Accessing and developing the required biophysical datasets and data layers for Marine Protected Areas network planning and wider marine spatial planning purposes

Report No 4: Task 2H. Development of a Benthic Productivity Datalayer: Assessing the Available Approaches

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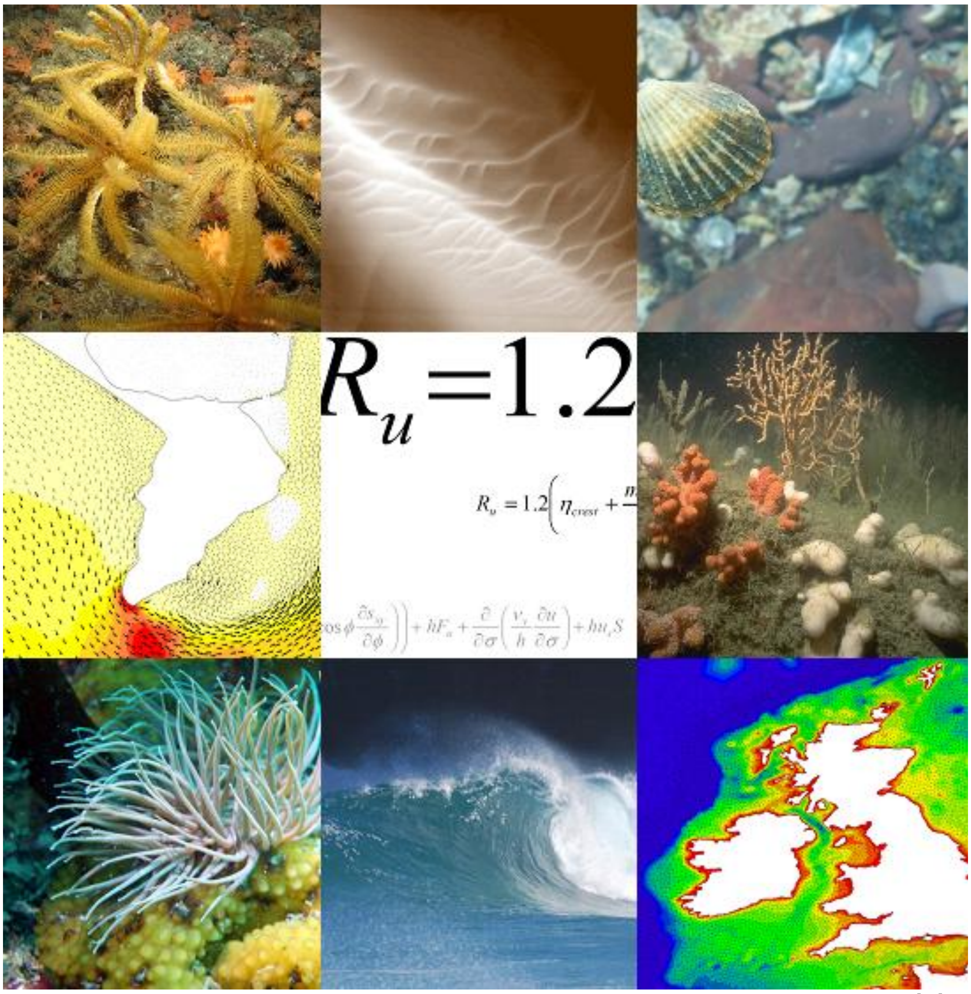

Project Title: Accessing and developing the required biophysical datasets and data layers for Marine Protected Areas network planning and wider marine spatial planning purposes

Report No 4: Task 2H. Development of a Benthic Productivity Datalayer: Assessing the Available Approaches

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Executive Summary

The UK is committed to the establishment of a network of marine protected areas (MPAs) to conserve marine ecosystems and marine biodiversity. MPAs can be a valuable tool to protect species and habitats. They can also be used to aid implementation of the ecosystem approach to management, which aims to maintain the 'goods and services' produced by the normal functioning of the marine ecosystem that are relied on by humans.

A consortium[1] led by ABPmer have been commissioned (Contract Reference: MB0102) to develop a deliver a series of biophysical datalayers to aid the selection of a network of Marine Conservation Zone (MCZ) in England and Wales (and the equivalent MPA measure in Scotland) under the Marine and Coastal Access Bill. Such datalayers will also be of use in taking forward marine planning in UK waters. The overall aim of the project is to ensure that the best available information is available for the selection of MPAs in UK waters, and that these data layers can be easily accessed and utilised by those who will have responsibility for selecting sites. The project has been divided into a number of discrete tasks, one of which was to review and assess methodologies for the development of a 'benthic productivity' datalayer.

