as a habitat. Bergen op zoom, Holland: Government Institute for Fishery Investigations. pp.115.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O. & Banta, G.T. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Marine Ecology Progress Series, **466**, 285-302.

Lalli, C.M. & Parsons, T.R. 2006. Biological Oceanography An Introduction. Oxford: Elsevier Butterworth-Heinemann.

Larson, A.A., Stachowicz, J.J. & Hentschel, B.T. 2009. The effect of a tube-building phoronid on associated infaunal species diversity, composition and community structure. Journal of Experimental Marine Biology and Ecology. **381.** 126-135.

Le Pape, O., Guérault, D. & Désaunay, Y. 2004. Effect of an invasive mollusc, American slipper limpet *Crepidula fornicata*, on habitat suitability for juvenile common sole *Solea solea* in the Bay of Biscay. Marine Ecology Progress Series, **277**, 107-115.

Lenihan, H.S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs**, 63(3),** 251-275.

Lesser, M.P. & Kruse, V.A. 2004. Seasonal temperature compensation in the horse mussel, *Modiolus modiolus*: metabolic enzymes, oxidative stress and heat shock proteins. Comparative Biochemistry and Physiology, **137,** 495–504.

Levinton, J. S. 2001. Marine Biology - Function, Biodiversity, Ecology. New York: Oxford University Press.

Liang, I. 2002. Effect of salinity on growth and survival of king scallop spat (*Pecten maximus*). Aquaculture, **205,**171-181.

Libes, S.M. 1992. An Introduction to Marine Biogeochemistry. USA: John Wiley & Sons.

Limpenny, S.E., Barrio Froján, C., Cotterill, C., Foster-Smith, R.L., Pearce, B., Tizzard, L., Limpenny, D.L., Long, D., Walmsley, S., Kirby, S., Baker, K., Meadows, W.J., Rees, J., Hill, J., Wilson, C., Leivers, M., Churchley, S., Russell, J., Birchenough, A.C., Green, S.L. & Law, R.J. 2011. The East Coast Regional Environmental Characterisation. Cefas Open report 08/04. 287pp.

MacTavish, T., Stenton-Dozey, J., Vopel, K. & Savage, C. 2012. Deposit-Feeding Sea Cucumbers Enhance Mineralization and Nutrient Cycling in Organically-Enriched Coastal Sediments. PLoS ONE, 7 (11).

Maddox, D., Poiani, K. & Unnasch, R. 1999. Evaluating management success: Using ecological models to ask the right management questions. In: Sexton, W.T., Malk, A.J., Szaro, R.C. & Johnson, N.C. (Eds.) Ecological Stewardship. Oxford, UK: Elsevier Science, p563-584 http://www.sound-science.org/MaddoxEtAl1999.pdf

Manley, P., Zielinski, W.J., Stuart, C.M., Keane, J.J., Lind, A.J., Brown, C., Plymale, B.L. & Napper, C.O. 2000. Monitoring ecosystems in the Sierra Nevada: the conceptual model foundation. Environmental Monitoring and Assessment, **64**, 139-152. http://www.fs.fed.us/psw/publications/zielinski/manley1.pdf

MarLIN. 2006. *BIOTIC - Biological Traits Information Catalogue.* Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. Available from: www.marlin.ac.uk/biotic. [Accessed 11/08/15]

Martin, S., Thouzeau, G., Chauvaud, L., Jean, F., Guerin, L. & Clavier, J. 2006. Respiration, calcification, and excretion of the invasive slipper limpet, *Crepidula fornicata* L.: Implications for carbon, carbonate, and nitrogen fluxes in affected areas. Limnology and Oceanography, **51**, 1996-2007.

Masselink, G. & Hughes, M.G. 2003. Introduction To Coastal Processes & Geomorphology. London: Hodder Arnold.

