JNCC
Joint Nature Conservation Committee

JNCC Report
No: 585

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

Coates, D.A., Alexander, D., Herbert, R.J.H. & Crowley, S.J.

June 2016

0963-8901

For further information please contact:

Joint Nature Conservation Committee
Monkstone House
City Road
Peterborough PE1 1JY
www.jncc.defra.gov.uk

This report should be cited as:

Coates, D.A., Alexander, D., Herbert, R.J.H. & Crowley, S.J. 2016. Conceptual Ecological Modelling of Shallow Sublittoral Sand Habitats to Inform Indicator Selection. Marine Ecological Surveys Ltd - A report for the Joint Nature Conservation Committee. *JNCC Report No. 585*. JNCC, Peterborough

Summary

The purpose of this study is to produce a series of conceptual ecological models (CEMs) which represent shallow sublittoral sand 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 sand’. This definition includes those habitats which fall into the EUNIS Level 4 classifications A5.23 Infralittoral Fine Sand, A5.24 Infralittoral Muddy Sand, A5.25 Circalittoral Fine Sand and A5.26 Circalittoral Muddy Sand, 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 sand habitats. In addition to this, four detailed sub-models were produced. Each focussed on a particular functional group of fauna within the habitat: “suspension and deposit feeding infauna”, “small mobile fauna and tube dwelling species”, “mobile epifauna, scavengers and predators”, and “attached epifauna and macroalgae”. 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.

Contents

1 Introduction

In order to manage the marine environment effectively it is necessary for decision makers to have access to suitable tools for identifying the state of marine biodiversity and 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 straight forward 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.

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 focussed on producing a series of CEMs for the marine habitat ‘Shallow Sublittoral Sand’, 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), 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.

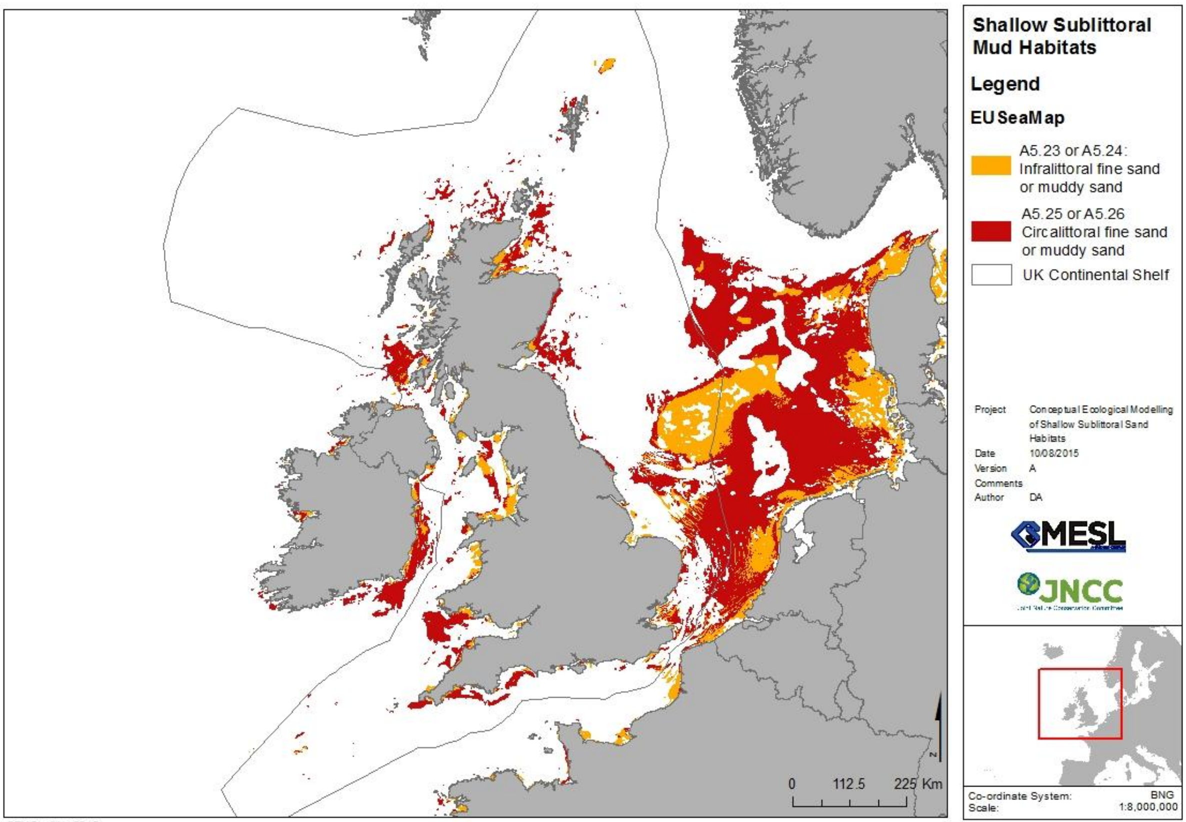
1.1 Habitat Background

The Marine Strategy Framework Directive (MSFD) predominant habitat type ‘Shallow Sublittoral Sand’ covers more than 80,000km^2 of the UK seabed and has the potential to support a range of biodiversity. Sublittoral sand habitats are found in a range of environments, generally inshore. The habitat is characterised by clean medium to fine sands or non-cohesive slightly muddy sands which are generally subject to some degree of wave action or tidal currents (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 sand habitat covers four 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) fine sand, Infralittoral muddy sand, circalittoral (defined as the zone between which 1% light attenuation reaches the seabed and the bottom of the wave base, 50-70m depth) fine sand and circalittoral muddy sand (McBreen *et al* 2011; Cochrane *et al* 2010). The distribution of EUNIS Level 4 biotopes which represent infralittoral and circalittoral sand habitats in the vicinity of the UK is shown in Figure 1.

---

[1] http://eunis.eea.europa.eu/



©EUSeaMap2012

Figure 1. The distribution of shallow sublittoral sand habitats around the UK, split by infralittoral and circalittoral zones. Data is taken from the EUSeaMap broad-scale modelled habitat mapping project[2].

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):

A5.23 (SS.SSa.IFiSa): Infralittoral Fine Sand:
- **A5.231** (SS.SSa.IFiSa.IMoSa) - Infralittoral mobile clean sand with sparse fauna
- **A5.232** (SS.SSa.IFiSa.ScupHyd) - *Sertularia cupressina* and *Hydrallmania falcata* on tide-swept sublittoral sand with cobbles or pebbles
- **A5.233** (SS.SSa.IFiSa.NcirBat) - *Nephtys cirrosa* and *Bathyporeia* spp. in infralittoral sand
- **A5.234** (SS.SSa.IFiSa.TbAmPo) - Semi-permanent tube-building amphipods and polychaetes in sublittoral sand

A5.24 (SS.SSa.IMuSa) - Infralittoral Muddy Sand:
- **A5.241** (SS.SSa.IMuSa.EcorEns) - *Echinocardium cordatum* and *Ensis* spp. in lower shore and shallow sublittoral slightly muddy fine sand
- **A5.242** (SS.SSa.IMuSa.FfabMag) - *Fabulina fabula* and *Magelona mirabilis* with venerid bivalves and amphipods in infralittoral compacted fine muddy sand
- **A5.243** (SS.SSa.IMuSa.AreISa) - *Arenicola marina* in infralittoral fine sand or muddy sand
- **A5.244** (SS.SSa.IMuSa.SsubNhom) - *Spisula subtruncata* and *Nephtys hombergii* in shallow muddy sand