Given the uncertainty over suitable methods to employ for datalayer development, this review has concentrated on soft-sediment productivity, as approaches in this area are most developed and tested. Soft-sediments are the most wide-spread type of marine benthic habitat in UK waters so that development of a methodology to map production/productivity for these habitats would be valuable to cover a broad extent of the seabed. The primary production of vegetated habitats has been well studied but these are very limited in their extent, relative to UK waters as a whole. Methods of assessing productivity on hard substrate are poorly developed, currently work is being undertaken to refine models and develop measures of productivity for hard substrates but these will not report in the time-scale of this project (before 2012). The focus on soft-sediment productivity ensures that the outputs of the study will be applicable across the majority of the UK Continental Shelf.

This document was the product of the review process. As benthic productivity is not currently widely used to inform environmental management, the report begins by providing a background to the review, defining key terms and outlining relevant information on food chains and the flow of energy and cycling of matter in ecosystems. A distinction was made between secondary production, the production of organic material (biomass) and secondary productivity, which is the rate of production over a specified area and time. The report, therefore, provides a clearly defined context to the reviewed approaches. ABPmer also organised a one-day workshop, where experts from research and other institutions were invited to discuss the issues around mapping benthic productivity. Specifically, opinions and feedback were sought on the approaches that could be used to construct a productivity datalayer and the use of this to deliver management objectives. The meeting notes

[1] ABPmer, MarLIN, Cefas, EMU Limited, Proudman Oceanographic Laboratory (POL) and Bangor University

are provided as an appendix to this report (Appendix 1). The workshop also acted as a form of peer-review to complement the research and reporting undertaken by ABPmer. Experts were also invited to comment on the draft report, which was circulated electronically, and to provide feedback.

Methods of assessing the benthic secondary productivity of macroinvertebrates, in soft-sediments can be broadly categorised into four approaches; direct methods; empirical modelling; expert-judgement and proxy indicators of habitat productivity. Each available approach is briefly described in the report and the strengths and weaknesses in relation to datalayer development are outlined in a following section.

While direct methods (cohort and size based approaches), were acknowledged to provide the most accurate, quantitative, assessments of productivity, workshop attendees agreed they were completely unsuitable for the production of a datalayer, due to prohibitive sampling and processing requirements. Empirical modelling approaches have greater potential for use in datalayer development, as, in general, the productivity estimates are derived from more easily measured characteristics of assemblages. The complexity of models varies from those that use one or two measured parameters to assess the production of samples, to multivariable predictive models. Depending on data availability these approaches were considered suitable for assessments of broad-scale production and, the workshop agreed, that promising models should be explored further.

The final approaches considered are based on more qualitative approaches to assessing secondary production and these approaches have some degree of overlap. These are the use of expert judgement, combined with literature information, to subjectively rank areas based on production. While such an approach does provide a pragmatic approach to developing a production datalayer on a UK CS wide basis, the workshop felt, strongly that the use of expert judgement was too subjective and, as an exercise, would be unrepeatable and unvalidated These strong objections meant that expert judgement was not considered a suitable approach in this review. An alternative approach is to select factors that have been identified as influential on amounts of production and productivity rates, and use these as proxy indicators. Workshop participants suggested that these were potentially useful to develop a datalayer but that the approaches require further trialling and validation.

In relation to these available approaches, the utility of the layer to fulfil management objectives was considered and recommendations were made, regarding the development of a datalayer. Based on feedback from the workshop, and the review process, it was proposed that a pilot study should be conducted to test the performance of three potential approaches, two of these are based on empirical modelling 1) Approaches developed by Thomas Brey (Brey et al. 1996, Brey, 1999b), 2) the Duplisea *et al*. (2002) model modified by Jan Hiddink (Hiddink, 2006). Also it was suggested that modelling work was undertaken to identify proxy indicator variables of production. If these approaches were applied to the same area then the results of these could be compared to determine if the more cost-effective, proxy indicator approach, could be applied rather than the more data intensive models.

The results from the pilot study would therefore inform on, the feasibility of constructing a UK wide datalayer, the approaches that could be utilised and the cost of this. If alternative approaches to the Brey model, did not perform adequately, then this would suggest that data requirements might prevent the construction of a cost-effective UK wide datalayer.