Mattson, S. & Cedhagen, T. 1989. Aspects of the behaviour and ecology of *Dyopedos monacanthus* (Metzger) and *D. porrectus* Bate, with comparative notes on *Dulichia tuberculata* Boeck (Crustacea: Amphipoda: *Podoceridae*). Journal of Experimental Marine Biology and Ecology, **127(3**), 253-272.

McBreen, F., Askew, N., Cameron, A., Connor, D., Ellwood, H. & Carter, A. 2011. UKSeaMap 2010: Predictive mapping of seabed habitats in UK waters. *JNCC Report, No. 446*. JNCC, Peterborough.

McGee, B.L. & Targett, N.M. 1989. Larval habitat selection in *Crepidula* (L.) and its effect on adult distribution patterns. Journal of Experimental Marine Biology and Ecology, **131**, 195-214.

Meadows, P.S., Meadows, A. & Murray, J.M.H. 2012. Biological modifiers of marine benthic seascapes: Their role as ecosystem engineers. 157-158. 31-48.

Mermillod-Blondin, F. 2011. The functional significance of bioturbation and bio-deposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. Journal of the North American Benthological Society, **30(3),**770-778.

Middelburg, J.J. & Soetaert, K. 2004. Chapter 11. The role of sediments in shelf ecosystem dynamics. In: Robinson, A. & Brink, K.H. (ed). The Sea, volume 13. Cambridge :Harvard University Press., pp. 353-374.

Munn, C.B. 2004. Marine Microbiology - Ecology & Applications. Oxon: Garland Science/ BIOS Scientific Publishers.

Navarro, J.M. & Thompson, R.J. 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dillwyn) during the spring diatom bloom. Journal of Experimental Marine Biology and Ecology, **209**, 1-13.

Naylor, P. 2011. Great British Marine Animals, 3rd Edition. Cornwall, UK : Deltor Publishing.

Neal, K. & Avant, P. 2008. Owenia fusiformis. A tubeworm. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme [on-line]. Plymouth: Marine Biological Association of the United Kingdom. Available from: http://www.marlin.ac.uk/speciesimportance.php?speciesID=4001 [cited 29/10/2014].

Noffke, A., Hertweck, G., Kroncke, I. & Wehrmann, A. 2009. Particle size selection and tube structure of the polychaete *Owenia fusiformis*. Estuarine, Coastal and Shelf Science, **81**, 160-168.

Noon, B. R. & McKelvey, K. 2006. The process of indicator selection. USDA Forest Service Proceedings RMRS-P-42CD: 944-951.

Norling, K., Rosenberg, R., Hulth, S., Gremare, A. & Bonsdorff, E. 2007a. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment, Marine Ecology Progress Series**, 332**, 11–23.

Norling, P. & Kautsky, N. 2007b. Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. Marine Ecology Progress Series. **351**, 163-175.

Norling, P. & Kautsky, N. 2008. Patches of the mussel *Mytilus* sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea**. 4,** 75-87.

Nybakken, J.W. 2001. Marine Biology, An Ecological Approach. Fifth. San Francisco Ed. Benjamin Cummings, 516pp.

Pandolfi, J.M., Robertson, D.R. & Kirtley, D.W. 1998. Roles of worms in reef-building. Coral Reefs. **17(2)** 120.

Papaspyrou, S., Gregersen, T., Cox, R.P., Thessalou-Legaki, M. & Kristensen, E. 2005. Sediment properties and bacterial community in burrows of the ghost shrimp *Pestarella tyrrhena* (Decapoda: Thalassinidea). Aquatic Microbial Ecology, **38**, 181-190.

Passarelli, C., Olivier, F., Paterson, D.M. & Hubas, C. 2012. Impacts of biogenic structures on benthic assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. **465**, 85-97.

Paterson, D.M. & Black, K.S. 1999. Water flow, sediment dynamics and Benthic biology. Advances in Ecological Research**. 29**, 155-193.