A5.25 (SS.SSa.CFiSa) - Circalittoral Fine Sand:

---

[2] http://jncc.defra.gov.uk/page-5020

- **A5.251** (SS.SSa.CFiSa.EpusOborApri) - *Echinocyamus pusillus*, *Ophelia borealis* and *Abra prismatica* in circalittoral fine sand
- **A5.252** (SS.SSa.CFiSa.ApriBatPo) - *Abra prismatica*, *Bathyporeia elegans* and polychaetes in circalittoral fine sand

A5.26 (SS.SSa.CMuSa) - Circalittoral Muddy Sand:
- **A5.261** (SS.SSa.CMuSa.AalbNuc) - *Abra alba* and *Nucula nitidosa* in circalittoral muddy sand or slightly mixed sediment
- **A5.262** (SS.SSa.CMuSa.AbraAirr) - *Amphiura brachiata* with *Astropecten irregularis* and other echinoderms in circalittoral muddy sand

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 sand 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 sand habitats, along with associated confidence and knowledge gap analyses.
2. Create a hierarchical set of control models to represent shallow sublittoral sand 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 sands) 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 project species list 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. *Sertularia cupressina, Nephtys cirrosa, 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:

- *Ampelisca brevicornis* to represent semi-permanent tube-building amphipods,
- *Chamelea gallina to represent* venerid bivalves.

Alternative methods of reducing the list, e.g. grouping fauna by major taxonomic group or using a higher taxonomic classification, were ruled out. This could result in the loss of critical information on relevant ecosystem processes and/or functions, and species level information is required for effective results.

The Excel Add-In TREx (Taxonomic Routines for Excel) was used to check taxonomic information (spelling and name changes) about the species selected. A manual check of species names was conducted to identify any species of conservation importance or alien

---

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

species to the UK. As a result, no species of conservation importance were identified from the full list of species.

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 the Worksheet 3b (Sublittoral Sand Sediment CEM Literature Review and Ancillary Information Spreadsheet) which accompanies this report.

A revised list of 57 benthic species to be considered within the immediate scope of the project was taken forward for review in the literature, as shown in Appendix 1 and the ‘Species Selection’ worksheet in the spreadsheet which accompanies this report.

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.

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 sand 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[5] indicated that a number of taxa have changed nomenclature. These are listed below:

- *Amphiura brachiata* is now known as *Acrocnida brachiata*
- *Corophium crassicorne* is now known as *Crassicorophium crassicorne*
- *Exogone hebes* is now known as *Parexogone hebes*
- *Fabulina fabula* is now known as *Tellina (Fabulina) fabula*
- *Laminaria saccharina* is now known as *Saccharina latissima*
- *Mysella bidentata* is now known as *Kurtiella bidentata*
- *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 Sand CEM Literature Review and Ancillary Information – Version 1.0). The information logged was divided into the following sections (worksheets):

- **Overview:** Information on the content of every worksheet.
- **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:** All taxa associated with the project biotopes.
- **Species Selection:** The final list of species to be included in the scope of the project, refined to the key characterising taxa representative of all the project biotopes.
- **Trait Selection:** 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.
- **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

---

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

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:** Confidence assessment used for assigning confidence to individual sources. Confidence is taken as the lowest common denominator for both quality and applicability.
- **Definitions:** Species trait definitions

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 200 peer-reviewed and grey literature sources were reviewed as part of this project. The information gathered during the literature review is detailed and summarised in the accompanying data logging pro forma spreadsheet. Specific evidence on ecosystem interactions or species traits which inform the models is presented and discussed throughout Section 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*, *Nephtys cirrosa*, *Liocarcinus depurator* and *Flustra foliacea* were well researched, as were many of the burrowing polychaete worms such as *Arenicola marina* and *Spiophanes bombyx.* Fewer sources were available for poorly studied species such as the cumacean *Diastylis rathkei*, and some smaller interstitial species.

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 sand 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 sand habitats in the UK, although it was not always possible to find suitable information. In some cases information has been taken from comparable habitats (such as intertidal sand or sandbank habitats), using comparable taxa likely to perform the same functions, and from comparable global locations. This has been reflected in the ‘limitations in evidence’ column in the data logging spreadsheet (worksheet ‘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 results of the conservation status checks indicated that none of the species from the full biotope complement were of particular conservation importance.

3.1 Knowledge Gap Assessment

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 sand 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. Information gathered on the ecosystem interactions which occur in shallow sublittoral sand habitats has been incorporated into the confidence assessments associated with each of the models produced by this project, as described in Section 4.2. It is important to note that the level of information sourced during the literature review (and thus the associated confidence assessment) was a factor of the time and resource limitations of the project. This is further discussed in Section 6.

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 sand 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 sand 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 does not address the individual species identified within each biotope, but instead considers the sublittoral sand habitat as a whole and the broad ecological groups that occur within it.

Sub-Models

The sub-models have been designed to show a greater level of detail for specific ecological aspects of the shallow sublittoral sand habitat and therefore will inform the selection of monitoring aspects at a meaningful ecological scale.

Functional groups of the sublittoral sand habitat were identified for the key characterising species selected for each biotope. 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. Expert judgement was applied where analyses did not place species into discrete clusters.

Three ecological groups described by Tillin and Tyler-Walters (2014) were not included as part of the sub-models for shallow sublittoral sand as no key characterising species from the sublittoral sand biotopes belonged to these groups: Ecological group 2 (Temporary or permanently attached surface dwelling or shallowly buried larger bivalves) and Ecological groups 9 and 10 (Burrowing hard-bodied and soft-bodied species).

Based on the study carried out by Tillin and Tyler-Walters (2014), seven of the ten ecological groups were used to categorise the selected species into four functional groups (Table 4).

Each of these will form the basis of a sub-model for shallow sublittoral sand habitats as identified in Figure 2.

Ecological group 8a and 8c (Echinoderms) were split across two sub-models, separating the suspension/deposit feeding echinoderms from the predatory echinoderms as they differ in ecosystem inputs (food sources) and output processes (e.g. different biodeposition and bioturbation rates, see model outputs).

