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Conceptual Ecological Modelling of Sublittoral Rock Habitats to Inform Indicator Selection

Alexander, D., Coates, D. A., Tillin, H. & Tyler-Walters, H.

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For further information please contact:

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

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Summary

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

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

The project scope included those habitats defined as ‘sublittoral rock’. This definition includes those habitats that fall into the EUNIS Level 3 classifications A3.1 Atlantic and Mediterranean high energy infralittoral rock, A3.2 Atlantic and Mediterranean moderate energy infralittoral rock, A3.3 Atlantic and Mediterranean low energy infralittoral rock, A4.1 Atlantic and Mediterranean high energy circalittoral rock, A4.2 Atlantic and Mediterranean moderate energy circalittoral rock, and A4.3 Atlantic and Mediterranean low energy circalittoral rock as well as the constituent Level 4 and 5 biotopes that are relevant to UK waters. A species list of characterising fauna to be included within the scope of the models was identified using an iterative process to refine the full list of species found within the relevant Level 5 biotopes.

A literature review was conducted using a pragmatic and iterative approach to gather evidence regarding species traits and information that would be used to inform the models and characterise the interactions that occur within the sublittoral rock habitat. All information gathered during the literature review was entered into a data logging pro-forma spreadsheet that 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 multivariate analysis approach was adopted to assess ecologically similar groups (based on ecological and life history traits) of fauna from the identified species to form the basis of the models. A model hierarchy was developed based on these ecological groups. One general control model was produced that indicated the high-level drivers, inputs, biological assemblages, ecosystem processes and outputs that occur in sublittoral rock habitats. In addition to this, seven detailed sub-models were produced, which each focussed on a particular ecological group of fauna within the habitat: ‘macroalgae’, ‘temporarily or permanently attached active filter feeders’, ‘temporarily or permanently attached passive filter feeders’, ‘bivalves, brachiopods and other encrusting filter feeders’, ‘tube building fauna’, ‘scavengers and predatory fauna’, and ‘non-predatory mobile fauna’. Each sub-model is accompanied by an associated confidence model that presents confidence in the links between each model component. The models are split into seven levels and take spatial and temporal scale into account through their design, as well as magnitude and direction of influence. The seven levels include regional to global drivers, water column processes, local

inputs/processes at the seabed, habitat and biological assemblage, output processes, local ecosystem functions, and regional to global ecosystem functions.

The models indicate that whilst the high level drivers that affect each ecological 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.

Physical drivers which influence the ecosystem were found to be of high importance for the sublittoral rock habitat, with factors such as wave exposure, water depth and water currents noted to be crucial in defining the biological assemblages. Other important factors such as recruitment/propagule supply, and those which affect primary production, such as suspended sediments, light attenuation and water chemistry and temperature, were also noted to be key and act to influence the food sources consumed by the biological assemblages of the habitat, and the biological assemblages themselves.

Output processes performed by the biological assemblages are variable between ecological groups depending on the specific flora and fauna present and the role they perform within the ecosystem. Of particular importance are the outputs performed by the macroalgae group, which are diverse in nature and exert influence over other ecological groups in the habitat. Important output processes from the habitat as a whole include primary and secondary production, bioengineering, biodeposition (in mixed sediment habitats) and the supply of propagules; these in turn influence ecosystem functions at the local scale such as nutrient and biogeochemical cycling, supply of food resources, sediment stability (in mixed sediment habitats), habitat provision and population and algae control. The export of biodiversity and organic matter, biodiversity enhancement and biotope stability are the resulting ecosystem functions that occur at the regional to global scale.

Features within the models that are most useful for monitoring habitat status and change due to natural variation have been identified, as have those that may be useful for monitoring to identify anthropogenic causes of change within the ecosystem. Biological, physical and chemical features of the ecosystem have been identified as potential indicators to monitor natural variation, whereas biological factors and those physical /chemical factors most likely to affect primary production have predominantly been identified as most likely to indicate change due to anthropogenic pressures.

Contents

1 Introduction

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

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

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

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

One such method proposed for selecting suitable indicators is the use of Conceptual Ecological Models (CEMs). CEMs are representations of the ecological interactions that occur within a habitat, and 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; Maddox *et al* 1999; Manley *et al* 2000).

The present report is focussed on producing a series of CEMs for the marine habitat ‘Sublittoral Rock’. The models produced by this project will be used to inform indicator selection for the monitoring of this habitat type in UK waters. CEMs have previously been developed for the habitat type ‘shallow sublittoral coarse sediments’ (Alexander *et al* 2014) from which this project follows. It is intended that CEMs will eventually be produced for a selection of habitat types defined under the UK Marine Biodiversity Monitoring R&D Programme (UKMBMP). The sublittoral rock models produced by this project will demonstrate the ecological components and processes that occur across spatial and temporal scales within non-anthropogenic impacted ecosystems (control models). These control models, 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

Sublittoral rock habitats are highly diverse and widespread around the UK. The sublittoral area can be separated into two zones on the basis of the dominant biological assemblage; the infralittoral (algal dominated) and the circalittoral (animal dominated). The boundary between these two zones is principally defined by the availability of light. The infralittoral

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

zone typically supports various algae communities, predominantly kelp species and erect seaweeds with associated understory fauna. Circalittoral rock habitats may include coralline algae in shallower areas and support a wide range of animal species including attached suspension feeders and mobile grazers and predators. Both biological zones may be subject to considerable wave and water current energy inputs and may comprise topographically complex environments that support a large diversity of marine life (Connor *et al* 2004).

This project uses the UK marine habitat classification (Connor *et al* 2004), as translated in EUNIS (European Nature Information System[2]), to provide a structure to the study. The sublittoral rock habitat covers two biological zones at EUNIS Level 3: infralittoral rock habitats, defined as those areas between the mean low water line and the maximum depth at which 1% light attenuation reaches the seabed; and circalittoral rock habitats, defined as the zone between which 1% light attenuation reaches the seabed and the bottom of the wave base (approximately 50-70m depth) (Cochrane *et al* 2010; McBreen *et al* 2011). It should be noted that several biotopes included in the project scope are referred to as ‘deep’ (A4.12 and A4.121), although they do occur within the depth ranges described above (Connor *et al* 2004). The distribution of EUNIS Level 2 biotopes which represent infralittoral and circalittoral rock habitats in the UK is shown in Figure 1.

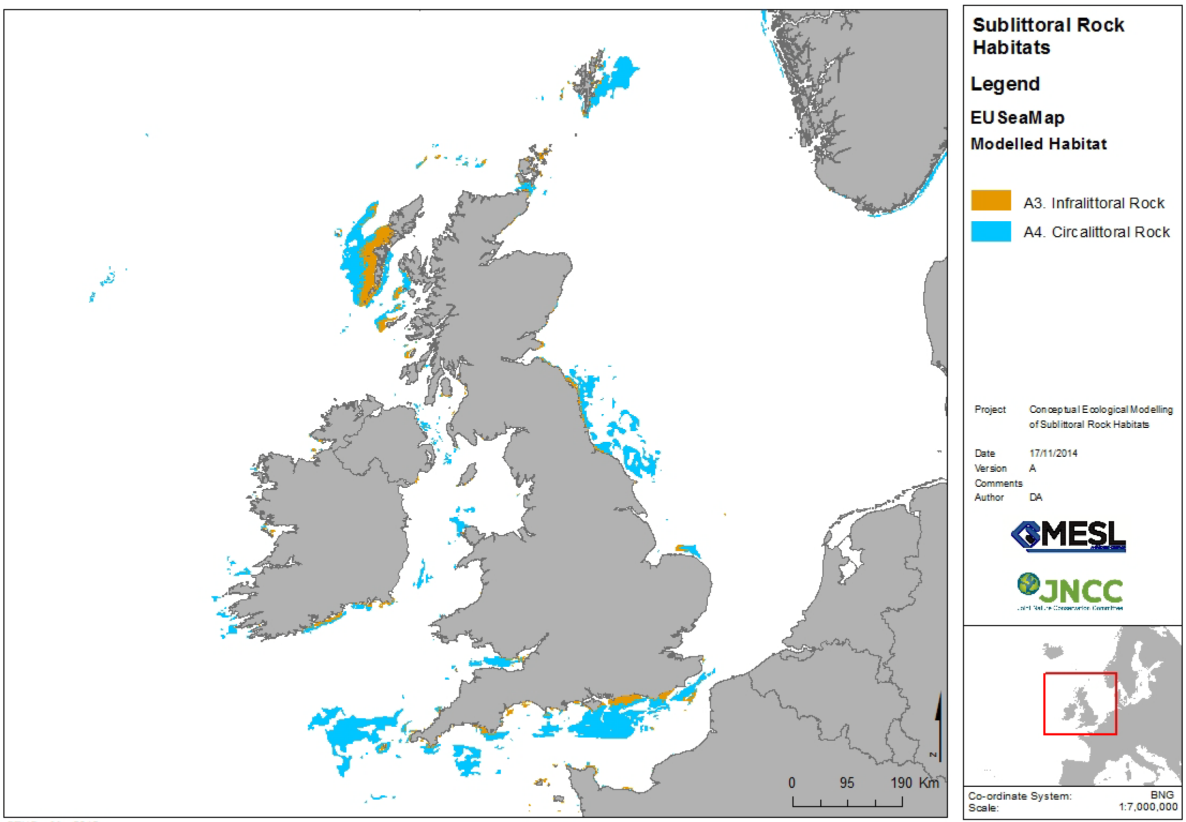

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Figure 1. The distribution of sublittoral rock habitats around the UK, split by depth zone. Data is taken from the EUSeaMap broad-scale modelled habitat mapping project[3].

A complete list of the level 3, level 4 and level 5 EUNIS biotopes included in the scope of this project is presented in the worksheet entitled ‘Habitat Characterisation’ in the data logging proforma that accompanies this report and in Appendix 3.

Some biotopes have been excluded from the habitat definition as they are not relevant to the UK. Two biotopes with very restricted extent were also excluded from the project scope due

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

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

to each being found in one place: A3.114 Sparse *Laminaria hyperborea* and dense *Paracentrotus lividus* on exposed infralittoral limestone (west coast of Ireland); and A4.136 *Suberites* spp. with a mixed turf of crisiids and *Bugula* spp. on heavily silted moderately wave-exposed shallow circalittoral rock (east of the Isle of Anglesey).

1.2 Project Aims

The aim of this project is to produce a series of Conceptual Ecological Models (CEMs) to demonstrate the ecological links, environmental drivers, ecosystem processes and ecosystem functions that occur in sublittoral rock 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 were as follows:

1. Collate and review available information on the environmental and ecological aspects of sublittoral rock habitats, along with associated confidence and knowledge gap analyses.
2. Define ecological groups within the biological assemblages of sublittoral rock habitats.
3. Create a hierarchical set of control models to represent shallow sublittoral coarse sediment habitats and relevant subsystems.
4. 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.
5. Describe how the driving influences (ecosystem drivers), biological assemblage groups and output processes 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 distribution and variability.
- Biological traits of the key species identified, including features such as life history, environmental preference, feeding habitat and ecosystem services provided.
- Ecosystem functions provided by the habitat/species, whether physical, chemical or biological and an assessment of the scales at which these functions occur.

In order to effectively conduct the literature review, specific research areas of the project were defined as follows:

- **Environmental Driver** – the physical, biological and chemical controls that operate on an ecosystem, shape its characteristics and determine its faunal and floral composition across all spatial scales.
- **Ecosystem Function** – the physical, chemical and biological process outputs of the ecosystem that are interconnected with other biotic and abiotic cycles.

- **Ecosystem Process** – the processes through which the flora/fauna and ecosystem are able to provide ecosystem functions.
- **Species Trait** – a biological characteristic of a certain taxa relating to their life-history, ecological interactions or environmental preference.

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

2.1 Species Selection

As it was judged that the majority of environmental drivers affecting each biotope would likely be similar in nature on a general level, and the main ecosystem processes/functions would also be similar at a functional group level (allowing for differences driven by varying energy inputs), it was decided that the key and most variable aspect of the final models would likely be the characterising flora/fauna themselves.

An initial review of all taxa associated with the project biotopes yielded a list of 255 species as described in the biotope descriptions (Connor *et al* 2004).

An initial review of the biotope descriptions (Connor *et al* 2004) identified a list of 255 species that have been recorded as occurring within the biotopes. It was not possible within the time-scales of the project to conduct a full literature review on the full species list. In addition, considering all species within the models was considered undesirable as some species may not be wholly representative of sublittoral rock habitats, either occurring across many biotopes including sedimentary types, or conversely be restricted, at low abundances, to one or two biotopes. Based on the author’s expert knowledge, species understood not to be fully representative of sublittoral rocky habitats were removed from the list.

To help focus the task within the allotted timescales, the list of species to be included in the scope of the project was refined to the key characterising taxa representative of all the project biotopes. All taxa named in the biotope titles were automatically included in the project species list. The biotope descriptions listed in Connor *et al* (2004) were then interrogated and any species that were noted as important or characterising in the biotope commentary, but not included in the biotope titles, were included. This yielded a list of 159 characterising taxa, which was considered to still be too large for the scope of the project.

The full species list (255 taxa) was then subject to a detailed review, and species or groups understood, based on the expert knowledge or judgement of the authors, to be important or distinct in terms of ecosystem function and traits were flagged up for inclusion.

To ensure that the species selected for more detailed review and inclusion in the models were representative of the taxonomic and functional range of species present within the biotopes, a further selection step was applied. The list of named and important taxa was split into high-level functional groups (foliose brown algae, grazing gastropod, anemone *etc*.) based on taxonomy, expert opinion and a limited initial literature review. The functional groups were then refined based on a combination of taxonomic Order, growth form and feeding preference to give 43 groups. The depth zone and habitat energy preference from the biotopes in which the species were listed was also recorded. The species list was then systematically reduced by selecting one species to represent each rudimentary functional

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

group, ensuring that all habitat and energy preferences were covered by the species selected. Where multiple species from the same functional group existed that were found in the same depth zone/energy habitat, preference was given to species considered more common (using expert judgement), or for which traits information was available via the MarLIN Biological Traits Information Catalogue database[6].