Pazos, A.J., Roman, G., Acosta, C.P., Abad, M. & Sanchez, J.L. 1997. Seasonal changes in condition and biochemical composition of the scallop *Pecten maximus* L. from suspended culture in the Ria de Arousa (Galicia, N.W. Spain) in relation to environmental conditions. Journal of Experimental Marine Biology and Ecology, **211**, 169-193.

Pechenik, J. A., Ambrogio, O.V. & Untersee, S. 2001. Predation on juveniles of *Crepidula fornicata* by two crustaceans and two gastropods. Journal of Experimental Marine Biology and Ecology, **384,** 91-98.

Pechenik, J.A., Blanchard, M. & Rotjan, R. 2004. Susceptibility of larval *Crepidula fornicata* to predation by suspension-feeding adults. Journal of Experimental Marine Biology and Ecology, **306**, 75-94.

Pillay, D. & Branch, G.M. 2011. Bioengineering effects of burrowing Thalassinidean shrimps on marine soft-bottom ecosystems. Oceanography and Marine Biology: An Annual Review. **49**. 137-192.

Porter, J. 2012. Seasearch Guide to Bryozoans and Hydroids of Britain and Ireland. Marine Conservation Society.

Pretterebner, K., Riedel, B., Zuschin, M. & Stachowitsch, M. 2012. Hermit crabs and their symbionts: Reactions to artificially induced anoxia on a sublittoral sediment bottom, Journal of Experimental Marine Biology and Ecology **411**, 23–33.

Probert, P.K. 1984, Disturbance, sediment stability, and trophic structure of soft-bottom communities, Journal of Marine Research, **42**, 893-921.

Qian, P.Y. 1999. Larval settlement of polychaetes. Hydrobiologia. **402**, 239-253.

Queiros, M., Birchenough, S., Bremner, J., Godbold, J., Parker, R., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P., Van Colen, C., Van Hoey, G. & Widdicombe, S. 2013. A bioturbation classification of European marine infaunal invertebrates, Ecology and Evolution, **3**, 11.

Reise, K. 2002. Sediment mediated species interactions in coastal waters. Journal of Sea Research. 48, 127-141.

Reiss, H., Degraer, S., Duineveld, G.C.A., Kröncke, I., Aldridge, J., Craeymeersch, J., Eggleton, J.D., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Pohlmann, T., Rachor, E., Robertson, M., vanden Berghe, E., van Hoey, G. & Rees, H.L. 2010. Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. – ICES Journal of Marine Science. **67**, 278–293.

Reubens, J.T., Braeckman, U., Vanaverbeke, J., Van Colen, C., Degraer, S. & Vincx, M. 2013. Aggregation at windmill artificial reefs: CPUE of Atlantic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) at different habitats in the Belgian part of the North Sea. Fisheries Research **139**, 29-34.

Rhoads, D.C. & Young, D.K. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research, **28 (2),** 150-178.

Rigolet, C., Dubois, S.F. & Thiebaut, E. 2014. Benthic control freaks: Effects of the tubiculous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities. Journal of Sea Research, **85,** 413-427.

Ross, D.M. 1965. Preferential Settling of the Sea Anemone *Stomphia coccinea* on the Mussel *Modiolus modiolus*. Science, **148**, 527-528.

Saravia, S., van der Meer, J., Kooijman, S.A.L.M. & Sousa, T. 2011. Modelling feeding processes in bivalves: A mechanistic approach. Ecological modelling, **222,** 514-523.

Schratzberger, M. & Warwick, R.M. 1999. Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. Journal of Experimental Marine Biology and Ecology, **235**, 255-271.

Seiderer, L.J. & Newell, R.C. 1999. Analysis of the relationship between sediment composition and benthic community structure in coastal deposits: Implications for marine aggregate dredging, ICES Journal of Marine Science, **56**, 757–765.

Siegel, D.A., Mitarai, S., Costello, C.J., Gaines, S.D., Kendall, B.E., Warner, R.R. & Winters, K.B. 2008. The stochastic nature of larval connectivity among nearshore marine populations. PNAS, **105** 8974-8974.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation **83,** 247-257.