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

Table 4. Relationship between the sub-models of the shallow sublittoral sand 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 4: Infaunal very small to medium sized suspension and/or deposit feeding bivalves	Suspension and deposit feeding infauna
Group 5: Small-medium suspension and/or deposit feeding polychaetes	
Group 8a. Echinoderms – Subsurface urchins	
Group 7. Very small to small, short lived (<2 years) free-living species defined on size and feeding type	Small Mobile Fauna and Tube/Burrow Dwelling Crustaceans
Group 3: Mobile epifauna, mobile predators and scavengers	Mobile Epifauna, predators and scavengers
Group 6: Predatory polychaetes	
Group 8c. Echinoderms – Free-living interface suspension/deposit feeders, Amphiuras, ophiurids	
Group 1. Temporary or permanently attached epifauna	Temporary or permanently attached epifauna and macroalgae

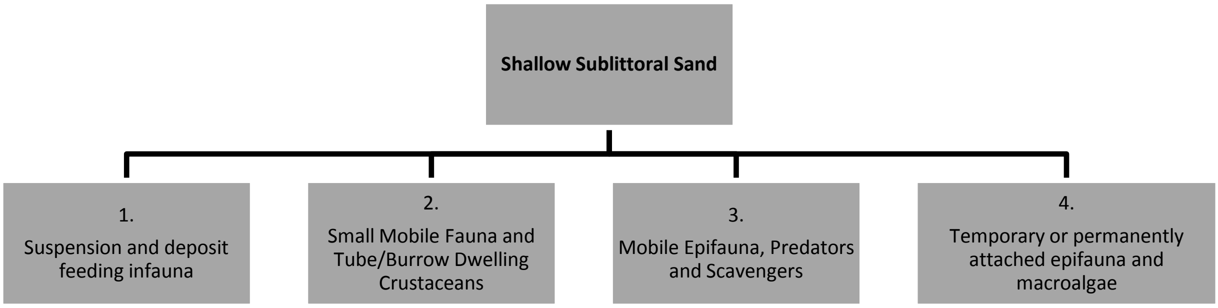


Figure 2. Shallow sublittoral sand habitat CEM hierarchy. The top level of the flowchart represents the general control model, with the four sub-models each documenting a specific functional group within this habitat.

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 specifies 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.

Ecosystem Drivers:

- **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.

Ecosystem 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.

DRIVING INFLUENCES	
1. Regional to Global Drivers	
Geology	Underlying rock or substratum
Depth	Distance between water surface and sea bed
Wave Exposure	Hydraulic wave action
Water Currents	Movement of water masses by tides and/or wind
Climate	Short term meteorology and long-term climatic conditions
Propagule Supply	Supply of larvae, spores and/or regenerative body fragments
2. Water Column Processes	
Primary Production	The production of new organic substances through photosynthesis
Suspended Sediment	Particles of sediment which have become elevated from the seabed and are being kept suspended by turbulence within the water column
Light Attenuation	The penetration of light in the water column
Water Chemistry & Temperature	The chemical and physical characteristics and composition of the water column, excluding dissolved oxygen. This parameter is inclusive of salinity, nutrients, chemicals in the water column and water temperature
Dissolved Oxygen	The dissolved oxygen concentration in the water column above the seabed. Dissolved oxygen was separated from Water Chemistry as it is an important driving force in sand and muddy sand habitats
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)
- Diatoms	Single-celled algae with a cell well of silica
- POM (Particulate Organic Matter)	Non-living material derived from organic sources within the water column
- Detritus	Organic waste and debris contained within seabed sediments
- Phytobenthos	Plants and algae attached to the seabed
- Bacteria & Fungi	Prokaryotic microorganisms & eukaryotic unicellular microorganisms
- Meiofauna	Small benthic invertebrates (<1mm)
- Carrion	Dead and decaying animal flesh
- Living Prey	Live prey items such as benthic infauna or interstitial fauna
Seabed Mobility	Movement of sediment on the seabed
Recruitment	The process by which juvenile organisms join the adult population. Combines settlement and early mortality
4. Habitat and Biological Assemblage (Tillin & Tyler-Walters 2014)	
Suspension and deposit feeding infauna	Suspension and deposit feeding infauna which includes burrowing bivalves, burrow dwelling and tube building polychaetes together with interface suspension/deposit feeding brittle stars and sub-surface dwelling echinoderms
Small mobile fauna and tube/burrow dwelling crustaceans	Small, short-lived amphipods, cumaceans, isopods and mysids, which are free-living (inhabit the sediment surface and are unattached) or those crustaceans which dwell in semi-permanent tube or burrow structures

Mobile Epifauna, Predators and scavengers	Mobile scavenging and predatory crabs, polychaetes, fish, echinoderms and gastropods
Temporary or permanently attached epifauna and macroalgae	Erect, shorter lived and soft-bodied epifauna together with the primary producer kelp (macroalgae)
OUTPUTS	
5. Output Processes	
Secondary Production	Amount of biomass created as a direct result of consumption
Biodeposition	The process by which filter feeding organisms capture particulate matter from the water column and deposit into the sediments
Bioturbation	Sediment re-working by marine fauna
Bioengineering	Faunal modification of the natural habitat, e.g. tube building, burrow creation *etc.*
Supply of Propagules	The production and transportation of larvae, spores or body fragments capable of regeneration
6. Local Ecosystem Functions	
Food Resources	The growth of prey items as a food resource for other organisms
Nutrient Cycling	Cycling of organic and inorganic nutrients that involves processing into a different chemical form
Biogeochemical Cycling	The cycling of organic carbon and nitrogen into different chemical forms
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
Population Control	Control of lower trophic level organism population through predation
7. Regional to Global Ecosystem Functions	
Export of Biodiversity	Export of biodiversity, including propagules, outside of the habitat
Export of Organic Matter	Export of organic material outside of the habitat, such as food sources *etc*.
Biodiversity Enhancement	Enhancements in biodiversity within the habitat resulting from increased sediment stability and habitat provision
Biotope Stability	Stability of the habitat through the habitat provision and increased sediment stability (including carbon sequestration)

4.1.4 Model Interactions

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

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

The strength of influence between sub-model components is indicated by the thickness of the connecting line and is based on the magnitude scoring matrix presented in Table 2.

Driving influences are shown in uniform black within the models, whereas outputs are coloured to indicate whether they are positive or negative in accordance with Table 1. Feedback within the models is indicated with a dashed line.

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

In order to differentiate between driving factors 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

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

The most variable aspect of each model is the biological assemblage. 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 variation in the models, and are defined by the sub-selection of fauna being addressed. The fauna covered in each model characterise the output processes, and in turn the ecosystem functions at the local to global scales.

4.2 Model Confidence

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

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

Wherever possible, the links in each of the models are informed by evidence gathered as part of the literature review. However some links are informed by expert judgement in cases where no references could be identified within the project timescales. In these cases, confidence can only be medium (for those relationships certain to exist), or low (for those relationships which possibly exist but are not evidenced). No high confidence links can exist when expert judgement alone 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 produced models are conceptual designs that have been created for the specific habitats and selected species only. As a result, not every existing link within the ecosystem is presented. Links are shown if they are regarded as potentially important for habitat monitoring purposes. 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 and 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 for the shallow sublittoral sand habitat in this report refer to the new species names where applicable.

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 4-8. The models should be interpreted in consultation with the biotope/model matrix presented in Appendix 3. Reference should also be made to the ‘Habitat Characterisation’ worksheet in the 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.

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 sand 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 sand 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. 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 one of the major defining factors of shallow sublittoral sand habitats with a high relevance in both the circalittoral and infralittoral zones (Basford *et al* 1990). 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). Water depth has a major influence on the habitat and its exposure to wave action (Connor *et al* 2004; Brown *et al* 2002a).