The Excel Add-In TREx (Taxonomic Routines for Excel) was used to check taxonomic information (spelling and name changes) about the species selected. TREx was also used to identify whether any of the total of 255 originally identified species were of conservation importance or alien species to the UK. This check resulted in three species, *Echinus esculentus*, *Eunicella verrucosa* and *Nucella lapillus* being added to the selection list.

A revised list of 76 benthic species to be considered within the immediate scope of the project was taken forward for literature review, as shown in Appendix 1 and in the accompanying ‘Project Species’ worksheet.

2.2 Species Traits Selection

Species traits provide information regarding the biology and ecology of living organisms. Species traits are an essential consideration within the model, impacting on the ecosystem functions and feedback influences within the habitat. Following the methodology undertaken in Alexander *et al* (2014), a comprehensive list of biological traits was collated from the MarLIN 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 45 biological traits, which was further refined based on other comparable studies (e.g. Van der Linden *et al* 2012; Bolam *et al* 2014; Tillin & Tyler-Walters 2014) and through expert opinion to give a manageable list of 18 relevant traits for inclusion in the project. The list of 18 traits is shown in the accompanying spreadsheet (‘Trait Selection’ worksheet), including a short justification for the inclusion of each trait. Standardised trait categories (based on those indicated in the MarLIN BIOTIC database) were utilised wherever possible in the literature review. The traits selected for this project are similar to those used in Alexander *et al* (2014), however differ slightly in reflection of the different nature of the hard substrata in rock habitats.

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 sublittoral rock habitats;
ii) the ecosystem processes and functions that the constituent taxa and biotopes are likely to produce; and
iii) the interactions that may occur between components and levels of the final models.

This information was initially identified using peer-reviewed papers which were the preferred literature source as they were thought to be the most reliable. These were then supplemented with information from other sources. Multiple electronic databases (Science Direct, Web of Knowledge, Wiley Online Library) were searched using a list of key words (included in Appendix 2) which ensured that all databases were thoroughly interrogated, and allowed a systematic approach to the literature review.

A ‘grey literature’ search (i.e. literature that has not been peer-reviewed, such as articles, theses, technical reports, agency publications *etc*) was also undertaken following the same

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[6] http://www.marlin.ac.uk/biotic

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, *etc*).

Where possible, an attempt was made to utilise sources relating to information from the UK; in some cases, the search was widened beyond the UK to locate information relevant to the research topic. The implications of this are discussed in the confidence assessment presented in Section 7.

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

- *Sertularia argentea* is a synonym of *Sertularia cupressina* var. *argentea*
- *Pomatoceros triqueter* is now known as *Spirobranchus triqueter*

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

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 Rock CEM Literature Review and Ancillary Information Version 0.2) and were developed in conjunction with the project steering group and in accordance with Alexander *et al* (2014). The information logged was divided into the following sections (worksheets):

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

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

- **Reference Summary**: Source information, full reference, abstract, summary of relevant material extracted and source confidence. Each reference was given a unique code used to identify the source throughout all sheets.

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

2.4.1 Magnitude and Direction of Influence

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

Table 1. Assessment of direction of interaction (Alexander *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. increased habitat complexity links to enhanced biodiversity.
Negative	The CEM component being considered has a negative/destabilising influence on the component it is linked to, e.g. the presence of high kelp in a habitat may lead to reduced sediment transport.
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 by this project is a key consideration. Confidence has been assessed in a number of ways. The confidence matrix utilised for individual evidence sources is shown in Tables 3a-c. This uses parameters such as source quality (peer-reviewed/non peer-reviewed) as shown in Table 3a, and applicability of the study (whether the source is based on data from the UK and relates to specific model features or not) as shown in Table 3b.

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

Confidence in the individual sources gathered as part of the literature feeds into confidence in the resulting models produced by this project. Confidence in the models and the methodology applied is described in Section 7.

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 6.

The majority of biological traits information was obtained from peer-reviewed and grey literature (such as the MarLIN BIOTIC database) and from taxonomic identification books and keys. Predominantly, the information obtained from journals was research that had been carried out internationally from comparable temperate regions, but in most cases can still be applied to UK species. During the literature review, it became apparent that information was more readily available for larger, common species, or those that are commercially exploited, but less so for rare and ambiguous taxa.

Due to the paucity of information relating to driving factors on specific biotopes, a focus was given to generic drivers likely to affect all sublittoral rock habitats, although a large emphasis was placed on the energy level of the environment. In some cases, studies from the rocky intertidal zone have been used to provide proxy data for the subtidal zone, as it is apparent that considerably more effort has gone into intertidal research than subtidal. A degree of expert opinion has been used to infer the linkages between some key environmental driving factors and the biological communities. Many of the sources identified relating to environmental drivers were overarching papers that did not relate to a specific location or range. Preference was given to sources describing ecosystem function in sublittoral rock habitats in the UK, although it was not always possible to find suitable information. Where data is particularly limited in applicability, this has been reflected in the ‘limitations’ column in the accompanying spreadsheet and in the source confidence score. Information for the majority of interactions was taken from peer-reviewed articles, with either a high or medium confidence level.

The results of the conservation status checks indicated that the majority of the species selected are assumed to be native to the UK. The dog whelk *Nucella lapillus* is listed under the OSPAR convention, the pink sea fan *Eunicella verrucosa* is protected by the Wildlife and Countryside Act 1981 and is a priority species for conservation under the Natural Environment and Rural Communities Act 2006. The edible urchin *Echinus esculentus* is also listed as ‘Near Threatened’ on the IUCN Red List[8].

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

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

3.1 Knowledge Gap Assessment

A moderate-high level of information was gathered to inform the project as part of the literature review. An ongoing and systematic knowledge gap assessment is being undertaken in order to evaluate the nature of this data and to identify any areas where additional effort was needed to gather evidence to inform the models.

The ‘Faunal Traits Summary’ worksheet in the accompanying spreadsheet indicates the degree of evidence that has been sourced for species trait information. The majority of floral and faunal traits have a high level of information recorded. Information on basic traits, such as mobility type and size for example, are complete for all taxa covered by the project. Less information was sourced for more complex aspects, such as species connectivity to other habitats and species, species status as a key prey item, and whether a taxon is likely to have a naturally highly variable population. In some cases, expert opinion has been used to input trait information, as indicated in the ‘Faunal Traits Summary’ worksheet. Expert opinion carries a lower confidence score (see Table 3a).

Information gathered on the ecosystem interactions that occur in sublittoral rock habitats has been incorporated into the confidence assessments associated with each of the models produced by this project, as described in Section 2.5. Those interactions that are well informed by multiple sources have a high associated confidence. Where literature evidence could not be sourced, expert judgement has been used to inform interactions between ecosystem components (see Section 2.5). Expert judgement carries a lower confidence score (see Table 6) but is considered appropriate for those traits and interactions deemed to be well known and/or understood, despite a lack of references (whether actual or could not be sourced within the project timescales). This is fully highlighted in the confidence models that accompany each conceptual ecological model (see Section 7). 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 7.

Literature sources detailing the interactions between high-level environmental drivers are relatively generic 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 that could not be informed by expert judgement.

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

4 Defining Ecological Groups

The ecological groups defined are intended to form the basis of the Conceptual Ecological Models produced as the outputs for this project. Incorporating each characterising species separately in the models was considered unworkable due to the great number of assessments required and the lack of information available for many species, and therefore Ecological Groups have been used to present group information. By identifying Ecological Groups from the list of characterising species selected for inclusion in the project scope (as described in Section 2.1), a basis for the models can be developed.

Multivariate analysis was used as an exploratory tool to assess the traits of all characterising species selected in order to identify functionally similar groups of species that are likely to be influenced by the same drivers and support ecosystem function within the models. These groups have been termed ‘Ecological Groups’. The methodology presented in Tillin and Tyler-Walters (2014) has been utilised for this aspect of the project, given the comparable (though not identical) project objectives.

Biological traits information gathered during the initial literature search was used to populate a trait-species matrix. Table 4 shows the traits selected for this stage of the project, and the categories within that trait to which a species could be matched (adapted from the MarLIN BIOTIC database). This subset of traits was selected based on their usefulness in determining ecological groups, using the information provided in Tillin and Tyler-Walters (2014) and expert judgement, for example the trait ‘Mobility’ is important in determining which animals group together in terms of moving around the environment, and the trait ‘Typical Food Types’ indicates the different food sources each species feeds upon, allowing functionally similar taxa to be grouped together. Some traits, such as ‘Lifespan’ and ‘Connectivity to other taxa’, whilst deemed useful in informing the models themselves, were not considered overly important as a factor in determining ecological function, and were omitted from informing the creation of the Ecological Groups, in part due to a lack of suitable information and as it was deemed through expert judgement that other traits were more suitable to group taxa by. The traits selected for inclusion in this project vary slightly from those selected in Tillin and Tyler-Walters (2014) due to the differing objectives of the studies. A rationale for trait selection in this exercise is presented in the ‘Trait Selection’ worksheet in the spreadsheet which accompanies this report.

Following the methodology in Tillin and Tyler-Walters (2014), each biological trait for each species was assigned a numerical value using information gathered as part of the literature review so that the matrix could be interrogated statistically. Where a species expressed one specific trait category within the trait, a score of 1 was assigned to the relevant field. Where a species could express several trait categories, the score of 1 was split equally between all relevant fields. For example, when considering the trait ‘resource capture’, the bryozoan *Electra pilosa* is recorded as an active filter feeder only and thus receives a score of 1 within this field. The barnacle *Balanus crenatus* is recorded as both an active and a passive filter feeder, so receives a score of 0.5 in each relevant field, and the polychaete *Harmothoe* is recorded as a scavenger, a grazer and a predator, thus receives a score of 0.33 in each relevant field. This process was repeated for all species and for all traits until the matrix was completed. Empty fields in the matrix were assigned a score of zero as the analytical software does not allow missing variables.

Table 4. Biological traits and associated trait categories used to define Ecological Groups for species associated with sublittoral rock habitats. Information regarding the trait categories is largely taken from the MarLIN BIOTIC database (MarLIN 2006). Full definitions are included in the project definitions worksheet in the data logging pro-forma that accompanies this report. Traits were identified for inclusion in this exercise based on the methodology presented in Tillin and Tyler-Walters (2014) and using expert judgement[9].

Trait	Trait categories	Trait	Trait categories	Trait	Trait categories
Mobility	Permanently attached Temporarily attached Burrower Crawler Swimmer	Substratum preference	Bedrock Cobbles Gravel Sand Mixed Algae	Tidal stream preference	Very weak (negligible) Weak (<1kn) Moderately strong (1-3kn) Strong (3-6kn) Very strong (<6kn)
Typical food types	Particulate organic matter Plankton (phyto- and zoo-) Detritus Small invertebrates/ live prey Carrion Photoautotroph Microorganisms Algae	Maximum body size	Very small (<1cm) Small (1-2cm) Small-medium (3-10 cm) Medium (11-20cm) Medium-large (21-50cm) Large (>50cm)	Resource capture	Passive suspension feeder Active suspension feeder Deposit feeder Scavenger Predator Primary producer
Physiographic preference	Open coast Offshore seabed Enclosed coast Sheltered coast	Habitat	Attached Free-living Burrow-dwelling Tubiculous Erect	Salinity preference	Full (30-40psu) Variable (18-40psu) Reduced (18-30psu) Low (<18psu)
Environmental position	Infauna Epifauna Epilithic	Depth preference	Infralittoral Circalittoral Deep circalittoral		

4.1 Data Analysis

The resulting species-trait matrix was imported to PRIMER v6 statistical software (Clarke & Warwick 2001) for analysis, in order to help determine the ecological groups. A Bray-Curtis similarity matrix was created based on the untransformed and un-standardised values for each trait. The trait data were already considered to be standardised since the contribution to each trait category summed to 1 and no further data transformations were considered necessary. Patterns and similarities within the species traits were explored using both non-metric multidimensional scaling (nMDS) plots and cluster analysis (based on group averaging).

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[9] kn – knots and psu – practical salinity units.

The nMDS plot produced is shown in Figure 2. This shows several distinct clusters of species that have similar biological traits. A manual cut-off of 60% similarity on the dendrogram was used to aid interpretation of the nMDS plot, based on expert judgement. A number of nMDS plots were produced using different combinations of the traits shown in Table 4 as variables. Predominantly these traits included tidal stream preference, depth zone, species size, food types and habitat preference, as expert judgement deemed these to be the most important traits in defining the ecological groups for a conceptual ecological model of a control system (i.e. where human pressures are absent or negligible). None of the re-runs using alternative combinations of variables yielded any stronger groupings than those presented in Figure 2, thus it was deemed that it was best to use the greatest number of variables available to inform the ecological groups.

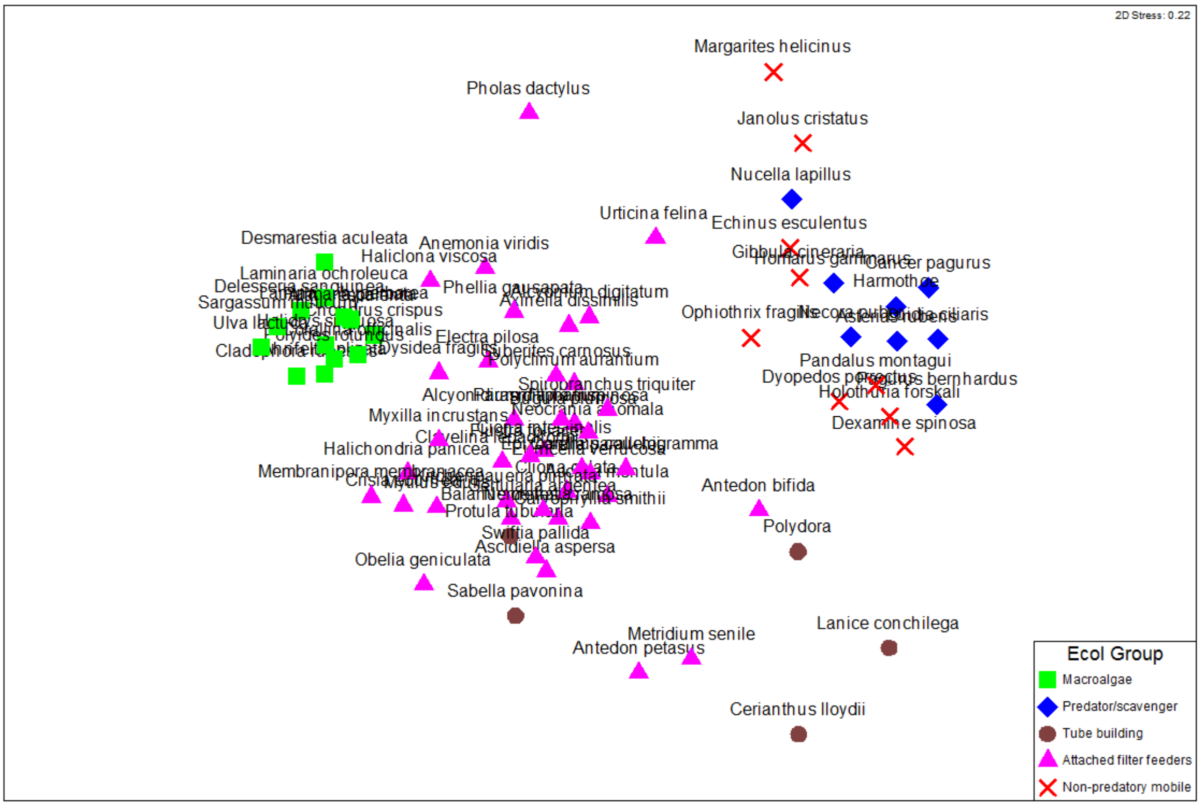

Figure 2. Non-metric multidimensional scaling ordination, shown in 2D format, based on Bray-Curtis similarity of coded traits for the selected project species. Colours show ecological groupings defined using expert judgement and the outputs of the cluster analysis.