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1. Introduction

1.1 Project Background

1.1 The UK is committed to the establishment of a network of marine protected areas (MPAs) to conserve marine ecosystems and marine biodiversity. MPAs can be a valuable tool to protect species and habitats. They can also be used to aid implementation of the ecosystem approach to management, which aims to maintain the 'goods and services' produced by the normal functioning of the marine ecosystem that are relied on by humans.

1.2 As a signatory of OSPAR the UK is required to establish an ecologically coherent network of well-managed MPAs. The UK is already in the process of completing a network consisting of Special Areas of Conservation (SACs) and Special Areas of Protection (SPAs), collectively known as Natura 2000 sites to fulfil its obligations under the EC Habitats Directive (92/43/EEC). Through provisions in the Marine and Coastal Access Bill a network of Marine Conservation Zones (MCZs) will be designated in England and Welsh territorial waters and UK offshore waters. The Scottish Government is also considering equivalent Marine Protected Areas (MPAs) in Scotland. These sites are intended to help to protect areas where habitats and species are threatened, and to also protect areas of representative habitats. For further information on the purpose of MCZs and the design principles to be employed see [http://www.defra.gov.uk/marine/biodiversity/marine-bill/guidance.htm, Defra, 2009].

1.3 Selection of MPAs should be based on the best available data and will come from a range of sources including biological, physical and oceanographic characteristics and socio-economic data such as the location of current activities. To ensure such data are easily available to those whom will have responsibility for selecting sites Defra and its partners[2] commissioned a consortium[1] lead by ABPmer Ltd and partners to take forward a package of work. New Geographical Information System (GIS) data layers to be developed included:

- Geological and geomorphological features;
- Listed habitats;
- Fetch and wave exposure;
- Marine diversity layer;
- Benthic productivity; and
- Residual current flow.

1.4 The current report provides a detailed review on approaches available for the development of a benthic productivity data layer, including recommendations for a preferred approach and methodology.

[2] Joint Nature Conservation Committee (JNCC), Countryside Council for Wales (CCW), Natural England (NE), Scottish Government (SG), Department of Environment Northern Ireland (DOENI) and Isle of Man Government.

1.2 Aims and Objectives

1.5 The aim of this project was to identify and review current approaches available for measuring secondary production by invertebrates and to assess the suitability of these for generating broad-scale benthic productivity maps of UK waters. The key aims of this element of the contract were:

- To complete an objective review of the current approaches available for the generation of benthic productivity maps, identifying their strengths and weaknesses and any refinements/modifications required; and
- To present the review in a clear report that includes an assessment of the value (and use) of creating such a datalayer for MPA site selection.

1.3 Format of Report

The report has been divided into eight sections. Section one provides an introduction to the project with section two outlining why the review was requested. Section three provides a discussion on the potential use and value of a benthic productivity datalayer, with section four outlining the adopted approach for the review and its final recommendations. Section five details the review of secondary production and methods of assessment, with section six detailing the strengths and weaknesses of the approaches to measuring productivity with section seven providing a discussion on the use and development of a Benthic Productivity Layer. Conclusions are presented in section 8.

2. Background

2.1 Sustaining marine productivity is encompassed in the UK Government's vision for the marine ecosystem, which is to maintain 'clean healthy, safe, productive and biologically diverse oceans and seas' (Defra, 2002). Measures of productivity (production of organic material per unit area and time) indicate the amount of matter/energy that is potentially available as reproduction stages or food (Brey, 2001). Production (of organic material) is a key ecosystem process that underpins ecosystem function. Benthic macroinvertebrates are an important part of the energy flow occurring in marine ecosystems, they link primary producers (which are an important food source for the benthos), and higher trophic (feeding) levels, (as prey items for fish). They can therefore be understood to be an important part of productivity of the seas, in terms of both ecosystem function (through organic matter cycling) and economic value-underpinning the production of commercial fish.

2.2 The creation of a benthic productivity datalayer may be a useful tool to discriminate between areas where productivity rates from benthic invertebrate communities differ. Given the importance of benthic invertebrate production of organic material to the ecosystem, this will aid the identification of areas that should be considered for protection as part of the MPA selection process.

2.3 Information on productivity has not been used widely for management purposes and much of the terminology relating to ecological fields has been developed in technical books and papers. In addition such terms are less intuitive than some of the terms associated with the assessment of sensitivity or diversity in ecology. Therefore this review begins by outlining the processes of production and productivity and defining associated terms, with particular reference to the marine environment.