- **Wave disturbance** is far more prominent in shallow waters of 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 sand habitats from 'exposed' to 'extremely sheltered' (Connor *et al* 2004). Increased wave exposure generally enhances the resuspension and sorting of sediments, increasing the concentration of suspended sediment in the water column, 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). 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** include both wind mediated flows and tides. Currents facilitate the transportation and deposition of fine sediment particles (suspended sediment) and together with wave action affect seabed mobility (Brown *et al* 2002a). Water currents also create a transport mechanism for the circulation of temperature and nutrients and sustain the supply of food and propagules to the seabed (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 are a highly important global driver for shallow sublittoral sandy sediments. The 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 sandy sediments (Ehrenhauss & Huettel 2004). These pore water flows enhance the nutrient efflux and oxygen penetration and consumption in sandy sediments (Libes 1992). Although water currents are likely to vary naturally in magnitude and direction through the seasons and annually (both tidal and non-tidal flows), variability is low in comparison to other components.

- **Propagule supply** is a major driver at the regional to global scale, and the only biological ecosystem driver. This driver also forms part of a feedback loop, indicating the importance of recruitment, which is necessary for the persistence of habitats. Connectivity to the same or other habitats is likely to be a key influence on propagule supply where larvae from associated or adjacent habitats are responsible for local recruitment. Propagule supply links to recruitment at the local input level of the models and drives the biological assemblages. 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 (Qian 1999). Not all impacting factors have been shown on the models in an effort to minimise unnecessary complexity.

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

- **Climate** is an important driver in the ecosystem and represents both long-term and short-term meteorological conditions within the model. Influenced by global, regional and local atmospheric and oceanographic conditions, this model component particularly influences water chemistry, dissolved oxygen, temperature and primary production (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.

Water Column Processes

At the second model level (water column processes), five 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, water chemistry & temperature and dissolved oxygen 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), particularly in the infralittoral zone. Larger macrophytes are less common in shallow sublittoral sand habitats due to the high sediment mobility often associated with the habitat and the lack of suitable attachment surfaces. Primary production is a temperature, nutrient (water chemistry) and light dependent process providing energy to drive plankton and marine food webs (Devlin *et al* 2008; Hiscock *et al* 2006). Primary production predominantly occurs in the shallow waters of the infralittoral zone (Jones *et al* 2000). As the top of the circalittoral zone is defined as receiving 1% light attenuation (Connor *et al* 2004) primary production is very low (Lalli & Parsons 2006). Light attenuation is driven by depth and suspended sediments in the water column (Devlin *et al* 2008; Masselink & Hughes 2003; Brown *et al* 2002a).

- **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. 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). 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 biogeochemical cycling (a local ecosystem function) to water chemistry and dissolved oxygen 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.

- **Dissolved oxygen** is an important factor of marine habitats and an integral part of water chemistry. 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).

- **Light attenuation** is another important factor of the shallow sublittoral sand 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 is of high relevance in the infralittoral zone but of comparatively less relevance in the circalittoral zone. 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. These drivers directly affect light attenuation through turbidity of the water column. 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 impact the physical and biological nature of the habitat on a more localised 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), POM and water chemistry and temperature (dissolved oxygen in particular) (Lalli & Parsons 2006; Levinton 2001; Nybakken 2001). Zooplankton are expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006), as POM derived from organic sources, including plankton, 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 particulate organic matter (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; Brown *et al* 2002a; Nybakken 2001).

- **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 stable sediments, such as burrowing bivalves, tube dwelling fauna and sessile epifauna are not likely to flourish in highly mobile environments due to the potential for smothering and difficulties in finding food. Filter feeding fauna, straining food particles from the water column, are likely to require some degree of current flow in order for transport of particulate food sources to be maintained, although currents that are too strong could result in a highly mobile seabed, with decreased sediment stability, and harsher living conditions (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). The sediment grain size will directly impact the biological assemblage as some functional groups have specific niche sediment requirements. In muddy sand 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 (Bilotta & Brazier 2008; Rhoads & Young 1970). The mineralisation of organic matter will decrease with decreasing grain size (fine sand to muddy sand) 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 (Nybakken 2001).

  Sediment type itself 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 drifts (or similar) (Limpenny *et al* 2011; Tappin *et al* 2011). As a result, surface sediments may be unconsolidated and could be prone to movement or winnowing (Masselink & Hughes 2003). Should this occur on a large scale, 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 applicable to the habitat as a whole at a general level. As output processes and ecosystem functions are heavily influenced by the characterising fauna of each habitat, the sub-models should be referred to for specific interactions (and references) related to one particular functional group.

Output processes from shallow sublittoral sand habitats can be broadly split into four main categories: secondary production, sediment processing, habitat modification and supply of propagules.

- **Secondary production** is a key process occurring within the shallow sublittoral sand habitats. Energy from lower trophic levels is converted to higher trophic levels through energy transfer (Lalli & Parsons 2006). This also provides ecosystem functions at the local scale by driving nutrient cycling (Lalli & Parsons 2006; Nybakken 2001). This process 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. Habitat modification is defined as the biological modification of the natural environment, through processes such as tube or reef building or the creation of permanent burrows. Supply of propagules is the product of reproduction and transport by currents, which feeds back to recruitment at the input level.

- **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 sand habitats and are heavily influenced by sediment processing (Mermillod-Blondin 2011; Norling *et al* 2007; Kristensen 2000; Probert 1984). These processes occur in part due to the representative fauna themselves through natural processes (such as uptake of nutrients, decay *etc.*) and secondary production (Mermillod-Blondin 2011; Norling *et al* 2007). These processes are also undertaken in part by microbial activity which may be exacerbated by the other biological features of the habitat, such as increased microbial activity 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 with higher mud content (Kristensen *et al* 2012).

- **Sediment stability** is 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 and 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, such as excessive burrowing (Meadows *et al* 2012).

- **Habitat provision** is the result of bioengineering of the natural environment (building of tubes and burrows) and the colonisation of species which are found within the habitats themselves by symbiotic, 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).

Regional to Global Ecosystem Functions

There are four regional to global scale ecosystem functions resulting from shallow sublittoral sand 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 difficult to represent within the conceptual models.

Other habitat types may lie adjacent to shallow sublittoral sand habitats, for example intertidal sand (Connor *et al* 2004). In terms of ecosystem drivers, connectivity is important for certain aspects of the models such as supply of propagules, nutrient cycling, temperature, and food resources. All components are likely to be affected to some degree by adjacent habitat types, depending on the spatial scales involved.

Connectivity to other habitats is also a factor to be considered at the ecosystem function level. Several of the identified regional to global ecosystem functions concern the export of matter or biodiversity from the shallow sublittoral sand 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 sand habitats, the habitats should not be thought of as operating in isolation, and connectivity to other habitats is likely to be key to maintaining their health.

5.2 Sub-model 1. Suspension and Deposit feeding infauna

5.2.1 Biological assemblage

The suspension and deposit feeding infauna sub-model represents fauna in the shallow sublittoral sand habitats that are deposit or suspension feeders or can switch between these two feeding methods (Tillin & Tyler-Walters 2014). Three main functional groups were identified for this model:

- Burrow dwelling bivalves e.g. *Abra alba*, *Ensis ensis*, *Kurtiella bidentata*
- Polychaetes
    - Burrow dwelling Polychaetes e.g. *Arenicola marina*, *Scoloplos armiger*
    - Tube building Polychaetes e.g. *Lanice conchilega*, *Owenia fusiformis*, *Spiophanes bombyx*
    - Crawlers e.g. *Aricidea cerrutii*
- Echinoderms:
    - Ophiurids e.g. *Acrocnida brachiata*
    - Subsurface dwelling Echinoderms e.g. *Echinocardium cordatum*, *Echinocyamus pusillus*

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. Certain species will also consume small living prey e.g. meiofauna, bacteria and fungi.