It should be noted that the interpretation of the resulting plots is subjective and based on the relative distances between data points (in this case the species). Species that are plotted closer together in the ordination plots are more similar in terms of the selected traits than species that are further apart. The nMDS plot shown in Figure 2 indicates several distinct groups of species. A degree of expert judgement has been utilised to define the ecological groups from the analyses and it should be noted that the data labels indicating group membership were added following the ordination, rather than representing a priori defined groups. The ecological groups are defined below:

Macroalgae

The group defined as macroalgae contains exclusively primary producers. The species comprising this group are ordinated as a tight cluster in the nMDS plot (shown in green in Figure 2), likely to be driven by their common food type and resource capture method, which is distinct from the other taxa considered.

Temporarily or permanently attached filter feeders
A large and diverse group (shown in violet in Figure 2), temporarily or permanently attached filter feeders includes both tight clusters of species and outlying taxa on the nMDS plot. Overall group similarity is thus relatively low, however all taxa are connected by their attached status and filter feeding traits. Species listed in this group mainly include bryozoans, hydroids, sea anemones, bivalves and sponges.

Tube-dwelling fauna
This small group of four species (shown in brown on Figure 2) was defined on the basis of the tube-dwelling trait as these taxa do not form a distinct group within the ordination plots or cluster analyses. There is some overlap with 'temporary or permanently attached fauna' as expected due to similarities in feeding type and habitat preferences expressed by these species.

Scavengers/Predatory Fauna
Scavengers and predatory fauna grouped together relatively clearly in the multivariate analysis, the majority of species comprising the group at the 60% similarity level in the cluster analysis (shown in blue on Figure 2). This group comprises predominantly crustaceans and echinoderms, along with other taxa, all connected by their predatory or scavenger traits.

Non predatory mobile fauna
This group encompasses a range of fauna (shown in red on Figure 2). Predominantly the link between species is their high mobility and preference for detritus feeding or grazing. Amphipods, echinoderms and gastropods comprise this group.

5 Model Development

5.1 Model Design

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

Due to the large degree of species overlap between biotopes, it was deemed more useful to divide the species into ecological groups and develop models based on these, rather than develop models for individual biotopes or energy levels, which would require a large number of models that would likely be highly similar (redundant) as many ecological groups are present in most, or all of the biotopes. The resulting models would also be far more complex as they would include a number of ecological groups. The idea of producing models by energy level and depth zone was explored, however this was ruled out due to the complexities described above and because it was thought that an ecological group-based approach would be more useful in determining indicator species than a complex energy/habitat-style approach. The proposed approach also aligns with the methodology and hierarchy developed in Alexander *et al* (2014).

5.1.1 Model Hierarchy

General Model

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

Sub-Models

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

Sub-models for this project have been based on the ecological groupings of species identified above and selected for inclusion within the project scope. The groups identified in Section 4 have been taken as a basis for each sub-model. Expert judgement and evidence derived from the literature review has been applied to ensure that the most similar species are represented in the same groups. Those species that are most similar to each other in terms of biological traits are ultimately likely to be affected by similar driving factors and will produce similar output processes and ecosystem functions.

The groups identified in Section 4 have been modified slightly to form the model hierarchy. As a very large group identified through the multivariate analyses, ‘Temporarily or permanently attached filter feeders’ has been split into three sub-models (shown as sub-models 2-4 below). Bivalves, brachiopods and other encrusting filter feeders have been separated out as a distinct group, and the remaining attached filter feeders according to whether they are active or passive feeders (see Appendix 3 for a full species list for each group). The proposed sub-models are shown below and in Figure 3:

1. Macroalgae.
2. Temporarily or permanently attached active filter feeders.
3. Temporarily or permanently attached passive filter feeders.
4. Bivalves, brachiopods and other encrusting filter feeders.
5. Tube building fauna.
6. Scavengers/Predatory fauna.
7. Non predatory mobile fauna.

The matrix presented in Appendix 3 details the relevant species against the allocated biotope classifications and conceptual ecological sub-model, therefore allowing a rapid reference guide to the sub-models and which species and/or biotopes they cover. This also shows a breakdown of major ecological groups that are represented within each of the sub-models.

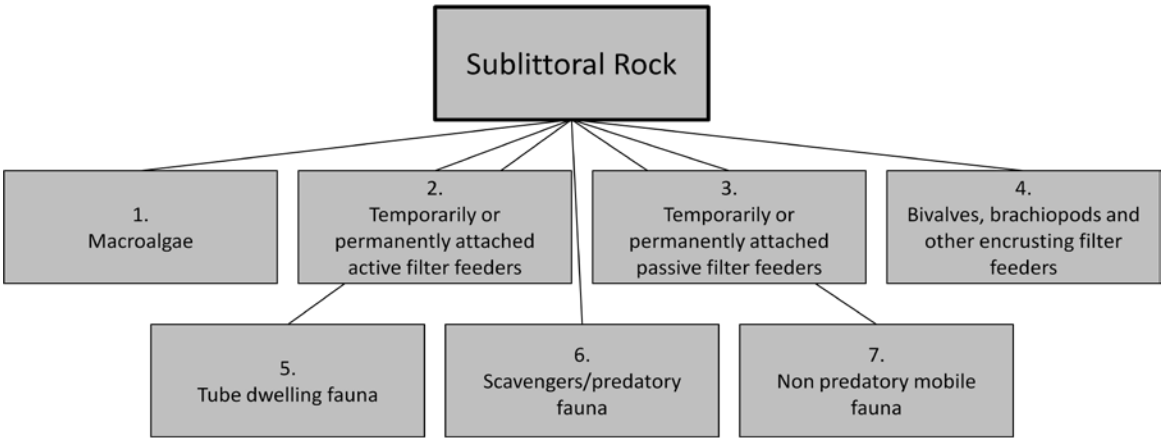

Figure 3. Sublittoral rock habitat CEM hierarchy. The top level of the flowchart represents the general control model, with the seven sub-models each documenting a specific functional group within this habitat. Sub models 2, 3 and 4 represent the same overall ecological group, although contain different major taxonomic groups, and have been split due to the size of the ecological group.

No differentiation is made in the hierarchy for fauna specifically related to the infralittoral or circalittoral zones due to the large degree of crossover apparent in drivers and function within the habitats. The characterising ecological groups (with the exception of macroalgae) occur in both zones, so separate models for the infralittoral and circalittoral would be redundant. The matrix presented in Appendix 3 indicates which species characterise which biotopes (as defined by this project), and indicates how each model relates to individual biotopes.

5.1.2 Model Levels

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

Ecosystem Drivers:

- **1. Regional to Global Drivers** – high-level influencing inputs to the habitat that drive processes and shape the habitat at a large scale, e.g. water currents, climate *etc*. These are largely physical drivers, which have an impact on the water column profile.
- **2. Water Column Processes** – processes and inputs within the water column that feed into local seabed inputs and processes, e.g. suspended sediment, water chemistry and temperature *etc*.
- **3. Local Processes/Inputs at the Seabed** – localised inputs and processes to the ecosystem that directly 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) that typifies the habitat. For the sub-models, fauna are categorised into functional groups and sub-functional groups as necessary. Example taxa characterising each group are named in the models, however for the full list of fauna related to each grouping, please see Appendix 3.

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 that are applicable on a local scale, whether close to the seabed or within the water column, e.g. nutrient cycling, habitat provision *etc*.
- **7. Regional to Global Ecosystem Functions** – ecosystem functions that occur as a result of the local processes and functions performed by the biota of the habitat at a regional to global scale, e.g. biodiversity enhancement, export of organic material *etc*.

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

ECOSYSTEM DRIVERS	
1. Regional to Global Drivers	
Depth	Distance between water surface and sea bed
Wave Exposure	Hydraulic wave action
Water Currents	Movement of water masses by tides and/or wind
Climate	Short term meteorology and long-term climatic conditions
Geology	Underlying rock or substratum
Propagule Supply	Supply of larvae, spores and/or regenerative body fragments
2. Water Column Processes	
Water Chemistry and 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
Primary Production	The production of new organic substances through photosynthesis
Dissolved Oxygen	The dissolved oxygen concentration in the water column above the seabed
Light Attenuation	The penetration of light in the water column
Suspended Sediment	Particles of sediment which have become elevated from the seabed and are being kept suspended by turbulence within the water column
3. Local Processes/Inputs at the Seabed	
Food Sources	Types of food ingested by the fauna represented in the models
- Plankton	Microscopic plants and animals which inhabit the water column (for the purposes of this study, phytoplankton and zooplankton have been grouped together)
- POM (Particulate Organic Matter)	Non-living material derived from organic sources within the water column
- Detritus	Organic waste and debris contained within seabed sediments
- Algae	Plants and algae attached to the seabed
- Carrion	Dead and decaying animal flesh

- Micro-organisms	Microbial organisms (e.g. bacteria, diatoms and protozoa)
- Small Invertebrates and Fish	Live prey items such as bivalves, polychaetes or small fish
Seabed Mobility	Movement of sediment on the seabed
Grazing and Predation	The predation of organisms by another
Recruitment	The process by which juvenile organisms join the adult population. Combines settlement and early mortality
4. Habitat and Biological Assemblage	
Macroalgae	Marine algae including red, green, brown and kelp variants
Attached Active Filter Feeders	Organisms attached to the seabed surface which are predominantly active filter feeders, e.g. create water flow to feed
Attached Passive Filter Feeders	Organisms attached to the seabed surface which are predominantly passive filter feeders, e.g. rely on natural water movement to feed
Bivalves, Brachiopods and Other Encrusting Filter Feeders	Boring and attached bivalves and brachiopods as well as other surface encrusting filter feeders
Tube Building Fauna	Tubicolous fauna that construct and live in tubes made from sedimentary material on the surface of the seabed
Scavengers and Predatory Fauna	Mobile scavenging and predatory crabs, echinoderms, polychaetes and molluscs
Non Predatory Mobile Fauna	Mobile fauna which are either predominantly grazers or which feed on detritus or POM
ECOSYSTEM OUTPUTS	
5. Output Processes	
Primary Production	The production of energy through the process of photosynthesis (typically by algae and plankton in the marine environment)
Secondary Production	Creation of biomass as a direct result of consumption
Bioengineering	Faunal modification of the natural habitat, e.g. tube building, boring organisms, algal canopy *etc*
Hydrodynamic Flow	Changes to water flow/movement as a result of organism activity
Biodeposition	The process by which organisms either deposit material onto the seabed, e.g. through the capture of particulate matter in the water column through filter feeding or the production of faeces/pseudo-faeces
Supply of Propagules	The production and transportation of larvae, spores or body fragments capable of regeneration
6. Local Ecosystem Functions	
Nutrient Cycling	Cycling of organic and inorganic nutrients that involves processing into a different chemical form
Biogeochemical Cycling	The cycling of organic carbon and nitrogen other than nutrients
Food Resources	The provision of food resources for other organisms
Population Control	Control of lower trophic level organism population through predation
Control of Algal Growth	Control of algal biomass through grazing pressure
Sediment Stability	Cohesion of sediments into a stable form more resistant to disturbance
Habitat Provision	Provision of living space for other organisms through surface attachment of increased habitat complexity
7. Regional to Global Ecosystem Functions	
Export of Biodiversity	Export of biodiversity, including propagules, outside of the habitat
Export of Organic Matter	Export of organic material outside of the habitat, such as food sources *etc*
Biodiversity Enhancement	Enhancements in biodiversity within the habitat resulting from increased sediment stability and habitat provision
Biotope Stability	Stability of the habitat through the habitat provision and increased sediment stability

For the purposes of this study ‘sublittoral rock’ incorporates those biotopes identified in the project scope, presented in Appendix 3. This includes biotopes comprising bedrock, boulders, cobbles, and in some cases mixed sediments. This range of substrata presents multiple habitat types and a highly diverse array of taxa to be studied.

5.1.4 Model Interactions

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

The links in the general model reflect driving influences, as well as positive and negative influences and feedback loops. However, the general model does not indicate the magnitude of influence for each interaction. This is a result of the general model summarising information from the habitat as a whole where multiple functional groups are being considered. Thus, in some cases, conflicting information on magnitude of influence of one component on another would need to be presented, which is not achievable. Where there was a necessity to show conflicting interaction direction within an ecological group, the process which represented the majority of compositional species was indicated.

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

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

In order to differentiate between driving factors that are most relevant in the infralittoral zone and those that 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.

5.1.5 Natural Variability

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

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

In common with Alexander *et al* (2014), natural variability is assigned a score of 1-3 where 1 represents low variability (small circle symbol on models), 2 medium variability (medium circle symbol on models) and 3 high variability (large circle symbol on models). Scores are based on an expert judgement estimate of the above criteria and are indicated on the models for environmental drivers and inputs at levels 1-3.