Smyth, D. & Roberts, D. 2010. The European oyster (*Ostrea edulis*) and its epibiotic succession. Hydrobiologia, **655,** 25-36.

Spalding, M.D., Gerald, H.E., Allen, R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., Mcmanus, E., Molnar, J., Recchia, C.A. & Robertson, J., 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas, Bioscience, **57 (7),** 573-583.

Tappin, D.R., Pearce, B., Fitch, S., Dove, D., Gearey, B., Hill, J.M., Chambers, C., Bates, R., Pinnion, J., Diaz Doce, D., Green, M., Gallyot, J., Georgiou, L., Brutto, D., Marzialetti, S., Hopla, E., Ramsay, E. & Fielding, H. 2011 The Humber Regional Environmental Characterisation. British Geological Survey Open Report OR/10/54. 357pp.

Thurstan, R.H., Hawkins, J.P., Raby, L. & Roberts, C.M. 2013. Oyster (*Ostrea edulis*) extirpation and ecosystem transformation in the Firth of Forth, Scotland. Journal for Nature Conservation, **21**, 253-261.

Tillin, H. & Tyler-Walters, H. 2014. Assessing the sensitivity of subtidal sedimentary habitats to pressures associated with marine activities. Phase 1 Report – Rationale and proposed ecological groupings for Level 5 biotopes against which sensitivity assessments would be best undertaken. *JNCC Report No. 512A*. JNCC, Peterborough.

Trigg, C., Harries, D., Lyndon, A. & Moore, C.G. 2011. Community composition and diversity of two *Limaria hians* (Mollusca: Limacea) beds on the west coast of Scotland. Journal of the Marine Biological Association of the United Kingdom, **91 (7),** 1403-1412.

Vader, W. 1984. Associations between amphipods (Crustacea: Amphipoda) and sea anemones (Anthozoa, Actiniaria). Australian Museum Memoir, **18(13),** 141-153.

Vallet, C., Dauvin, J.C., Hamon, D. & Dupy, C. 2001. Effect of the introduced common slipper shell on the suprabenthic biodiversity of the subtidal communities in the Bay of Saint-Brieuc. Conservation Biology, **15**, 1686-1690.

Van der Linden, P., Patrico, J., Marchini, A., Cid, N., Neto, J.M. & Marques, J.C. 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem, Ecological Indicators, **20**, 121–133.

Van Hoey, G., Guilini, K., Rabit, M., Vinca, M. & Degraer, S. 2008. Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems, Mar Biol, **154,** 1009–1019.

Vopel, K., Thistle, D. & Rosenberg, R. 2003. Effect of the brittle star *Amphiura filiformis* (Amphiuridae, Echinodermata) on oxygen flux into the sediment. Limnology and Oceanography. **48 (5).** 2034-2045.

Wallentinus, I. & Nyberg, C.D. 2007. Introduced marine organisms as habitat modifiers. Marine Pollution Bulletin, **55**, 323-332.

Wilding, C. & Wilson, E. 2009. *Swiftia pallida*. Northern sea fan. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme [on-line]. Plymouth: Marine Biological Association of the United Kingdom. Available from: http://www.marlin.ac.uk/speciesbenchmarks.php?speciesID=4407 [cited 05/11/2014].

Wingard, G.L. & Lorenz, J.J. 2014. Integrated conceptual ecological model and habitat indices for the southwest Florida coastal wetlands. Ecological Indicators, 44, 92-107.

Woodin, S.A., Wethey, D.S. & Volkenborn, N. 2010. Infaunal Hydraulic Ecosystem Engineers: Cast of Characters and Impacts, Integrative and Comparative Biology, **50 (2),** 176–187.

Zacharias, M.A. & Roff, J. 2001 Use of focal species in marine conservation and management: a review and critique. Aquatic Conservation: Marine and Freshwater Ecosystems, **11**, 59-76.

Ziervogel, K. & Forster, S. 2006. Do benthic diatoms influence erosion thresholds of coastal subtidal sediments? Journal of Sea Research, **55**, 43– 53.