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 (e.g. *Aricidea cerrutii*), are free-living within a burrow system (e.g. *Abra alba, Scoloplos armiger*) or construct robust tubes made from sediment particles (e.g. *Lanice conchilega*) or mucus (e.g. *Spiophanes bombyx*).

5.2.2 Ecosystem Drivers

Several key ecosystem drivers are likely to be of large influence to suspension and deposit feeding infauna in addition to those described for the general model. Other features common to all models may still be of high influence to shallow sublittoral sand habitats, however have been discussed under the context of the general model to avoid repetition of descriptions.

- **Propagule supply** is an important biological driver of suspension and deposit feeding infauna. Some of the species characterising this model are known to have a planktonic larval stage (MarLIN 2006) suggesting that connectivity to other habitats nearby could be an important aspect. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop. 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). As the tube building fauna are partially filter feeders, water currents are likely to also interact with the supply of particulate food sources. As a result, water chemistry, sediment type (Basford *et al* 1990), water currents and the availability of food sources (MarLIN 2006) are driving forces with a medium to large influence on the suspension and deposit feeding infauna in the shallow sublittoral sand habitat. Concentrations of fine sediments can have a negative influence on the filter-feeding mechanisms of suspension feeding infauna (Bilotta & Brazier 2008; Rhoads & Young 1970).

- **Seabed mobility** is also a large driver for this model. High levels of sediment mobility will likely prohibit colonisation by tube building fauna, as a relatively stable environment is required for successful habitat construction (Holt *et al* 1998). High seabed mobility may also disrupt the activity of burrowing fauna and prohibit the flow of water through burrows. This is likely to be at least in part influenced by a feedback loop from the sediment stabilising ecosystem function performed by tube builders, and the disruption to seabed stability caused by the bioturbation of burrowers (Meadows *et al* 2012; Woodin *et al* 2010; Paterson & Black 1999). Additionally, some tube building fauna acquire a degree of suspended sediment to construct their tubes, however most bioengineering fauna select sediment particles from the seabed itself and do not rely on suspended particles (Noffke *et al* 2009).

- **Food sources** for suspension and deposit feeding infauna are primarily plankton within the water column (both phytoplankton and zooplankton), POM, detritus and small living prey e.g. meiofauna, bacteria and fungi (MarLIN 2006; Fauchald & Jumars 1979). The availability of food resources is considered a key biological driver.

- **Physical environmental features** are also key drivers for suspension and deposit feeding infauna. In particular water currents are likely to interact with the supply of particulate food sources for suspension feeders. Water depth is also likely to have a large influence on the fauna represented by this model, although features such as geology are likely to have a lower influence.

Other driving influences directly acting on the biological assemblage include seabed mobility, temperature and dissolved oxygen, all of which must be within a range of tolerance in order for organisms to thrive (Lalli & Parsons 2006; Nybakken 2001).

5.2.3 Ecosystem Outputs

Several important ecosystem functions are performed by suspension and deposit feeding infauna.

- **Biodeposition** is a key output process performed by filter feeding infauna. Sediment particles and POM are trapped from the water column and deposited into the sediments through the excretion of waste material, creating a stabilising effect (Levinton 2001; Nybakken 2001). In response to elevated suspension sediment concentrations, certain bivalves 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 (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. Deposit feeding fauna find conditions more favourable under brittlestar beds as a result of the increased deposition of organic matter, enhancing the habitat provision in the area (Hughes 1998).

- **Bioengineering** is an output process which each of the sub-functional groups represented in the model engage in to some degree (Queiros *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). 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* 2007), 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). 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 (Queiros *et al* 2013). Both the building of tubes and body movements within them (e.g. feeding activity) enhance the biogeochemical fluxes in sublittoral muddy sand habitats, transporting oxygen and organic matter to deeper sediment layers (Rigolet *et al* 2014; Braeckman *et al* 2010). This creates a feedback loop to water chemistry, temperature and dissolved oxygen.

- **Bioengineering** through the construction of (semi-) permanent burrows or sedimentary tubes is a major output processes in this sub-model (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 and increased sediment stability through the creation of compacted or mucus lined sediment tunnels which increases shear stress resistance of sediments and restricts lateral inflow of water in the burrows (Probert 1984). These stable environments can provide an extended and protected platform for biogeochemical cycling bacteria to colonise along the burrow walls (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 from 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 arising from bioengineering. The tubes constructed by habitat modifiers enhance the habitat provision for other organisms increasing the colonisation of both macro- and meiofaunal species (Rigolet *et al* 2014; Larson *et al* 2009; Bolam & Fernandes 2003; 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).

- **Increased microbial activity** is another result of habitat modification. Tube-builders have the potential to create favourable conditions for the microbial activity in and around their tubes (Passarelli *et al* 2012) which increases the biogeochemical cycling of nutrients and oxygen in the shallow sublittoral muddy sand (Meadows *et al* 2012). Microbes can then increase sediment stability by increasing the adhesion between sediment particles (Probert 1984). At high densities, tube-building fauna stabilise the surrounding sediment by trapping sediment particles between their tubes (Woodin 2010; Van Hoey 2008; Pandolfi *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).

- **Secondary production** is an important function performed by suspension and deposit feeding infauna as they consume primary producers and organic material, and serve as an important food resource for multiple other organisms such as fish, crustaceans and polychaetes (Nybakken 2011; MarLIN 2006; Levinton 2001; Jones *et al* 2000; Francour 1997; Fauchald & Jumars 1979). Food processing through secondary production also cycles nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale. As the deposit feeding infauna consume POM and detritus a feedback loop exists from the export of organic matter to food sources.

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

5.3 Sub-model 2. Small Mobile Fauna and Tube/Burrow Dwelling Crustaceans

5.3.1 Biological assemblage

The small mobile fauna and tube/burrow dwelling crustaceans sub-model represents species which are considered to be ecologically similar (adapted from Tillin & Tyler-Walters 2014; See Table 4). The sub-model has been divided into two main functional groups:

- Amphipods
    - Burrow dwelling amphipods e.g. *Crassicorophium crassicorne, Urothoe elegans*
    - Tube building amphipods e.g. *Ampelisca brevicornis*
- Small mobile crustaceans
    - Cumaceans e.g. *Diastylis rathkei*
    - Isopods e.g. *Eurydice pulchra*
    - Mysids e.g. *Gastrosaccus spinifer*

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.

Most species in this sub-model are suspension or deposit feeders or can switch between both feeding methods. Suspension (filter) feeders separate particulate organic matter and plankton from the water column while deposit feeders typically consume detritus and organic matter in the surrounding sediment. The isopod *Eurydice pulchra* is a scavenger and will consume small invertebrates and microorganisms.

5.3.2 Ecosystem Drivers

Several key environmental drivers are likely to be of significant importance to suspension and small mobile fauna or tube/burrow dwelling crustaceans further to the links shown for the general habitat model. Other features common to all models may still be of high influence to shallow sublittoral sand habitats, however have been discussed under the context of the general model to avoid repetition of descriptions

- **Physical ecosystem drivers** such as water chemistry, sediment type (Basford *et al* 1990), seabed mobility and the availability of food sources (MarLIN 2006) are driving forces with a medium to large influence on the small mobile fauna and tube dwelling species in the shallow sublittoral sand habitat.