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

5.2 Model Confidence

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

The combined confidence for the interactions from multiple sources is scored in accordance with the protocol presented in Table 6 and is based on the combined confidence methodology developed in Alexander *et al* (2014). This assesses the number of sources related to one particular link within the model, the level of agreement between them and differentiates between sources of information (Alexander *et al* 2014).

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

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

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

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

Confidence results are presented in Section 7. 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.

5.3 Model Limitations

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

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

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

Confidence in the models is somewhat influenced by the extent of the literature review, time and budgetary constraints of the project. This is further discussed in Section 7.

6 Model Results

Each of the models produced is described and discussed in the following sections of this report. The models produced stand as an accompaniment to this report and are also included in Appendices 5-11. The models should be interpreted in consultation with the biotope/model matrix presented in Appendix 3. Reference should also be made to the ‘Habitat Characterisation’ spreadsheet which accompanies this report (tab 2 in Sublittoral Rock CEM Literature Review and Ancillary Information) for details of the physical parameters which define the habitat and each constituent biotope of sublittoral rock. Tab 7 in the same spreadsheet (interaction matrix) provides further information on the specific species within each ecological group that informed the interactions in the model.

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

It should be noted that information presented under each model heading is tied to the confidence assessments presented in Section 7. References for the information discussed are shown where literature sources have been found to back up the statements being made.

6.1 General Control Model and Common Model Components

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

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

6.1.1 Ecosystem drivers

Regional to Global Drivers

The majority of ecosystem drivers relate to the physical environment in the general model, especially at the regional to global scale. Several of the drivers are critical in defining the physical character of the habitat itself (such as depth), whereas others are crucial in determining the subsequent biological assemblage and resulting output processes (such as water currents).

Depth is a key defining factor of the sublittoral rock biotopes being considered in this project, through separation of infralittoral and circalittoral biotopes, and its influence on other critical drivers (Cusson & Bourget 2005; Eriksson & Bergstrom 2005; Basford *et al* 1990; Bolam *et al* 2010). Rocky sublittoral habitats are principally defined by the amount of physical energy (in the form of wave exposure and water currents) that the habitat is subject to, which is directly mediated by depth (Masselink & Hughes 2003). Water depth is also a major driving factor affecting key water-column processes, significantly affecting light attenuation (Devlin *et al* 2009) and temperature (Munn 2004), thus indirectly controlling primary production. Depth is therefore one of the major defining factors of the sublittoral rock habitats with a high relevance in both the circalittoral and infralittoral zones (Basford *et al* 1990).

Wave exposure is a dominant controlling factor in benthic assemblages in the sublittoral rock habitat (Little & Kitching 1996) (see ‘Habitat Characterisation’ spreadsheet for biotope-specific details). The limit of wave exposure is defined as the wave base, the maximum depth to which wave energy causes motion in the water column (Connor *et al* 2004). The effects of wave disturbance are far more prominent in shallower waters, that is, the infralittoral zone (Masselink & Hughes 2003; Brown *et al* 2002a). The greater the wave exposure, the greater the physical stresses in the environment, and therefore organisms are likely to need a greater degree of adaptation to thrive there (Little & Kitching 1996). Despite this, algal and faunal diversity has been shown to increase with wave exposure in some studies (e.g. Nauderhaug & Christie 2011). Wave exposure is also likely to have an influence on water column chemistry and oxygen availability due to mixing (Diaz & Rosenberg 1995; Brown *et al* 2002b). Wave exposure is defined as having moderate natural variability, based on current meteorological conditions including seasonal variation, cyclical fluctuations and the frequency of extreme events. For example, severe autumn storms can increase the impact of wave exposure, mixing of the water column and breakdown of summer thermoclines in deeper waters (Diaz & Rosenberg 1995).

Water currents are defined to include both current-mediated flow and tides (Reiss *et al* 2009). They provide a mechanism for transport of particulate matter, sediments (not relevant to bedrock environments), and components of the water chemistry and temperature profile, as well as supplying energy to the seabed (Hiscock *et al* 2004). The transport mechanism supplies food resources for filter feeding organisms, and influences water column chemistry and temperature through mixing (Chamberlain *et al* 2001; Biles *et al* 2003). Bottom-water circulation distributes dissolved oxygen in the water column and transfers oxygen from the surface to the seabed (Diaz & Rosenberg 1995). Although water currents do vary naturally in magnitude and direction through the seasons and annually (both tidal and non-tidal flows), natural variability is low in comparison to other components.

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

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 bedrock and post-glacial drift material have an influence on any pockets of sediments in the rock habitat. Many of the species included within the project scope require stable hard substrata in order to attach themselves, thus the presence of bedrock outcrops is of crucial importance. Equally, some species such as boring piddocks (e.g. *Pholas dactylus*) require soft bedrock outcrops into which they can burrow in order to thrive in the sublittoral rock environment (MarLIN 2006).

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

Water Column Processes

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

Water chemistry and temperature is a large component that incorporates several features grouped together for ease of presentation. Properties include salinity, temperature, nutrients and dissolved organic material, along with dissolved oxygen. These may be influenced by many regional to global drivers; however wave exposure, depth, water currents and climate are shown on the model as particularly important due to direct influences, such as climate on water temperature, water currents, nutrient transport, and wave exposure on dissolved oxygen mixing (e.g. Brown *et al* 2002b; Dutertre *et al* 2012). Photosynthesis is the most important source of dissolved oxygen in the marine environment, while wave and wind exposure facilitate the uptake of dissolved oxygen from the atmosphere and mixing into the water column (Brown *et al* 2002b). In addition to primary production, water chemistry and temperature links to biological components such as food sources and the biological community of the habitat, based on the need of organisms for dissolved chemicals in the water column (nutrients, calcium carbonate *etc*) and specific temperature requirements (Cusson & Bourget 2005; Bolam *et al* 2010). A feedback loop from biogeochemical cycling as a local ecosystem function to water chemistry also exists, signifying the re-supply of organic material to the water column (e.g. Libes 1992). Water chemistry and temperature is defined as having moderate variability, based on environmental drivers and potential for changes over the short and long term.

Primary production by phytoplankton and macroalgae is a crucial aspect of the sublittoral rock habitat models. Primary production predominantly occurs in the shallow waters of the infralittoral zone, (e.g. Jones *et al* 2000) and is a nutrient (water chemistry) and light dependent process that forms the basis of all marine food webs (Hiscock *et al* 2006; Devlin *et al* 2009). Primary production is also influenced by water chemistry (nutrients) and temperature as necessary factors for photosynthesis (Hily 1991; Lalli & Parsons 2006; Hiscock *et al* 2006). Primary production is presented in this project as an output process from the macroalgae sub-model and an input process influencing food resources for all other sub-models.

Light attenuation is another important factor of the sublittoral rock habitat. Influenced by depth (as described above) and suspended sediments (Masselink & Hughes 2003; Brown *et al* 2002a; Devlin *et al* 2009), and linking to primary production as well as directly to the fauna and flora of the habitat, this factor is of large importance, especially to the macroalgae communities that dominate many of the infralittoral biotopes. As the top of the circalittoral zone is defined as receiving 1% light attenuation (Connor *et al* 2004), primary production is largely confined to the boundaries of the infralittoral zone (e.g. Lalli & Parsons 2006). There is the potential for macroalgae species to negatively affect light attenuation through the production of thick canopies; this is further discussed in Section 6.2.3.

Suspended sediments, although not likely to be as prevalent in sublittoral rock habitats as opposed to soft sediment habitats, are still an important factor within the water column. Suspended sediments are mainly influenced by wave exposure, water currents and to a lesser degree geology (Brown *et al* 2002b), directly affecting light attenuation through turbidity of the water column. An increased suspension of fine sediments can influence the filter-feeding mechanisms of suspension feeding infauna.

Local Processes and Inputs at the Seabed

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

Seabed mobility, a proxy for the extent to which the habitat is affected by natural physical disturbance and a key driver in sedimentary habitats, has limited applicability to hard substrata. This factor has been included in the sublittoral rock models due to the inclusion of a small number of mixed sediment biotopes in the project scope, with varying degrees of sand and gravel contained therein. Environments with a high degree of seabed mobility are likely to be characterised by fauna tolerant of mobile sediments and sediment movement, or those which are able to consolidate loose substrata. Fauna that are filter feeders straining food particles from the water column are likely to require some degree of current flow in order for transport of particulate food sources to be maintained, although currents that are too strong could result in a highly mobile seabed, with decreased sediment stability, and harsher living conditions (Nybakken 2001; Masselink & Hughes 2003; Lalli & Parsons 2006).

Grazing and predation is a key local scale biological driver affecting both macroalgae and benthic faunal assemblages. Grazing herbivorous fauna are important controllers of algae in the sublittoral rock habitat (e.g. Nybakken 2001; Livore & Connell 2012; Dauvin *et al* 2013) and macrofaunal predatory taxa can have a likewise top-down limiting control on macrobenthic fauna.

Substrata/sediment type has a profound effect on the faunal and floral complement of a particular habitat. Many of the species considered in this project require a hard rocky surface to attach themselves to. Where softer sediments exist as opposed to exposed bedrock, such as in mixed sediment biotopes, the nature of these sediments is highly influential on benthic fauna. (Ellingsen 2002; Seiderer & Newell 1999; Basford *et al* 1990; Cooper *et al* 2011). Sediment type itself is influenced by multiple factors, including wave exposure, water currents, underlying geology, seabed mobility and to some extent the fauna itself (e.g. Brown *et al* 2002a). Whilst underlying geology may be an important driver of sediment type, it is important to note that many coarse sediment deposits found in UK waters are likely to be the product of Pleistocene-age drifts, or similar deposits (e.g. Limpenny *et al* 2011; Tappin *et al* 2011) which may rest on unrelated geological formations. As a result, surface sediments may be unconsolidated and could be prone to movement or winnowing (Masselink & Hughes 2003).

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

6.1.2 Ecosystem Outputs

Output Processes

The output processes described in this section are those that are generic to sublittoral rock habitats. As the type and level of output processes and ecosystem functions are driven by the characterising fauna of each habitat, the sub-models should be referred to for specific interactions (and references) related to one particular functional group.

Output processes from the sublittoral rock habitat can be broadly split into five main categories: primary production, secondary production, bioengineering, biodeposition and supply of propagules. These are sometimes described as ‘ecosystem services’, but for the purpose of this project are described as ‘processes’, as this project is not focused on the supply of services that have value to humans.

Primary production is an essential function performed by the macroalgal species that populate the rocky subtidal habitat. Through the process of photosynthesis, macroalgal assemblages produce energy which along with phytoplankton forms the basis of marine food webs (e.g. Nybakken 2001; Lalli & Parsons 2006). Primary production leads to the supply of food sources for secondary producers, plays an important role in biogeochemical and nutrient cycling (Nybakken 2001), and ultimately results in the export of organic matter outside of the immediate system (Nauderhaug & Christie 2011; Birkett *et al* 1998).

The major output process produced by macroalgae is primary production. As a result of this, macroalgae act as 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 food 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 (Nauderhaug & Christie 2011; Birkett *et al* 1998). The process of photosynthesis also leads to increased levels of dissolved oxygen in the water column (e.g. Lalli & Parsons 2006), indicated by the feedback link shown on the general model.

Secondary production (defined as converting energy to/from lower to higher trophic levels, although not necessarily from primary producers) follows on from this, and is a core process undertaken by all fauna as growth and consumption of other lower trophic level organisms occurs (Lalli & Parsons 2006). This is a key feature of the conceptual ecological models and a core output process which in turn drives important ecosystem functions at the local scale, such as provision of food resources and nutrient cycling (Nybakken 2001; Lalli & Parsons 2006), and leads indirectly to the export of organic matter and the export of biodiversity at the wider scale. This is a major influencing factor in increasing food and prey availability within the habitat.

Bioengineering, the modification of the natural environment by flora or fauna, is likewise an important output process in the rocky subtidal habitat. Both macroalgae and fauna have the capability of modifying the benthic environment, through the creation of living structures, the creation of burrows or the creation of tubiculous habitats. Bioengineering is an important factor especially in the rocky subtidal habitat as it promotes increased habitat complexity.

Biodeposition is a less prominent feature of the rocky subtidal habitat than compared to soft sediment habitats, although remains important especially where mixed sediment biotopes occur. Biodeposition largely refers to the capture of particulate matter in the water column by filter feeders and the transfer of this material to the benthic habitat, however it also refers to the production of faeces and pseudo-faeces by non-filter feeding organisms. Biodeposition therefore influences nutrient cycling, and impacts biogeochemical cycling. Wave exposure and water currents are likely to impact the dispersal of material amassed through biodeposition, especially so in hard substrata biotopes, however the link has not been indicated on the general model in order to facilitate presentation.

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 sublittoral rocky habitat and is essential for the maintenance of the 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 by the representative fauna of each ecological group 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, both naturally occurring as well as occurring as a function of the other biological features of the habitat (Mermillod-Blondin 2011; Kristensen *et al* 2012). Microbial activity leads to nitrogen and carbon fixation, which feeds back to water chemistry as an ecosystem input (Munn

2004; Bertics *et al* 2010). The role of microbes in the rocky subtidal habitat has been omitted from the models due to the increased level of complexity presenting these features would produce, and a lack of clear literature evidence to inform the links.

The ability of the habitat to produce food resources is represented as an ecosystem function, influenced by both primary and secondary production. This is through direct predation of primary producers and consumption of higher trophic level fauna by predators. Through the export of food resources from the habitat, this factor has the potential to influence regional to global ecosystem functions, as indicated on the model.

The provision of food resources as an ecosystem function is closely related to population/algae control. A function performed by grazing secondary producers and predators, population control is an important factor in rock habitats, especially where space is at a premium and the potential for biological dominance of the habitat by a limited number of species exists.

Sediment stability, although only particularly relevant to mixed sediment biotopes, is likely to be affected by the output processes of sediment processing and habitat modification. Consolidation of sediments by fauna is achieved in several ways, predominantly in the rocky environment by aggregations of fauna (such as *Mytilus edulis*), or through bioengineering (algal consolidation of sediment, presence of tube building fauna *etc*).