Zulkhe, R. 2001. Polychaete tubes create ephemeral community patters: *Lanice conchilega* (Pallas 1766) associations studied over six years. Journal of Sea Research, **46**, 261-272.

11 List of Appendices

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In addition to the appendices listed, a spreadsheet containing ancillary electronic information supporting the literature review also accompanies this report, as referred to within the main report sections.

Appendix 1 – List of Species Included in Project Scope

Please see accompanying spreadsheet for full species list and details of how this list was refined. It should be noted that accepted scientific names are used, rather than exact names as listed in biotope descriptions (see Section 2.3. for details).

Abra alba
Alcyonium digitatum
Ampelisca tenuicornis
Amphilectus fucorum
Amphipholis squamata
Amphiura filiformis
Apseudopsis latreillii
Ascidiella aspersa
Asterias rubens
Balanus crenatus
Buccinum undatum
Calyptraea chinensis
Cancer pagurus
Cereus pedunculatus
Cerianthus lloydii
Chaetopterus variopedatus
Chaetozone setosa
Chamelea gallina
Crepidula fornicata
Echinus esculentus
Eudorella truncatula
Flustra foliacea
Halichondria bowerbanki
Hydrallmania falcata
Kirchenpaueria pinnata
Kurtiella bidentata
Lanice conchilega
Leptopentacta elongata
Limaria hians
Liocarcinus depurator
Luidia ciliaris
Maera grossimana
Mediomastus fragilis
Melinna palmata
Metridium senile
Modiolus modiolus
Monocorophium sextonae
Necora puber
Nemertesia antennina
Ophiothrix fragilis
Ostrea edulis
Pagurus bernhardus
Pecten maximus
Philine quadripartita
Prionospio fallax
Psammechinus miliaris
Sabella pavonina
Sagartia elegans
Scoloplos armiger
Sertularia argentea
Spirobranchus triqueter
Styela clava
Thyasira flexuosa
Tubificoides benedii
Urticina felina
Venerupis corrugata

Appendix 2 – List of Keywords used as search terms

Amphipod
Annelida
Annual variation
Anoxia
Bacteria
Benthic
Biodeposition
Bioengineering
Biogeochemical process
Bioirrigation
Biological driver
Biotope
Bioturbation
Bioturbation
Bivalve
Brittlestar
Burrowing
Circalittoral
Climate
Climate variation
Coarse mixed sediment
Crustacea
Currents
Currents
Deposit feeder
Depth
Depth range
Dissolved oxygen
Driver
Echinodermata
Ecology
Ecosystem functioning
Ecosystem process
Ecosystem service
Environmental driver
Environmental position
Epifauna
Feeding behaviour
Feeding Habits
Feeding method
Filter feeding
Food resource
Food web
Function
Functional group
Geology
Growth form
Habitat
Habitat provision
Habitat stability
Holothuroidea
Hydrodynamic flow
Hypoxia
Infauna
Influence
Infralittoral
Interaction
Interstitial
Lifespan
Light attenuation
Macrofauna
Marine
Microbial activity
Mixed sediment
Mobility
Muddy mixed sediment
Natural variability
Natural variation
Nitrogen flux
Nutrient cycling
Nutrient provision
Ocean acidification
Organic Carbon
Organic matter
Physical driver
Physiographic
Phytoplankton
Polychaete
POM
Predator
Prey
Primary production
Relationship
Response
Role
Salinity
Seabed energy
Seabed mobility
Seasonal variability
Secondary production
Sediment
Sediment dynamics
Sediment resuspension
Sediment stability
Sediment transport
Sparse fauna
Species trait
Sublittoral
Substratum
Subtidal
Suspension feeder
Suspension feeding
Temperature
Temporal variability
Tidal stress
Tolerance
Trophic level
Tube dwelling
Turbidity
Variability
Variation
Water chemistry
Water composition
Water flow
Wave energy

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