- **Food sources** for small mobile fauna or tube/burrow dwelling crustaceans mainly consist of particulate organic matter, (phyto-) detritus, micro-algae and benthic diatoms. Most species also consume micro-organisms from the bottom deposit and other small invertebrates associated with sandy shores (e.g. other copepods, small amphipods and polychaetes) (MarLIN 2006).

- **Propagule supply** is an important biological driver of small mobile fauna or tube/burrow 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. 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

Bioturbation, bioengineering, biodeposition and secondary production are the major output processes performed by mall mobile fauna or tube/burrow dwelling crustaceans in the shallow sublittoral sand habitat.

- **Bioturbation** is an important output process of the small mobile fauna or tube/burrow dwelling crustaceans sub-model through the physical shallow burrowing and ploughing activities which are related to the feeding activity of the infauna. 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). 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* 2007), 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 undertaken by the fauna represented by this sub-model (MarLIN 2006; Levinton 2001). The amphipod *Ampelisca tenuicornis* constructs mats which enable them to form dense aggregations. Both the burrow dwelling and tube building amphipods will enhance the habitat provision for other organisms (Rigolet *et al* 2014). These micro-habitats increase sediment stability through the creation of compacted or mucus lined burrows and mats (Probert 1984). Burrow dwellers and tube-builders 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).

- **Biodeposition** is another key output process performed by the small mobile fauna or tube/burrow dwelling crustaceans. Particulate matter is strained from the water column by the fauna and subsequently deposited into sediments through the excretion of waste material (Levinton 2001; Nybakken 2001). 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). These processes are linked to the export of organic matter at a wider scale and to water column chemistry through a feedback loop.

- **Secondary** production is an important function performed by the crustaceans and small mobile fauna represented in this sub-model. The species shown are important secondary producers, consuming other fauna, primary producers and organic material. In turn crustaceans themselves serve as an important food resource for multiple other organisms such as flatfish, crabs and larger polychaetes (MarLIN 2006; Smith 2004; Valentin 1977). As some organisms are consumed by other taxa represented within this model, a feedback loop exists from food resources as a local ecosystem function to food sources as a local input at the seabed (MarLIN 2006; Jones *et al* 2000). Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale.

5.4 Sub-model 3. Mobile Epifauna, Predators and Scavengers

5.4.1 Biological assemblage

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

- Mobile Epifauna, Predators and Scavengers
    - Crustaceans e.g. *Carcinus maenas, Pagurus bernhardus*
    - Echinoderms e.g. *Asterias rubens, Ophiura ophiura*
    - Pisces e.g. *Ammodytes tobianus*
- Predatory Polychaetes
    - Burrow dwelling polychaetes e.g. *Glycera lapidum, Nephtys cirrosa*
    - Crawlers e.g. *Parexogone hebes, Pholoe inornata*
- Predatory Gastropods e.g. *Philine quadripartita*

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.

5.4.2 Ecosystem Drivers

A wide range of ecosystem drivers are shown to affect mobile epifauna, predators and scavengers. Other features common to all models may still be of high influence to shallow sublittoral sand habitats, however have been discussed under the context of the general model to avoid repetition of descriptions.

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

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

- **Sediment type** is expected to have a smaller 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. 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 fine muddy sand (MarLIN 2006). For most epifauna, water depth is a greater influencing factor than sediment composition (Basford 1990).

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

Detritus, the organic matter contained within seabed sediments or on the seabed, is also an important food source for scavenging fauna such as the hermit crab *Pagurus bernhardus* and polychaete *Glycera lapidum* (MarLIN 2006). Detritus in the marine environment is influenced by a number of factors, including the abundance of marine life (Lalli & Parsons 2006; Brown *et al* 2002a; Nybakken 2001). Not all the relevant factors influencing detritus availability are indicated on the model for the sake of simplicity.

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

Beside living prey, zooplankton and phytoplankton are also important food sources for the lesser Sand Eel, *Ammodytes tobianus* (MarLIN 2006).

5.4.3 Ecosystem Outputs

Secondary production, biodeposition, bioturbation, the supply of propagules and population control are the principal ecosystem outputs performed by mobile epifauna, predators and scavengers.

- **Secondary production** is a key process occurring within the shallow sublittoral sand 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. Food resources in shallow sublittoral sand habitats may be negatively affected by a high population of active predators.

- **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. Conversely, some species represented in the models, such as *Pagurus bernhardus,* may offer additional habitat provision to symbionts and epibiota (Pretterebner *et al* 2012), enhancing the biodiversity at regional to global ecosystem levels.

- **Biodeposition** is performed by the mobile epifauna, predators and scavengers. 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 and Branch, 2011). These processes are linked to the export of organic matter at a wider scale and to water column chemistry through a feedback loop. Deposit feeding fauna find conditions more favourable under brittlestar beds as a result of the increased deposition of organic matter, enhancing the habitat provision in the area (Hughes 1998).

- **Bioturbation** occurs when mobile epifauna, predators and scavengers moderately rework (bioturbate) the shallow sublittoral sand habitat (Vopel 2003; Schratzberger & Warwick 1999; Ambrose 1993), mainly through ploughing activities related to their feeding behaviour or by physically burrowing. Scavengers such as crabs continuously disturb and aerate the sediment through their ploughing feeding movements which increases the potential for biogeochemical cycling and enables smaller organisms (e.g. nematodes) to penetrate to deeper layers of the sediment (Reise 2002; Schratzberger & Warwick 1999). Excessive bioturbation can have a destabilising effect on the sediment (Ciutat *et al* 2006).

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

5.5 Sub-model 4. Attached Epifauna and Macroalgae

5.5.1 Biological assemblage

The attached Epifauna and macroalgae sub-model differs from the other three models as it contains both faunal and algal species. The sub-model is further divided into three ecological groups:

- Erect, shorter lived Epifauna
    - Hydrozoans e.g. *Hydrallmania falcata, Sertularia cupressina*
- Soft-bodied Epifauna
    - Bryozoans e.g. *Flustra foliacea, Alcyonidium diaphanum*
    - Anemones e.g. *Urticina felina, Cerianthus lloydii*
- Macroalgae
    - Kelp e.g. *Saccharina latissima*

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 attached Epifauna and macroalgae sub-model contains both secondary and primary producers. The hydrozoans and bryozoans are suspension feeders mainly feeding on plankton, detritus and organic matter. Anemones can be suspension feeders (*Cerianthus lloydii*) or predators (*Urticina felina*). The macroalgae represent kelp which is a primary producer in the shallow sublittoral sand habitat. Along with other primary producers macroalgae form the basis of the marine food web.