Habitat provision is the result of bioengineering of the natural environment and the colonisation of species that are found within the biotope themselves by symbiotic or commensal organisms (Vader 1984; Pretterebner *et al* 2012). This in turn has the potential to enhance biodiversity at the regional and global scale, as well as contributing habitat complexity and 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 the processes occurring on sublittoral rock habitats. The export of both organic matter and biodiversity are provided for by the supply of propagules, secondary production and production of food resources. Biotope stability and biodiversity enhancement are directly influenced by sediment stability, population and algae control, and habitat provision (Nybakken 2001; Lalli & Parsons 2006).

6.1.3 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 as connectivity varies at spatial and temporal scales which have not been elucidated or are difficult to represent generically.

There are various marine habitat types around the UK that may be found in close proximity to sublittoral rock habitats which do not exist in isolation and are intrinsically linked, for example littoral rock (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 sublittoral rock 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 that occur in sublittoral rock 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.

6.2 Sub-model 1. Macroalgae

6.2.1 Biological assemblage

The macroalgae sub-model represents algal primary producers in the sublittoral rock habitat. This model differs from the other sub-models produced in that no faunal species are represented within this sub-model. Whilst there is variation within the macroalgal species included in the project scope, most algal species are subject to the same driving factors and produce relatively similar ecosystem outputs and functions. Macroalgal species have therefore been split into more specific ecological groups for representation within the model as follows:

- Kelp e.g. *Laminaria hyperborea*
- Brown algae e.g. *Halidrys siliquosa*
- Green algae e.g. *Ulva lactuca*
- Red algae e.g. *Palmaria palmata*

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

Along with other primary producers, macroalgae form the basis of the marine food web, and as such are a key functional group within the rocky subtidal habitat. The macroalgae sub-model relates almost exclusively to the infralittoral zone, as macroalgal species are largely absent from the relatively light devoid circalittoral zone.

Algal species are found in a range of energy levels and on various substratum types (Connor *et al* 2004) although they require relatively clear water and suitable surfaces to attach holdfasts to in order to thrive. Algal species have the potential to be significant bioengineers, as some species (notably kelps) produce large canopies, under which complex understorey communities can develop (Birkett *et al* 1998).

6.2.2 Ecosystem Drivers

Physical environmental drivers are of great importance to macroalgal species. Regional to global and local drivers such as depth, wave exposure, water currents, and the nature of the seabed habitat are noted to be important in algal distribution (Eriksson & Bergstrom 2005). Depth is a crucial factor in determining macroalgal assemblage presence, diversity and biomass (Eriksson & Bergstrom 2005). Principally this is through light attenuation (see Section 6.1.1), rather than the physical impacts of depth and moderation of wave exposure (Kregting *et al* 2013).

Algal species require the presence of surfaces suitable for attachment in order to establish holdfasts for themselves. These occur predominantly in hard substrata environments where the seabed is stable and not likely to be subject to physical disturbance. Further to this, sediment deposition has been shown to significantly affect local structure and diversity of macroalgal assemblages (Moore 1972; Airoldi 1997). Erect algae are more likely to be affected than other growth forms and growth of large numbers of algal species have been shown to be enhanced in periods of reduced sedimentation (Airoldi 1997). As a consequence, stable rocky habitats are more suitable for most algal species rather than coarse mixed sediments or other sediment types.

Wave exposure is an important factor controlling the morphology, structure, diversity and abundance of macroalgae (Wernberg & Connell 2008), with species diversity showing an increase with elevated wave exposure (Nauderhaug & Christie 2012). Studies have also shown that in the presence of epiphytic algae, species richness increases with wave exposure (Nauderhaug & Christie 2011). Water currents are likewise noted as important controlling factors of macroalgal distribution, especially for juveniles. The flow of water is considered to be an important physical driving factor (Kregting *et al* 2013), thought to moderate habitat suitability through effects on sediment accretion and removal, as well as being responsible for the supply of nutrients and gases and the dispersal of oxygen and propagules.

In addition to the main driving physical factors, macroalgae are heavily influenced by factors affecting rates of primary production, such as light attenuation (e.g. Jones *et al* 2000), climate (Merzouk & Johnson 2011), water column chemistry and temperature, including nutrient content (Hily 1991; Lalli & Parsons 2006; Hiscock *et al* 2006).

As for all sub-models, propagule supply is an important biological driver for macroalgae. Recruitment into the adult population will drive the biological assemblage directly, in turn producing propagules and completing the feedback loop.

Grazing and predation is another key biological driver affecting macroalgal assemblages. Due to their role as secondary producers, non-predatory grazing fauna are important controllers of algae in the sublittoral rock 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 (e.g. Nybakken 2001; Livore & Connell 2012; Boaventura *et al* 2002; Dauvin *et al* 2013). This is further discussed in Section 6.8.3.

6.2.3 Ecosystem Outputs

Macroalgae in the sublittoral rock habitat is responsible for a multitude of output processes that lead to several key ecosystem functions at varying scales, notably primary production, bioengineering, habitat provision and the export of organic matter.

The major output process by macroalgae is primary production. Through the process of photosynthesis, macroalgal assemblages produce energy that, along with phytoplankton and marine plants, forms the basis of the majority of marine food webs. As a result of this, macroalgae act as 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 food 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 (Nauderhaug & Christie 2011; Birkett *et al* 1998). The process of photosynthesis also leads to increased levels of dissolved oxygen in the water column (e.g. Lalli & Parsons 2006), indicated by the feedback link shown on the model.

Habitat modification through bioengineering is one of the most important output processes in this model besides primary production. The degree of bioengineering is highly variable between species, with kelps and large sized algae being more prominent engineers. Prominent ecosystem functions resulting from bioengineering includes habitat provision, influence on hydrodynamic flow and impacts on sediment stability. Bioengineering by macroalgae is noted to have a potential influence on localised hydrodynamic flows by disrupting water currents (Eckman *et al* 1989; Duggins *et al* 1990). In turn 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). However, bioengineering is noted to negatively affect light attenuation, with the blades of mature kelps being noted in some studies to form a canopy layer which, under certain conditions, may cut off as much as 90% of the incident irradiance (Birkett *et al* 1998).

The canopy layer formed by some algal species enhances the habitat provision for other organisms, increasing the colonisation of both macro- and meiofaunal species and by providing a refuge to species that are otherwise highly susceptible to predation (Birkett *et al* 1998). The increased physical structure and habitat complexity afforded by macroalgal species also provides a growth surface for epiphytic species (Duggins *et al* 1990), and those species that graze upon the algae themselves. Kelp biotopes, with their high species diversity, high biomass and high rates of productivity are also important nursery areas for a diverse range of species. It is likely that juvenile forms of all the animals that are present as adults in the kelp bed make use of the habitat as a nursery area (Birkett *et al* 1998). Macroalgae species can also enhance biotope stability by binding together mixed sediments (where these occur), and creating more stable habitats (Duggins *et al* 1990).

In common with other models, the supply of propagules is another key output process of macroalgae in sublittoral rock habitats. 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.

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

6.3 Sub-model 2. Temporarily or Permanently Attached Active Filter Feeders

6.3.1 Biological assemblage

The temporarily or permanently attached active filter feeders sub-model represents a large group of fauna commonly linked by their attachment to the seabed and practice of creating water flow to strain food resources from the water column or actively capturing food items. Several groups were formed for this sub-model based on species taxonomy and common traits:

- Actiniaria e.g. *Metridium senile*
- Ascidians and tunicates e.g. *Ascidia mentula, Clavelina lepadiformis*
- Porifera e.g. *Axinella dissimilis, Myxilla incrustans*

Typically the fauna that constitutes this sub-model are found on either hard rock substrata or stable mixed substrata. The fauna occurs throughout both the infralittoral and circalittoral zones, and across high-, medium- and low-energy environments.

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.

6.3.2 Ecosystem Drivers

Physical environmental drivers are likely to be of significant importance to attached active filter feeders, as detailed for the general control model. Physical driving influences that affect the distribution of attached, active filter feeding organisms include wave exposure, depth, water currents and climate (e.g. Nybakken 2001; Little & Kitching 1996; Lalli & Parsons 2006).

As sessile filter feeders, the fauna represented within this model are reliant on transport of food resources suspended within the water column. Active filter feeders are able to create their own water flow to ensure the passage of suspended food items past feeding mechanisms, however a supply of food sources within the water column is a necessary starting point. Primary food sources of attached active filter feeders include particulate organic matter, plankton, detritus and small invertebrates and fish.

Plankton (both phytoplankton and zooplankton) and particulate organic matter (POM) are primary sources of food for Porifera, ascidians and Actiniaria (MarLIN 2006; Hily 1991; Hayward *et al* 1996). Phytoplankton, as primary producers, are heavily influenced by water chemistry and temperature (including nutrient availability) and light attenuation (e.g. Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000; Hiscock *et al* 2006). Other larger-scale drivers such as water currents and wave exposure (promoting water column mixing) will also influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley 1972; Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000). Phytoplankton are generally more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may reduce the importance of this food source at the top of the circalittoral (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) (Levinton 2001; Nybakken 2001; Lalli & Parsons 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006). POM derived from organic sources including plankton is an important food source in both the infralittoral and circalittoral zones (Nybakken 2001; Lalli & Parsons 2006; MarLIN 2006).

Other important food sources for this ecological group include small invertebrates and fish (MarLIN 2006), bacteria (Myers 2001) and suspended detritus (Millar, 1970). Small invertebrates and fish may be those that are native to the sublittoral rock habitat, or those from connected habitats. Not all factors affecting living prey are indicated in the model in order to minimise complexity. Detritus in the marine environment is influenced by a number of factors, including abundance of marine life (Nybakken 2001; Lalli & Parsons 2006; Brown *et al* 2000a); likewise not all of the links for which are indicated on the model for the sake of simplicity.

Seabed mobility is a minor consideration in the model. Some species of Porifera are known to be slow growing and long lived (MarLIN 2006; Bell 2008), thus are unlikely to settle or thrive in a mobile mixed sediment environment that is subject to routine disturbance.

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

6.3.3 Ecosystem Outputs

Secondary production is a key process occurring within the sublittoral rock habitat, whereby energy from lower trophic levels is converted to higher trophic levels through energy transfer (Lalli & Parsons 2006). This in turn provides ecosystem functions at the local scale by driving nutrient cycling (Nybakken 2001; Lalli & Parsons 2006) and is a major influencing factor in increasing food and prey availability within the habitat. Food processing through secondary production also serves to cycle nutrients in the ecosystem and contributes to an overall export of biodiversity and organic matter from the habitat at the regional to global scale.

Biodeposition is likewise an important process that occurs in the sublittoral rock habitat, although the local effects of this may be of limited extent in high-energy environments or on hard rock substrata. Being active filter feeders, Porifera, Ascidiacea and Actiniaria engage in capture of food matter from the water column and the transfer of energy from the pelagic to the benthic environment (Nybakken 2001). Actiniaria, Ascidiacea and Porifera play an important role in benthic–pelagic coupling as part of the benthic suspension feeding community, transferring energy to the benthos from the water column and releasing metabolites, waste, gametes, and offspring back into the water column (Levinton 2001; Bell 2008; Daly *et al* 2008).

Bioengineering is a major output process performed by Porifera. Some sponge species may grow to be large in size, and as such produce multiple ecosystem functions. These include impacts on near-bed hydrodynamic flow in dense sponge patches (Bell 2008), increased sediment and habitat stability through the stabilisation and consolidation of habitat in the rocky subtidal zone, binding boulders to rock (Bell 2008) and habitat provision (MarLIN 2006, Bell 2008). Porifera are noted to act as microhabitats for a range of other species (Bell 2008) and have been shown to increase bacterial biomass within the ecosystem (Bell 2008). Porifera may also engage in bioengineering through erosion activity. *Cliona celata,* for example, bores its way into soft rock such as limestone, and can be an important bioeroder in the sublittoral rock habitat (Bell 2008; Naylor 2011). Actiniaria are likewise noted to be providers of habitat to other organisms (Vader 1984). In turn, this can lead to increased habitat stability and biodiversity enhancement across larger spatial scales.

Porifera, Ascidiacea, and Actiniaria engage in nutrient cycling and biogeochemical cycling, although to a fairly limited degree outside the confines of the secondary production process. Being large filter feeders, Porifera are known to remove nutrients and from the water column, and are important factors for carbon flow and nitrogen fixation in the marine environment (Bell 2008).

As a food resource, ascidians and anemones are of limited importance, although Porifera are known to be consumed by a range of organisms including fish, molluscs, crustaceans and echinoderms (Bell 2008).

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

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

6.4 Sub-model 3. Temporarily or Permanently Attached Passive Filter Feeders

6.4.1 Biological assemblage

The temporarily or permanently attached passive filter feeders sub-model represents those species that are attached to the seabed and rely on natural water currents to transport food resources. The model is similar in nature to the active filter feeders model, and indeed the two models have only been split in order to facilitate presentation. Several groups were formed for this sub-model based on species' taxonomy and common traits:

- Bryozoans e.g. *Crisia eburnea, Electra pilosa*
- Hydrozoans e.g. *Obelia geniculata, Nemertesia ramosa*
- Crinoids e.g. *Antedon bifida*
- Hard corals, octocorals and seafans e.g. *Caryophyllia smithii*, *Alcyonium digitatum, Eunicella verrucosa*

Typically the fauna that constitutes this group is found on either hard rock substrata or stable mixed substrata. Such fauna occurs throughout both the infralittoral and circalittoral zones, and across high-, medium- and low-energy environments.

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

6.4.2 Ecosystem Drivers

Physical environmental drivers are likely to be of significant importance to attached passive filter feeders, as detailed for the general control model. Physical factors that affect the distribution of organisms include wave exposure, depth, water currents and climate (e.g. Nybakken 2001; Little & Kitching 1996; Lalli & Parsons 2006).

Being filter feeders, the fauna represented within this model are reliant on food resources suspended within the water column. Passive filter feeders are dependent on water currents to transport food resources to them, and are unable to create water flow themselves or actively hunt. Primary food sources of attached passive filter feeders include microorganisms, particulate organic matter, plankton and detritus.