5.5.2 Ecosystem Drivers

Attached epifauna and macroalgae inhabit the surface of the seabed in the identified biotopes, and are thus subject to a range of physical environmental drivers, in addition to those detailed for the general habitat model. Other features common to all models may still be of high influence to shallow sublittoral sand habitats, however have been discussed under the context of the general model to avoid repetition of descriptions

- **Physical drivers** such as water chemistry, sediment type (Basford *et al* 1990), seabed mobility and the availability of food sources (MarLIN 2006) are driving forces with a medium to large influence on the epifauna and macroalgae sub-model in the shallow sublittoral sand habitat. Concentrations of fine sediments can have a negative influence on the filter-feeding mechanisms of the suspension feeding fauna (Bilotta & Brazier 2008; Rhoads & Young 1970). Macroalgae are heavily influenced by factors affecting rates of primary production, such as light attenuation (Jones *et al* 2000), climate (Merzouk & Johnson 2011), water column chemistry and temperature, including nutrient content (Hiscock *et al* 2006; Lalli & Parsons 2006; Hily 1991).

- **Grazing and predation** is a key biological driver affecting the macroalgal species. Due to their role as secondary producers, non-predatory grazing fauna are important controllers of algae in the sublittoral sand habitat. Certain urchins and gastropods in particular are noted as voracious grazers and their feeding activity can be a controlling factor for the distribution and diversity of algae (Dauvin *et al* 2013; Livore & Connell 2012; Boaventura *et al* 2002; Nybakken 2001).

- **Food sources** for hydrozoans, bryozoans and anemones mainly consist of plankton (both phytoplankton and zooplankton), dissolved organic matter and detritus (MarLIN 2006). As a predator, the anemone *Urticina felina* will consume prawns, crabs, young fish and jellyfish.

- **Propagule supply** is an important biological driver of the attached epifauna and macroalgae 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. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

5.5.3 Ecosystem Outputs

Key output processes performed by attached epifauna and macroalgae include secondary production, primary production, biodeposition, habitat provision and the supply of propagules.

- **Secondary production** is a key process occurring within the shallow sublittoral sand 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.

- **Biodeposition** is another output process performed by the Hydrozoans, Bryozoans and anemones, although the magnitude of interactions is relatively small for these fauna compared to other models. 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). These processes are linked to the export of organic matter at a wider scale and to water column chemistry through a feedback loop.

- **Primary production** is the major output process undertaken by macroalgae which in this model is illustrated by a feedback loop. Through the process of photosynthesis, macroalgal assemblages obtain energy which, along with phytoplankton and marine plants, forms the basis of the majority of marine food webs. Kelp is only a small part of the shallow sublittoral sand habitat although it may dominate in neighbouring habitats (e.g. sublittoral rock habitats) producing a food resource for other fauna, through direct grazing and the production of detritus. The high productivity of kelp forests in comparison to other marine biotopes suggests that the surrounding coastal areas are dependent on the kelp biotopes as a major source of energy (Birkett *et al* 1998). Studies have shown that up to 90% of kelp production is estimated to enter the detrital food webs as particulate or dissolved organic matter, being exported from the immediate area of the kelp bed (Norderhaug & Christie 2011; Birkett *et al* 1998). The process of photosynthesis also leads to increased levels of dissolved oxygen in the water column (Lalli & Parsons 2006).

- **Habitat provision** through bioengineering is an important output process of macroalgae (especially kelp). Prominent ecosystem functions resulting from bioengineering includes habitat provision, influence on biogeochemical cycling and impacts on sediment stability. Bioengineering by macroalgae is noted to have a potential influence on localised hydrodynamic flows by disrupting water currents (Duggins *et al* 1990; Eckman *et al* 1989), indicated by the feedback link shown on the model. This has the potential to offer shelter from currents to other organisms (Duggins *et al* 1990), and is also noted to result in increased deposition of sediments contained within the water column near the sea bed (Eckman *et al* 1989) enhancing biotope stability. Bioengineering can negatively affect light attenuation, with the blades of mature kelps forming a canopy layer which, under certain conditions, may cut off as much as 90% of the incident irradiance (Birkett *et al* 1998).

- **Supply of propagules** is another key output process of the attached epifauna and macroalgae sub-model. Supply of propagules as an output process is important for the continuation of the habitat, and links back to recruitment as an input feature to the export of biodiversity at the regional to global scale.

6 Confidence Assessment

The confidence models which form a supplement to this report are included in Appendices 9-12. 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, and coloured according to whether literature evidence or expert opinion informs each connection. As detailed in Section 4.2, the confidence of these links is divided into two types within the models, informed by either literature sources or expert opinion, following the pro forma shown in Table 6.

In general, a high level of literature has been sourced to inform the models, thus confidence is relatively high for each sub-model. Expert judgement has been used to inform some links within each model where necessary, which has resulted in lowered confidence in some instances. Should any new information be collated on shallow sublittoral sand 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 literature review and generally have a high confidence.

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

Confidence was largely dependent on how well a particular functional group and its ecosystem functions had been studied. For example, the suspension and deposit feeding infauna sub-models generally has a high confidence reflecting the large amount of literature and research that has been carried out on the relevant 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 sand habitats which appear most useful for monitoring habitat status in the context of natural variation in the environment have been identified. Identification of these components will allow monitoring programmes to take account of how the habitat is varying naturally, so that any changes detected can be put within this context. These components have been identified through assessment of the model components and their interactions and are presented in Table 7. Habitat components presented in Table 7 have been further refined into sub-components to indicate specific features of the shallow sublittoral sand 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 ecological aspects of shallow sublittoral sand 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 sand 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 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* 2007). Sediment stability is thought to be a useful indicator to measure natural variation in the ecosystem through variations in these connecting 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.	High (supported by large amount of literature evidence)	All
Burrow Dwelling Fauna	Abundance and diversity of burrow dwelling fauna	Burrow dwelling fauna are a key part of the shallow sublittoral sand habitat. They contribute to several output processes and ecosystem functions at varying scales (Pillay & Branch 2011; Jones *et al* 2000). 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. Queiros *et al* 2013; Reise 2002; Levinton 2001). 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-models 1, 2 & 3
Bioengineering	Seabed rugosity	Bioengineering is performed by several ecological groups represented within the models (species such as *Ampelisca brevicornis, Lanice conchilega, Arenicola marina etc*.). As an output process, bioengineering is predominantly influenced by the faunal assemblage of the habitat, thus variability in the 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*	High (supported by large amount of literature evidence)	All

		2012; Porter 2012; Friedrichs 2009; Dobbs & Scholly 1986). Bioengineering is thought to be a good indicator to assess natural variation within the shallow sublittoral sand 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 sub-model 1)
Benthic Infauna (suspension and deposit feeding fauna)	Abundance and diversity of benthic infauna	Benthic infauna are a crucial part of the shallow sublittoral sand 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.	Medium (informed by both expert judgement and literature evidence)	All (sub-model 1 in particular)
Recruitment	Planktonic larvae production	Recruitment is a key biological factor which affects fauna related to shallow sublittoral sand 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 useful as these would likely be the most susceptible to natural variation. Defining species to specifically monitor cannot be stated without further literature evidence, although some studies do exist which could be used to address this (e.g. Hiscock *et al* 2005).	Medium (largely informed by expert judgement)	All

8 Monitoring components to identify anthropogenic causes of change

Table 8 presents key driving influences and output processes of the shallow sublittoral sand habitat which are likely to be sensitive to anthropogenic pressures operating on the ecosystem, and as such may be useful for monitoring to identify anthropogenic causes of change in the environment. Definitions of each of the pressures, along with relevant benchmarks (from Tillin *et al* 2010), are presented in Appendix 13. It should be noted that no consideration has been given to the monitoring methodology or practicality of including these features in a monitoring programme at this stage. 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 sand 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 sand 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 13.