Plankton (both phytoplankton and zooplankton) and particulate organic matter (POM) are primary sources of food for bryozoans, hydrozoans, crinoids and corals (Hancock 1965; MarLIN 2006; Porter 2012; Wilding & Wilson 2009). Phytoplankton, as primary producers, are heavily influenced by water chemistry and temperature (including nutrient availability) and light attenuation (e.g. Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000; Hiscock *et al* 2006). Other larger-scale drivers such as water currents and wave exposure (promoting water-column mixing) will also influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley 1972; Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000). Phytoplankton is generally more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents can reduce the importance of this food source at the top of the circalittoral (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) (Levinton 2001; Nybakken 2001; Lalli & Parsons 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006). POM derived from organic sources, including plankton, is an important food source in both the infralittoral and circalittoral zones (Nybakken 2001; MarLIN 2006; Lalli & Parsons 2006).

Other important food sources of this ecological group include microorganisms (including diatoms and microalgae) and detritus (Wilding & Wilson 2009; Hancock 1956; MarLIN 2006). Microorganisms and detritus in the marine environment are influenced by a number of factors, including marine life (Nybakken 2001; Lalli & Parsons 2006; Brown *et al* 2000a), not all of the links for which are indicated on the model for simplicity.

Seabed mobility is a minor consideration in the models, although may influence the biological assemblage. Some species found within this habitat are known to be slow growing and long lived (MarLIN 2006), thus are unlikely to settle or thrive in a mobile mixed sediment environment that is subject to routine disturbance.

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

6.4.3 Ecosystem Outputs

Secondary production is a key process occurring within the sublittoral rock habitat, whereby energy from lower trophic levels is converted to higher trophic levels through energy transfer (Lalli & Parsons 2006). This in turn provides ecosystem functions at the local scale by driving nutrient cycling (Nybakken 2001; Lalli & Parsons 2006), and is a major influencing factor in increasing food and prey availability within the habitat. 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. Several of the organisms represented in the ‘attached passive filter feeders’ sub-model are regarded as important prey resources in the habitat (MarLIN 2006).

Biodeposition is likewise an important process that occurs in the sublittoral rock habitat, although the local effects of this may be of limited extent in high-energy environments or on hard rock substrata. Being passive filter feeders, bryozoans, hydrozoans, crinoids and hard corals engage in the filtering of food particles from the water column and the transfer of energy from the pelagic to the benthic environment (Nybakken 2001). Hydroids are noted as especially important in transferring energy from pelagic to benthic ecosystems (Gili *et al* 1997), although all filter feeders play some role in transferring energy to the benthos from the water column and releasing metabolites, waste, gametes, and offspring back into the water column (Levinton 2001).

Bioengineering is undertaken by the species included within the ‘passive filter feeder’ sub-model, although to a lesser degree than the active filter feeders. Some bryozoans, hydroids, crinoids and hard corals do however obtain a large size (MarLIN 2006) and as such can be considered bioengineers. This has the potential to influence near-bed hydrodynamic flow and provide habitat for other organisms (Porter 2012). These output processes and local ecosystem functions in turn can lead to increased habitat stability and biodiversity enhancement across larger spatial scales.

Bryozoans, hydrozoans, crinoids and hard corals engage in nutrient cycling and biogeochemical cycling, although to a fairly limited degree outside the confines of the secondary production process. Being potentially large filter feeders, the fauna represented in this model is likely to remove significant amounts of nutrients from the water column, and is a likely important factor for carbon flow and nitrogen fixation in the marine environment

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

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

6.5 Sub-model 4. Bivalves, Brachiopods and Other Encrusting Fauna

6.5.1 Biological assemblage

The bivalves, brachiopods and other encrusting fauna sub-model represents a sub-section of the filter feeding functional group of species included in the project scope. The following functional groups are represented within the model:

- Boring bivalves e.g. *Pholas dactylus*
- Attached bivalves e.g. *Mytilus edulis*
- Brachiopods e.g. *Neocrania anomala*
- Encrusting filter feeders e.g. *Balanus crenatus*, *Spirobranchus triqueter*

These fauna are generally found attached to rock or other hard substrata. Feeding predominantly occurs through the organisms filtering food particles from the water column.

Bivalves, brachiopods and encrusting fauna occur throughout both the infralittoral and circalittoral zones, although some species, such as the encrusting filter feeders, are more widely distributed than others. Representative species included within this model are found throughout all energy environments.

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.

6.5.2 Ecosystem Drivers

Bivalves, brachiopods and encrusting fauna predominantly inhabit niches in hard substrata where the physical conditions allow for attachment. As such, larval settlement (propagule supply) is an important regional to global driver, as are water currents and wave exposure.

Physical environmental drivers are likely to be of significant importance to attached bivalves, brachiopods and encrusting fauna, as detailed for the general control model. Physical factors that affect the distribution of organisms include wave exposure, depth, water currents and climate (e.g. Nybakken 2001; Little & Kitching 1996; Lalli & Parsons 2006).

Bivalves, brachiopods and encrusting fauna are typically filter feeders, and whilst they may be able to create localised current flows, are predominately reliant of the natural flow of water to supply food resources. Typical prey types include plankton, POM, microorganisms and detritus.

Plankton (both phytoplankton and zooplankton) and POM are primary sources of food for bivalves, brachiopods and encrusting fauna in the sublittoral rock habitat (MarLIN 2006). Phytoplankton, as primary producers, are heavily influenced by water chemistry and temperature (including nutrient availability) and light attenuation (e.g. Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000; Hiscock *et al* 2006). Other regional to global drivers such as water currents and wave exposure (promoting water column mixing) will also influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley 1972; Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000). Phytoplankton are generally 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 (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) (Levinton 2001; Nybakken 2001; Lalli & Parsons 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006). POM derived from organic sources including plankton is an important food source in both the infralittoral and circalittoral zones (Nybakken 2001; MarLIN 2006; Lalli & Parsons 2006).

Other important food sources of this ecological group include microorganisms (including diatoms, microalgae and bacteria) and detritus (MarLIN 2006). Abundance of Microorganisms and detritus in the marine environment are influenced by a number of factors, including abundance of marine life (Nybakken 2001; Lalli & Parsons 2006; Brown *et al* 2000a), not all of the links for which are indicated on the model for the sake of simplicity.

Seabed mobility is a minor consideration in the models, although may influence the biological assemblage. Some species found within this habitat are likely to require stable environments to survive, thus are unlikely to settle or thrive in a mobile mixed sediment environment, which is subject to routine disturbance.

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

6.5.3 Ecosystem Outputs

Bivalves, brachiopods and encrusting fauna support several important ecosystem outputs, notably secondary production. Bivalves, both boring and attached species, are also significant bioengineers and provide habitats for other species.

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

Bioengineering is an output process performed by boring and attached bivalves. Boring bivalves such as *Pholas dactylus* burrow into soft rock structures and bioerode the substrata, creating a warren of burrows. Attached bivalves such as *Mytilus edulis* can form large aggregations, which modify the natural habitat and lead to numerous ecosystem functions, including principally habitat provision.

Mytilus aggregations are particularly important features of the sublittoral rock habitat, noted to have a positive effect on habitat structure and habitat complexity (Norling & Kautsky 2007), influences on nutrient and biogeochemical cycling (Norling & Kautsky 2008; Meadows *et al* 2011), current flow and sediment deposition (Dent & Dekker 2013).

Habitat provision is a key function of attached bivalves, providing shelter and a potential food supply to other organisms. The presence of a single attached bivalve individual has been shown to increase habitat species richness and biomass (Norling & Kautsky 2007), and boring bivalves are thought to provide refuge for other species in the burrows they carve. Habitat provision is also afforded by brachiopods, providing an organic surface for algae and encrusting fauna to colonise.

Filter feeding by bivalves, brachiopods and encrusting fauna results in biodeposition, although in common with other models the effects or benefits of this are likely to be reduced on hard substrata or in high-energy environments. Nonetheless, the species represented by this sub-model do capture food matter from the water column and thus facilitate the transfer of energy from the pelagic to the benthic environment (Nybakken 2001), transferring energy to the benthos from the water column and releasing metabolites, waste, gametes, and offspring back into the water column (Levinton 2001; Daly *et al* 2008). This process contributes to nutrient and biogeochemical cycling in the habitat.

Where bivalves or brachiopods occur on coarse and mixed substrates, the fauna may act to bind sediments together. Bivalves attach themselves to the seabed via sticky byssus threads, which may help to consolidate sediments, and increase sediment stability, in turn leading to potential biodiversity enhancement within the habitat and biotope stability at the wider scale.

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

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

6.6 Sub-model 5. Tube Building Fauna

6.6.1 Biological assemblage

The tube building fauna sub-model represents fauna in the sublittoral rock habitat that construct and live in erect, rigid tubes attached to the seabed. The majority of fauna represented in this model are solitary tube building species, with the exception of *Polydora spp.* which can form dense aggregations. Two main taxonomic groups have been identified within the fauna that comprises this model:

- Anemones e.g. *Cerianthus lloydii*
- Polychaetes e.g. *Sabella pavonina, Protula Tubularia, Lanice conchilega*

The fauna that constitutes this group are predominantly filter feeders that form either hard calcareous secretions or capture sediment particles in order to form the protective tubes they inhabit. Tube-building fauna are found in a range of sublittoral rock biotopes, in both the infralittoral and circalittoral zones (although are more common in the circalittoral; Connor *et al* 2004) and in a range of energy environments.

It should be noted that the tube-dwelling anemone *Cerianthus lloydii* is typically found in mixed sediment biotopes and is thus not considered a true 'rock' species. The inclusion of this species is justified by its presence in several sublittoral rock biotopes that contain mixed sediments. *Cerianthus lloydii* is the only anemone found within this group. *Sabella pavonina* and *Lanice conchilega* are likewise often found in mixed sediment biotopes (Connor *et al* 2004).

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

6.6.2 Ecosystem Drivers

Physical environmental drivers are likely to be of significant importance to attached tube-building fauna, as detailed for the general control model. Physical factors that affect the distribution of organisms include wave exposure, depth, water currents and climate (e.g. Nybakken 2001; Little & Kitching 1996; Lalli & Parsons 2006).

Near-bed current flows affect the settlement of larvae of tube-building organisms. Water currents form an important factor in determining where this functional group can establish itself in a certain area; relatively strong hydrodynamics can reduce larval settlement due to the detachment of larvae from the seabed (Qian 1999; Coates *et al* 2013). Water currents are likely to also interact with the supply of particulate food sources.

Tube-building fauna are typically passive filter feeders and strain food particles from passing water currents. Typical food types include POM and plankton, although some species are known to also feed on detritus.

Plankton (both phytoplankton and zooplankton) and POM are primary sources of food for both tube building anemones and polychaetes (MarLIN 2006; Hayward *et al* 1996). Phytoplankton, as primary producers, are heavily influenced by water chemistry and temperature (including nutrient availability) and light attenuation (e.g. Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000; Hiscock *et al* 2006). Other larger-scale drivers such as water currents and wave exposure (promoting water column mixing) will also influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley 1972; Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000). Phytoplankton is generally 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 (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) (Levinton 2001; Nybakken 2001; Lalli & Parsons 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006). POM derived from organic sources including plankton is an important food source in both the infralittoral and circalittoral zones (Nybakken 2001; MarLIN 2006; Lalli & Parsons 2006).

Another important food source for tube building polychaetes is detritus (MarLIN 2006). Detritus in the marine environment is influenced by a number of factors, including abundance of marine life (Nybakken 2001; Lalli & Parsons 2006; Brown *et al* 2000a), not all of the links for which are indicated on the model for the sake of simplicity.

Seabed mobility is a weak driver for this model, given the generally stable nature of sublittoral rock habitats. However in mixed sediment habitats where variability in seabed stability may be a variable, it is thought that sediment instability could prohibit colonisation by tube-building fauna, as a relatively stable environment is required for successful habitat construction (Holt *et al* 1998).

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

6.6.3 Ecosystem Outputs

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

Habitat modification through the construction of tubes (bioengineering) is one of the most important output processes in this model. The degree of bioengineering is highly variable between species with certain taxa creating individual tubes of cemented sedimentary particles, others forming dense aggregations of tubes (such as *Polydora spp*.) and others forming hard calcareous structures.

The habitat modification and creation of tubes has an influence on several local ecosystem functions in the sublittoral rock habitat, notably habitat provision for other organisms (Rigolet *et al* 2014). The tubes enhance the habitat provision for other organisms and provide a refuge to species which are otherwise highly susceptible to predation (Larson *et al* 2009; Rigolet *et al* 2014). Tube builders also create favourable conditions for microbial activity in and around their tubes (Passarelli *et al* 2012), increasing the biogeochemical cycling of nutrients in the habitat (Meadows *et al* 2012).

The tubes created by the fauna in this model may have a minor effect on 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), particularly where these fauna occur in dense aggregations. Reduced hydrodynamic flow is likely to lead to enhanced sediment stability in mixed sediment biotopes, which coupled with the sediment trapping characteristics of the tube structures themselves (Woodin 2010; Van Hoey 2008; Kirtley & Tanner 1968), can lead to enhanced biotope stability, and thus potentially biodiversity enhancement at the wider scale.

Biodeposition is another key output process performed by the three functional groups of the tube-building fauna model. Being predominantly filter feeders, tube-building fauna are engaged in the transfer of matter from the water column to the benthic environment (Nybakken 2001), although the localised benefits of this are likely to be more prominent in mixed sediment environments, as opposed to hard substrata or in high-energy environments. Tube-building fauna are important secondary producers, consuming primary producers and particulate matter detritus.

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

6.7 Sub-model 6. Scavengers and Predatory Fauna

6.7.1 Biological assemblage

The scavengers and predatory fauna sub-model includes those species that actively hunt or scavenge other living organisms within the sublittoral rock habitat. Four taxonomic groups have been identified within this sub-model:

- Crustaceans e.g. *Cancer pagurus, Necora puber*
- Echinoderms e.g. *Asterias rubens, Luidia ciliaris*
- Polychaetes e.g. *Harmothoe spp*.
- Molluscs e.g. *Nucella lapillus*

Scavenging and predatory fauna typically have a high degree of mobility and a large body size. They are regarded as important secondary producers and are vital for population control in the sublittoral rock environment. Fauna from this group is found in all sublittoral rock biotopes, across both the infralittoral and circalittoral zones and across all energy level environments.

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

6.7.2 Ecosystem Drivers

In addition to the physical drivers that influence species distribution (including wave exposure, depth, water currents and climate (e.g. Nybakken 2001; Little and Kitching 1996; Lalli & Parsons 2006), occurrence of scavengers and predatory fauna is driven principally by the availability of prey.

Carrion and living small invertebrates and fish are the key prey source consumed by the fauna in this sub-model (MarLIN 2006; Naylor 2011; 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.

Other food sources for the fauna represented by this group include detritus (MarLIN 2006), algae (Naylor 2011) and microorganisms (MarLIN 2006). *Necora puber* and *Harmothoe* spp. have been noted as consuming algae in the absence of abundant prey items (Naylor 2011). Not all links influencing food resources are shown on the model for the sake of simplicity.

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

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

6.7.3 Ecosystem Outputs

Secondary production is the key process occurring within the sublittoral rock habitat from scavenging and predatory fauna. Through consumption of prey, energy from lower trophic levels is converted to higher trophic levels through energy transfer (Lalli & Parsons 2006). This in turn provides ecosystem functions at the local scale by driving nutrient cycling (Nybakken 2001; Lalli & Parsons 2006), and is a major influencing factor in increasing food and prey availability within the habitat. In terms of wider regional to global ecosystem functions, secondary production ultimately leads to both export of organic matter and export of biodiversity.

As a consequence of high secondary production, predatory fauna act as significant top-down controllers of lower trophic level fauna in the sublittoral rock environment (Nybakken 2001; Little & Kitching 1996). In turn this leads to enhanced biotope stability by ensuring that population dynamics within the habitat are maintained, and that grazing fauna are not permitted to proliferate.

Habitat provision is afforded by some species within the sublittoral rock habitat, principally by species such as the hermit crab *Pagurus bernhardus*, which offers additional habitat provision to symbionts and epibiota (Pretterebner *et al* 2012), enhancing the biodiversity at regional to global ecosystem levels.

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

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

6.8 Sub-model 7. Non-Predatory Mobile Fauna

6.8.1 Biological assemblage

The non-predatory mobile fauna sub-model represents those species that are mobile and typically regarded as grazers in the sublittoral rock habitat. Three main ecological groups were identified within this model:

- Echinoderms e.g. *Holothuria forskali, Echinus esculentus* and *Ophiothrix fragilis*
- Gastropod molluscs e.g. *Gibbula cineraria, Margarites helicinus*
- Crustaceans e.g. *Pandalus montagui, Dexamine spinosa*

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

The species presented within this model are typically found throughout both the infralittoral and circalittoral zones, although some taxa such as *Echinus esculentus* found in a greater diversity of biotopes than others.

6.8.2 Ecosystem Drivers

Fauna represented within this model are principally grazers or detritivores, feeding on algae, detritus, or in some cases particulate matter and food sources within the water column.

Supply of food resources is a principal driving factor for non-predatory mobile fauna. Algae, plankton and detritus are key food sources for non-predatory mobile fauna (MarLIN 2006; Naylor 2011; EUNIS 2014; Mattson & Cedhagen 1989). Algae and phytoplankton are heavily influenced by factors affecting primary production, such as light attenuation, climate, and water-column chemistry and temperature, including nutrient content (Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000; Hiscock *et al* 2006). Other larger-scale drivers such as water currents and wave exposure (promoting water column mixing) are also likely to influence phytoplankton abundance through indirect links with water chemistry and temperature or suspended sediment and light attenuation (Eppley 1972; Hily 1991; Lalli & Parsons 2006; Jones *et al* 2000). Phytoplankton is likely to be more abundant in the infralittoral zone where photosynthesis can occur, although mixing of the water column and currents may make 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 (Nybakken 2001) although will also be influenced by other factors, including reproduction of benthic and epibenthic fauna (producing propagules and larvae in the water column), POM and water column chemistry (dissolved oxygen in particular) (Levinton 2001; Nybakken 2001; Lalli & Parsons 2006). Zooplankton is expected to be an important feature of both the infralittoral and circalittoral zones (Lalli & Parsons 2006).

POM and detritus are also important food sources for non-predatory fauna in both the infralittoral and circalittoral zones (Nybakken 2001; MarLIN 2006; Mattson & Cedhagen 1989; Lalli & Parsons 2006). Certain deposit feeders (e.g. *Janolus cristatus)* are also likely to consume small living organisms, such as bryozoans on the seabed (MarLIN 2006).

Physical environmental drivers are likely to be of significant importance to non-predatory mobile fauna, as detailed for the general control model. Physical factors that affect the distribution of organisms include wave exposure, depth, water currents and climate (e.g. Nybakken 2001; Little & Kitching 1996; Lalli & Parsons 2006).

Seabed mobility is likely to have a limited driving impact on non-predatory mobile fauna as most species are likely to be highly adaptable to physical disturbance given their elevated mobility compared to other fauna (Kaiser *et al* 1998).

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

6.8.3 Ecosystem Outputs

Non-predatory mobile fauna are important secondary producers, consuming primary producers and organic material, and in turn serving as an important food resource for multiple other organisms such as fish, crustaceans, molluscs and polychaetes (Francour 1997; Levinton 2001; MarLIN 2006; Fauchald & Jumars 1979; 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.

Due to their role as secondary producers, non-predatory grazing fauna are important controllers of algae in the sublittoral rock habitat. Certain urchins and gastropods in particular are noted as voracious grazers and their feeding activity can be a controlling factor for the distribution of kelps and other algae (Livore & Connell 2012; Boaventura *et al* 2002; Dauvin *et al* 2013).

Grazing organisms can have both positive and negative effects on the sublittoral rock habitat. Control of algal growth can lead to increased biotope stability through maintenance of the ecological equilibrium, and enhancement of biodiversity through the clearance of patches of thick algae and allowing new life to flourish, especially in thick and potentially sheltered and light-limited understorey communities (Livore & Connell 2012; Boaventura *et al* 2002). Both echinoderms and gastropod molluscs can, however, have a negative effect on biodiversity enhancement when the rate of grazing becomes too high within a habitat. Grazing by *Gibbula cineraria* for example has been shown to have a negative effect on recruitment in developing epifaunal communities by removal of juveniles and removal of habitat structure (Turner & Todd 1991). Likewise, urchins have been shown to be a destructive force in some sublittoral rocky habitats where grazing occurs in elevated levels, and ‘urchin barrens’ develop (Nybakken 2001; Livore & Connell 2012).

Biodeposition is an output process performed by non-predatory mobile fauna, especially those that may also capture particulate matter from the water column in addition to feeding on detritus or grazing. Selective suspension feeding ophiuroids, such as *Ophiothrix fragilis* for example, play a major role in the pelago-benthic transfer of particles from the water column to benthic habitats (Davoult & Gounin 1995; Norderhaug & Christie 2011) that drives both biogeochemical and nutrient cycling (Levinton 2001; Nybakken 2001). This process is linked to the export of organic matter at regional to global ecosystem levels.

In common with other models, the supply of propagules is another key output process. Most fauna represented within this 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.

Non-predatory mobile fauna provides four regional to global ecosystem functions that are based on the output processes and local ecosystem functions in the model; the export of organic, the export of biodiversity, biodiversity enhancement and increased biotope stability.

7 Confidence Assessment

The confidence models that form a supplement to this report are included in Appendices 12-18. The confidence models replicate the components and layout of each of the sub-models described in Section 6. No confidence assessment has been undertaken for the general model due to the need for conflicting information to be presented. To form the confidence models, ancillary information (such as natural variability and biological zone) has been removed from the model structure and the connecting links between model components have been weighted to indicate strength of confidence supporting the links. As detailed in Section 5.2, the confidence of these links is divided into two types within the models, informed by either literature sources or expert opinion, following the pro forma shown in Table 6. Links in the confidence models are colour coded to reflect this.

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

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

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, macroalgae and attached fauna have a generally high confidence reflecting the large amount of literature and research that has been carried out on the related species and their importance within the ecosystem.

8 Monitoring habitat status and change due to natural variation

Using the information gathered during the literature review and presented in the models, the features of sublittoral rock habitats that may be most useful for monitoring habitat status in the context of natural variation in the environment have been identified. Identification of these aspects would allow monitoring to take account of how the habitat type is varying naturally, so that any changes detected can be put within this context. These features have been identified through interrogation of the model components and their interactions and are presented in Table 7. All model components have been assessed regardless of strength of interaction.

Habitat components have been selected to fulfil this role that have a large magnitude of effect on the structure and functioning of the habitat, a generally low level of natural variability, and those that operate at the 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 component that could be monitored in Table 7. Confidence in the model components has been assigned based on the protocols presented in Sections 2.5 and 5.2.

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 that are useful for monitoring to determine habitat change due to natural variation; however those presented are considered the key components identified by this project through the CEMs. As stated above, considerations of methodology or practicality of application are outside the scope of this project.

Table 7. Key ecological CEM components of sublittoral rock habitats that could be most useful for monitoring habitat status and change due to natural variation. Components are listed in order of confidence for use as indicators for monitoring natural variation.

Habitat Component	Rationale	Component confidence in measuring Natural Variability	Relevant Models
Light Attenuation	Light attenuation is predominantly dependent on water turbidity and depth, although is also influenced by the presence of algae canopies in rock habitats. Whilst turbidity undergoes frequent short term fluctuations (e.g. from algal growth, storm events, tidal flows and seasonal changes), annual turbidity levels have a low level of natural variability; however, when changes do occur they will likely have a large magnitude of impact. Any change in light attenuation may impact primary production and food sources for fauna.	High (largely informed by literature evidence)	All - Sub-model 1 in particular.
Macroalgae	Macroalgae form a key ecological group in the sublittoral rock habitat. They are influenced by several naturally variable drivers at varying scales, principally those connected to primary production and physical stresses. A lot of macroalgal species are highly seasonal and produce numerous important output processes and ecosystem functions, changes in which have the potential to have large impacts on other organisms within the habitat. As such, it is considered that macroalgae diversity or biomass may be a highly suitable indicator for sublittoral rock ecosystem status change.	High (informed by expert judgement and literature evidence)	Sub-model 1
Water Chemistry and Temperature	Water chemistry and temperature is a key driver in the sublittoral rock habitat and has a strong influence over macroalgae species, such as the rate of photosynthesis (Lalli & Parsons 2006), in addition to affecting benthic fauna, which may also act as food sources (Cusson & Bourget 2005; Bolam *et al* 2010). Natural variation in water chemistry and temperature is likely to be relatively low (aside from seasonal variation), but impacts of change have the potential to be large, when they do occur and across a variety of scales. Water temperature, dissolved oxygen content and nutrient content of the water column are all potential key sub-components that could be targets for monitoring programmes.	High (informed by expert judgement and literature evidence)	All - Sub-model 1 in particular.
Wave exposure/ water currents	Wave exposure and water currents are dominant factors controlling the distribution of macroalgae and fauna in the sublittoral rock habitat (Little &	High (informed by expert judgement and	All

	Kitching 1996; Nauderhaug & Christie 2011) Natural variation in water currents is likely to be low (limited principally to any seasonal changes). Natural variability in wave exposure is likely to be marginally higher, affected by seasonal variability and potentially the presence of dense macroalgae. Despite the relatively stable nature of these factors, any change in their magnitude as a result of natural variation is likely to result in considerable changes to the characterising flora and fauna of the habitat, which are principally defined by their tolerance to water currents and wave exposure, in addition to other more stable factors such as depth. As such it is considered that these elements may be worth monitoring to assess habitat and status and change due to natural variation, especially given the ease of measuring this aspect.	literature evidence)	
Grazing and Predation	Grazing and predation is a natural ecological process which can exert strong influences on the biological assemblages found within the sublittoral rock habitat (Little & Kitching 1996). Levels of grazing and predation pressure are expected to be moderately stable over time, although are likely to be affected by seasonal variation and natural changes in population dynamics. Any change in grazing or predation rates has the potential to have large knock-on effects throughout the sublittoral rock habitat. It should be noted that where these species are highly mobile, vulnerable as by-catch, or commercially targeted they will likely not form reliable indicators.	Medium (informed by expert judgement and literature evidence)	All
Recruitment	Recruitment is a key biological factor that affects fauna related to sublittoral rock habitats at the 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 as a key driving factor given its large influence over benthic faunal composition. Defining species to specifically monitor cannot be stated without further literature evidence, although some studies do exist which could be used to address this (e.g. Hiscock *et al* 2005).	Medium (largely informed by expert judgement)	All

9 Monitoring features to identify anthropogenic causes of change

Table 8 presents key aspects of the sublittoral rock habitat that 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 (OSPAR 2011), along with relevant benchmarks (Tillin *et al* 2010), are presented in Appendix 19. It should be noted that no consideration has been given to the monitoring methodology or practicality of including these features in a monitoring programme at this stage.

The assessment presented in Table 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 sublittoral rock habitats will be produced by JNCC following a detailed sensitivity assessment of the ecological groups of the habitat type during 2015/16. The information presented below for the biological assemblages is therefore only a preliminary assessment.

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 that are useful for monitoring to determine habitat status change due to anthropogenic pressures; however those presented are the key components identified by this project.

Table 8. Key ecological aspects of sublittoral rock 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 19. Evidence for some features is provided in the form of literature sources in the text. Where these have not been provided expert judgement has been applied.