Pressure	Model Component	Rationale	Confidence
Physical damage or change to Habitat Structure	Suspended Sediment	Surface and sub-surface abrasion may enhance fine suspended sediments in shallow sublittoral sand habitats (Kenny & Rees 1994). Increased suspended sediment is likely to have a direct effect on light attenuation (Devlin 2008), reducing primary production by phytoplankton and algae, reducing food sources. Additionally increased suspended sediment may lead to the clogging of filtering mechanisms of suspension feeders (Bilotta & Brazier 2008).	High

	Seabed Mobility / Sediment Stability	Physical damage to shallow sublittoral sand 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 1998b) which can lead to a local decrease in the sediment stability of sublittoral sedimentary habitats (Ciutat *et al* 2007, 2006). 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 is 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
Removal of non-target species	Ecosystem functions	The removal of non-target species, principally through fishing activity, 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
Siltation rate changes, including smothering (depth of vertical sediment overburden)	Suspended Sediment	An increase in siltation is likely to be preceded by increased suspended sediments in the water column (Last *et al* 2011; Devlin 2008). Increased siltation rate changes through physical disturbance may lead to smothering of benthic fauna, in particular sedentary or species with limited mobility.	High
	Nutrient cycling	Nutrient cycling has the potential to be reduced as faunal communities are affected by smothering. Once the faunal community has become re-established nutrient cycling will potentially return to pre-event levels.	Medium

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 filter feeding mechanisms (Saraiva *et al* 2011). 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 sand 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 likely be lost.	High
	Sediment type	The changing of the physical habitat to another seabed type is likely to principally affect sediment type, assuming that sandy 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 (Munn 2004).	High (informed by literature evidence)
	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 sand 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 sand environment. In addition, benthic fauna and in particular 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 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 sediment, seabed mobility, supply of propagules, water chemistry and temperature) have been identified as potentially sensitive to pressures. Output processes of the shallow sublittoral sand habitat which have been identified as potentially useful monitoring aspects in relation to pressures include habitat provision, nutrient and biogeochemical cycling, sediment stability and various other ecosystem processes connected to these features.

10 References

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.

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.

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**, 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.

Birkett, D.A. & Maggs, C.A., Dring, M.J., Boaden, P.J.S. 1998. Infralittoral Reef Biotopes with Kelp Species (volume VII). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association of Marine Science (UK Marine SACs Project). 174 pages.

Boaventura, D., Alexander, M., Santina, P.D., Smith, N.D., Re, P., Cancela da Fonseca, L. & Hawkins, S.J. 2002. The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain. Journal of Experimental Marine Biology and Ecology, **267**, 185– 206.

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.

Brennand, H.S., Soars, N., Dworjanyn, S.A., Davis, A.R. & Byrne, M. 2010. Impact of Ocean warming and ocean acidification on larval development and calcification in the sea urchin *Tripneustes gratilla*. PLosOne. 5 (6).

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.

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.

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. Report for the Joint Nature Conservation Committee. *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, 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.

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

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.

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.

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 Reponses 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.

Duggins, D.O., Echman, J.E. & Sewell, A.T. 1990. Ecology of understory kelp environments. II. Effects of kelps on recruitment of benthic invertebrates. Journal of Experimental Marine Biology, **143**, 27-45.

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.

Eckman, J.E., Duggins, D.O. & Sewell, A.T. 1989. Journal of Experimental Marine Biology, **129**, 173-187.

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.

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.

Gross, J.E. 2003. Developing conceptual models for monitoring programmes. NPS Inventory and Monitoring Programme, USA.

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.
http://science.nature.nps.gov/im/monitor/docs/Conceptual_modelling.pdf
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.

Jones, H.F.E., Pilditch, C,A., Bryan, K.R. & Hamilton, D.P. 2011. Effects of infaunal bivalve density and flow speed on clearance rates and near-bed hydrodynamics, Journal of Experimental Marine Biology and Ecology, **401,** 20–28.

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. Peterborough, Joint Nature Conservation Committee. (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.

Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia, **426**, 1–24.

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.

Last K.S., Hendrick V.J., Beveridge C.M. & Davies A.J. 2011. Measuring the effects of suspended particulate matter and smothering on the behaviour, growth and survival of key species found in areas associated with aggregate dredging. Report for the Marine Aggregate Levy Sustainability Fund, Project MEPF 08/P76. 69pp.

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

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.

Livore, P. & Connell, S.D. 2012. Fine-scale effects of sedentary urchins on canopy and understory algae. Journal of Experimental Marine Biology and Ecology. **411**, 66–69.

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,563-584 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]

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

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.

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.

Merzouk, A. & Johnson, L.E. 2011. Kelp distribution in the northwest Atlantic Ocean under a changing climate. Journal of Experimental Marine Biology and Ecology, **400**, 90-98.

Middelburg, J.J. & Soetaert, K. 2004. Chapter 11. The role of sediments in shelf ecosystem dynamics. In: Robinson, A. & Brink, K.H. (Eds.). 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.

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.

Norderhaug, K.M. & Christie, H. 2011. Secondary production in a Laminaria hyperborea kelp forest and variation according to wave exposure. Estuarine, Coastal Shelf Science, **95**, 135-144.

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

Nybakken, J.W. 2001. Marine Biology, An Ecological Approach. Fifth Ed. San Francisco: 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.

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.

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.

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.

Smith, J. & Shackley, S.E. 2004. Effects of a commercial mussel *Mytilus edulis* lay on a sublittoral, soft sediment benthic community. Marine Ecological Progress Series, **282,** 185-191.

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.

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.

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

Valentin, C. & Anger, K. (1977): In-situ studies on the life cycles of *Diastylis rathkei* (Cumacea: Crustacea) , Marine Biology, **39,** 71-76.

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., Rabaut, M., Vincx, M. & Degraer, S. 2008. Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecystems. Marine biology, **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.

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.

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

11 List of Appendices

Appendix 1. List of Species Included in Project Scope
Appendix 2. List of Keywords used as Literature Review Search Terms
Appendix 3. Species/Biotope/Model Matrix
Appendix 4. General Control Model – Shallow Sublittoral Sand Habitats
Appendix 5. Sub-model 1. Suspension and Deposit Feeding Infauna
Appendix 6. Sub-model 2. Small Mobile Fauna or Tube/Burrow Dwelling Crustaceans
Appendix 7. Sub-model 3. Mobile Epifauna, Predators and Scavengers
Appendix 8. Sub-model 4. Attached Epifauna and Macroalgae
Appendix 9. Confidence model 1. Suspension and Deposit Feeding Infauna
Appendix 10. Confidence model 2. Small Mobile Fauna or Tube/Burrow Dwelling Crustaceans
Appendix 11. Confidence model 3. Mobile Epifauna, Predators and Scavengers
Appendix 12. Confidence model 4. Attached Epifauna and Macroalgae
Appendix 13. Description of Identified Anthropogenic Pressures
Appendix 14. Sublittoral Sand CEM Literature Review and Ancillary Information

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.