Pressure	Model Component	Rationale	Component confidence in measuring anthropogenic pressure
Removal of target species	Crustaceans, echinoderms and bivalves	Several species included in the project scope are commercially fished in certain areas around the UK (MarLIN 2006) and directly removed from the ecosystem. Target species include *Cancer pagurus*, *Homarus gammarus*, *Pandalus montagui*, *Mytilus edulis* and to a lesser extent *Echinus esculentus*. An expansion of edible seaweed harvesting would also potentially affect macroalgae. The removal of these species may result in disruptions to output processes and ecosystem functions such as predatory control of other organisms, the control of algal growth, bioengineering and biodeposition, as well as affecting the supply of propagules, in turn potentially influencing spawning stock biomass. However, Simberloff (1998) cautions that an indicator subject to single species management is no longer an indicator. This observation has substantial implications in marine systems, because some species that are readily observable are also harvested by humans to some degree and, therefore, make poor indicators (Zacharias & Roff 2001).	High

Local water-flow changes	Filter feeding fauna	Changes in local water flow has the potential to affect those fauna which rely on water currents for the supply of food sources, such as attached temporarily attached active and passive filter feeders, bivalves, brachiopods, other attached filter feeders and tube building fauna. Should the supply of food sources borne by water currents be interrupted, the fauna which rely on these may be impacted and subsequent output processes and ecosystem functions may be affected. Fauna and flora that rely on water currents for the removal of waste and the supply of nutrients may also be affected. Local water changes may also be accompanied by changes in siltation which may affect a range of species. In extreme instances siltation may change habitats from hard substratum to sedimentary habitats.	Medium
Local wave-exposure changes	Biological Assemblages	The distribution of fauna and flora in subtidal rock habitats is governed to a large extent by tolerance to pressures such as wave exposure (Little & Kitching 1996). A change in wave exposure through anthropogenic activity may alter habitat suitability for some species found within the affected habitat, resulting in decline of the species or out completion by another more suited to the new conditions. Macroalgae is considered to be a key ecological group that would indicate changes in response to altered wave exposure	Medium
Abrasion/disturbance of the substrate on the surface of the seabed	Tube building Fauna	Physical disturbances to the seabed can destroy the structures of tube-building fauna and impact the settlement and survival of propagules (Kenny & Rees 1994; Neal & Avant 2008; Dannheim *et al* 2014). Tube-building fauna may recover from substratum loss in mixed sediment environments (Boyd *et al* 2003; van Dalfsen *et al* 2000), although this is unlikely on hard surfaces where tube formation is a slow process. Incorporating fast recovering species as indicators in monitoring programmes would enhance the ability to quickly detect changes after anthropogenic activities.	High
	Echinoderms and attached epifauna	Echinoderms are relatively fragile and may decline in abundance after abrasion and physical disturbance of the seabed (Jennnings *et al* 2001). Attached epifaunal species are likely to be sensitive to surface and sub-surface abrasion through physical damage. Large emergent species that make up much of the architectural complexity of habitats are particularly vulnerable (Turner *et al* 1999; Thrush & Dayton 2002, Tillin *et al* 2006). Mobile species are likely to be more robust to impacts due to avoidance behaviour.	High
	Macroalgae	Macroalgal species are likely to be sensitive to abrasion caused by anthropogenic activities. This impact may physically affect the macroalgae structure or the holdfast with which it attaches itself to the substratum. Once removed from the substratum, many species of macroalgae cannot reattach themselves, so are likely to be lost from the habitat (Tyler-Walters 2007). There is the possibility that once removed, the macroalgae species may be replaced by others with a higher tolerance of physical abrasion, thus macroalgae species diversity is considered a good indicator of environmental changes in response to anthropogenic activity.	High

	Bioengineering (habitat complexity)	An increase in physical disturbance and levels of abrasion is likely to result in decreased habitat complexity, through damage to ecological groups of taxa that are typically responsible for the construction or formation of large biological structures in the sublittoral rock habitat. Damage to macroalgal species and large attached epifauna as a result of abrasion is likely to reduce habitat complexity, which may be a useful component of the habitat to monitor for signs of physical anthropogenic impact on the seabed. Epifaunal species are particularly vulnerable to abrasion and disturbance can physically damage and remove large emergent epifauna and biogenic substratum such as sponge beds (Pauly *et al* 1996; Auster 1998).	Medium
Changes in suspended solids (water clarity)	Light attenuation	An increase in suspended solids will reduce water clarity and will likely reduce light attenuation (Devlin 2008). This has the potential to limit primary production, resulting in possible impacts to output processes and secondary impacts on other organisms. This is also linked to the pressure ‘siltation rate change’.	High
	Suspended sediments	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
	Macroalgae	Long-term increases in the levels of suspended solids in the water column will likely reduce light attenuation and affect the ability of macroalgae to photosynthesise, possibly resulting in reduced biomass or species diversity, and will therefore impact output processes and ecosystem functions at all scales (Tyler-Walters 2007).	High
Siltation rate changes, including smothering	Suspended Sediments	Given that siltation rate changes are directly linked to suspended sediment concentrations (Devlin 2008), this factor is thought to be a key monitoring aspect for the sublittoral rock habitat.	High
	Tube building and attached filter feeding fauna	Siltation rate changes have the potential to negatively affect sessile, attached filter-feeding fauna and tube building fauna through physical smothering of the organisms structure (e.g. Riley 2005), and through clogging of the organisms feeding mechanisms (Saraiva *et al* 2011). Chronic siltation or acute episodes of siltation with large deposits may lead to the decline of these faunal assemblages, and in turn to disruption of output processes and ecosystem functions at both the local and wider scale. While some organisms may be adapted to recover from 'light' smothering, e.g. those taxa with mobile features or which have the ability to grow quickly (Last *et al* 2011), they are likely to be unable to cope with heavier and persistent increased sediment loads.	High
Nutrient enrichment	Macroalgae assemblages	Nutrient enrichment has the potential to positively affect macroalgal growth in the sublittoral rock environment. Macroalgal species may bloom in the presence of enhanced nutrient levels and as such algal biomass may be considered an indicator of ecosystem change, the rise in biomass can affect several key output processes and functions at varying scales, such as the export of organic matter, provision of habitat and food resources *etc*.	Medium

	Water chemistry	Nutrient enrichment is also likely to influence water chemistry and as is a directly measurable component within the sublittoral rock habitat. Changes in water chemistry are likely to have large effects within the habitat, principally affecting macroalgae and other primary producers.	High
Organic enrichment	Water chemistry and temperature	Organic enrichment from anthropogenic sources has the potential to have a large effect on water chemistry (Levinton 2001; Lalli & Parsons 2006). Direct loading of nutrients, organic matter and minerals is likely to have large effects on algal, benthic and epibenthic communities, and will alter ecosystem functions in a significant way (Munn 2004) although effects are better understood in sedimentary habitats. Organic enrichment of the natural environment is also likely to influence primary production (Hiscock 2006). Nutrients are known to be a limiting factor in primary production and an increased input could lead to phytoplankton blooms (e.g. Lalli & 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
	Scavengers and predatory fauna	Additional food supplies are deposited onto the seabed due to the discard of non-targeted species (bycatch) (e.g. Enever *et al* 2007). The introduction of additional food sources to the seabed can lead to an increase in abundance of mobile scavenging and predatory species such as *Pagurus* sp. in actively fished areas (Groenewold & Fonds 2000; Rumohr & Kujawski 2000; Bergmann *et al* 2002; Ramsay *et al* 1998; Dannheim *et al* 2014), with resulting effects on other ecological groups which are utilised as prey.	High

10 Examining the effects of different pressures on the system using Bayesian Belief Network Models – Potential for Further Study

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

Essentially a BBN is a formalised set of rules that indicates the probability of any ‘node’ in the system being in one of a number of fixed states. In practice, the node is any component box in the conceptual ecological model (e.g. grazing pressure or biodiversity enhancement).

A limited BBN approach has been trialled for the Conceptual Ecological Modelling of Shallow Sublittoral Mud Habitats project (Coates *et al* 2015). That project is highly similar in objectives and approach to the current study. Outputs from the BBN trail have been shown as a case study to demonstrate the practical application of this method to predictive ecosystem modelling.

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

The second factor in constructing a BBN is the probabilities of the interaction terms between nodes or compartments. Positive interactions between compartments mean that the probability of the target node *increasing*, would increase if the causative node was itself *increasing*, but would decrease if the causative node was *decreasing*. The network is parameterised using the assumption that the causative node is definitely *increasing*, and if this is the case, then the probability of the target node *increasing* is determined as a fixed value taken directly from the magnitude of effect indicated in the model.

The formulation of BBNs from the diagrammatic models produced is a relatively straightforward process, simply accounting for strength and confidence of each interaction, and can be presented in a relatively simple fashion. Further information regarding the BBN process can be found in Coates *et al* (in prep), Stafford *et al* (2014) and Stafford and Williams (2014). It is thought that by applying a BBN approach to the models produced in this project, a more robust method for identifying indicator species within the sublittoral rock habitat may be achieved. In theory the BBN approach would allow identification of key components of the ecosystem that vary the most in response to either natural or anthropogenic induced change, through the permutations of varying scenarios.

The full BBN methodology has not been applied to the rock CEM project due to time and resource constraints, however it is thought that further research into the applicability of this approach would be of benefit, and may ultimately result in a stronger method for indicator selection.

11 Conclusions

This project has demonstrated the links and interactions that occur within sublittoral rock habitats through a series of Conceptual Ecological Models. One general habitat model has been produced and seven detailed habitat sub-models, based on the representative ecological groups that define the habitat. Linkages within the models are well informed by the literature review, and thus confidence is generally high in the outputs. Expert judgement has been used to inform some interactions within the models, and confidence has been reduced in these instances. Should additional data be added to the project in the future, confidence could likely be improved.

The information presented in Tables 7 and 8 shows which components of the models may be useful for monitoring habitat status and change due to natural variation and anthropogenic pressure, respectively, and may be worth taking forward to inform indicator selection for this habitat type. Typically, local inputs to the habitat are those most likely to serve as features useful for monitoring change in the context of natural variation. Water column chemistry and temperature, suspended sediments and light attenuation are likely to be key monitoring aspects of the sublittoral rock physical and chemical environment. Biomass and diversity of macroalgal and faunal assemblages, in particular those that are active grazers or predators/prey species, are also useful monitoring features to assess habitat status and change due to natural variation from a biological point of view. It is recommended that further work is undertaken to identify specific species that would be useful to monitor from within the ecological groups to reflect natural variation in the biological community. It should be emphasised that the indicators identified are based on the models and consideration could not be given to whether these could be made operational, or the scales on which these should be assessed.

In terms of model components that may be useful for monitoring habitat status and change due to anthropogenic pressures, highest confidence is typically placed in the biological aspects of the habitat. Other localised input features have also been identified as potentially sensitive to pressures, especially those that affect photosynthesis and primary production. Various ecological groups within the ecosystem have been identified as important to monitor all the anthropogenic pressures, with macroalgae and filter feeding organisms of particular relevance. Physical and chemical components that have been identified as potentially useful monitoring aspects in relation to pressures include primarily those related to primary production, such as suspended sediments, light attenuation and water chemistry and temperature. It is recommended that further work is undertaken to identify specific species that would be useful to monitor the impacts of anthropogenic activity from within the identified ecological groups.

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13 List of Appendices

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In addition to the appendices listed, a spreadsheet containing ancillary electronic information supporting the literature review also accompanies this report, as referred to within the main report sections (Sublittoral Rock CEM Literature Review and Ancillary Information Version 1.0).

Appendix 1 – List of Species Included in Project Scope

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

Ahnfeltia plicata
Alaria esculenta
Alcyonidium diaphanum
Alcyonium digitatum
Anemonia viridis
Antedon bifida
Antedon petasus
Ascidia mentula
Ascidiella aspersa
Asterias rubens
Axinella dissimilis
Balanus crenatus
Bugula plumosa
Cancer pagurus
Caryophyllia smithii
Cerianthus lloydii
Chondrus crispus
Ciona intestinalis
Cladophora rupestris
Clavelina lepadiformis
Cliona celata
Corallina officinalis
Corella parallelogramma
Crisia eburnea
Delesseria sanguinea
Desmarestia aculeata
Dexamine spinosa
Dyopedos porrectus
Dysidea fragilis
Echinus esculentus
Electra pilosa
Epizoanthus couchii
Eunicella verrucosa
Flustra foliacea
Gibbula cineraria
Halichondria panicea
Haliclona viscosa
Halidrys siliquosa
Harmothoe
Holothuria forskali
Homarus gammarus
Janolus cristatus
Kirchenpaueria pinnata
Laminaria hyperborea
Laminaria ochroleuca
Lanice conchilega
Luidia ciliaris
Margarites helicinus
Membranipora membranacea
Metridium senile
Mytilus edulis
Myxilla incrustans
Necora puber
Nemertesia ramosa
Neocrania anomala
Nucella lapillus
Obelia geniculata
Ophiothrix fragilis
Pagurus bernhardus
Palmaria palmata
Pandalus montagui
Parasmittina trispinosa
Phellia gausapata
Pholas dactylus
Polyclinum aurantium
Polydora spp.
Polyides rotundus
Protula tubularia
Sabella pavonina
Sargassum muticum
Sertularia cupressina var. *argentea*
Spirobranchus triqueter
Suberites carnosus
Swiftia pallida
Ulva lactuca
Urticina felina

Appendix 2 – List of Keywords used as search terms

Algae
Amphipod
Anemone
Ascidian
Barnacle
Benthic
Benthic Species
Interactions
Benthic topography
Biodeposition
Bioengineer
Biogeochemical process
Biological composition
Biological driver
Biotope
Boring
Bivalve
Brittlestar
Brown algae
Bryozoa
Burrowing
Burrowing anemone
Coralline algae
Calcareous
Chemical driver
Circalittoral
Climate variation
Community
Connectivity
Crab
Crustacea
Currents
Deposit feeding
Depth
Dissolved oxygen
Driver
Ecosystem function
Ecosystem process
Ecosystem service
Environmental driver
Environmental position
Epibenthic
Epifauna
Errant polychaete
Feather star
Feeding
Feeding method
Filter feeding
Food resource
Food web
Functional group
Gastropod
Geology
Green algae
Growth form
Habitat provision
Habitat stability
Hydrodynamic flow
Hydroids
Holothuria
Infauna
Infralittoral
Interstitial
Kelp
Laminaria
Light attenuation
Macroalgae
Macrofauna
Macrophyte
Meiofauna
Microalgae
Microbial activity
Mobile Crustacea
Mobility
Nitrogen flux
Nudibranch
Nutrient cycling
Nutrient provision
Organic Carbon
Physical driver
Physiographic
Phytoplankton
Predator-Prey
Interactions
Prey
Primary production
Red algae
Rhodophyta
Rock
Salinity
Seabed energy
Seabed mobility
Seasonal variability
Secondary production
Sponge
Polychaete
Sediment
Sediment stability
Soft coral
Species trait
Spionidae
Sublittoral
Substratum
Subtidal
Suspension feeding
Temperature
Tidal stress
Tidal stream
Trophic level
Tube formation
Turbidity
Urchin
Water composition

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