2.4 Each ecosystem has a trophic structure of feeding relationships. The species present are assigned to trophic levels based on the way in which they obtain food. The trophic structure determines the flow of energy through the ecosystem and chemical cycling. Production refers to both the incorporation of energy and materials into the bodies of organisms (Campbell *et al*, 1999).

2.1 Terms and Definitions

2.1.1 Autotrophs and Primary Production

2.5 Depending on the way that they feed organisms can be classed either as autotrophs or heterotrophs. Autotrophs obtain simple inorganic substances from their environment and synthesise complex organic molecules. This process is called **primary production** and forms the basis of the food chain or food web in ecosystems. There are a number of types of primary production by autotrophs, some organisms use chemosynthesis to obtain energy from the oxidation of inorganic molecules e.g. sulphur bacteria at hydrothermal vents. In certain marine habitats such as hydrothermal vents and methane clathrates, primary production by chemosynthesis can support large numbers of animals.

2.6 Green plants contain chlorophyll and absorb solar energy and carbon dioxide to produce carbohydrates by the processes of photosynthesis. Photosynthesis by plants is dependent on solar energy reaching the system and the availability of key nutrients. The majority of carbon in marine systems is fixed by phytoplankton in coastal and ocean surface waters (where light penetrates). In inshore and coastal systems vegetation, including macroalgae, seagrasses and saltmarsh plants are important contributors to primary production. Although these may contribute less to overall production in the wider marine system, productivity rates within these habitats can be high. Saltmarsh habitats, for example, have some of the highest productivity rates globally (Waide *et al*, 1999). In shallow marine subtidal habitats, micro and macro algae and eelgrasses on the seabed are the major primary producers.

2.1.2 Heterotrophs and Secondary Production

2.7 Unlike autotrophs, heterotrophic organisms do not synthesise carbon compounds internally but ingest and then digest organic matter from the environment. Heterotrophic organisms consume the carbohydrates that result from primary production either directly (through feeding methods that result in the ingestion of plant material e.g. grazing, filter/suspension feeding and deposit feeding) or indirectly by ingesting other heterotrophic organisms that are alive or dead (predation, scavenging). Hence heterotrophic organisms are also referred to as consumers.

2.8 In highly turbid or deeper waters, secondary production by heterotrophic organisms, including bacteria, invertebrates and demersal fish, predominates, based on the recycling and regeneration of carbon based compounds (Crisp, 1984).

2.9 The organic matter ingested by heterotrophs is assimilated or excreted. The percentage that is assimilated varies according to the assimilation efficiency of the organism. Assimilated food can be used to meet the energetic requirements of the organism, through respiration or be directed into reproduction or growth. Together growth and reproduction are termed **secondary production**, although a distinction is usually made between somatic production (growth) and **gonad production** (reproduction). The **somatic production** of an individual is defined as the part of organic matter assimilated that is used to form new tissue by growth. Somatic production (P) is defined as the change in biomass (B) with time (Brey, 2001). Usually the term secondary production (the production of new biomass) refers to somatic production only. For some species it may not be possible to separate gonad and somatic productivity, although some studies have managed to do this for populations, e.g. the Antarctic scallop *Adamussium colbecki* (Heilmayer *et al*, 2003).

2.2 Measuring Production

2.10 Production is a measure of the rate of production of organic material and, therefore refers to a defined area and a defined time period. Measures therefore indicate the amounts of organic matter or energy incorporated and the unit area and time, e.g. g cm^{-2} yr^{-1} or kcal m^{-2} $year^{-}$ (Cusson & Bourget, 2005).

2.11 Primary production by plants is typically measured as **Net Primary Production**: the total amount of dry matter made by a plant in photosynthesis, minus the matter lost due to respiration and measured in units of dry weight per unit area per unit time. Primary production values can be calculated for single plants, for entire populations or for assemblages e.g. the primary production of a rainforest or a saltmarsh.

2.12 Secondary production by heterotrophic organisms, when defined as somatic production, is a measure of growth, e.g. the change in biomass, over a given time period. As for primary production, secondary production may be calculated for organisms, a population or an assemblage of organisms.

2.13 Benthic ecologists frequently report the ratio of production-to-(mean) biomass, (e.g. as P/B or production to mean biomass, $P:\overline{B}$) ratios for a unit of time. The calculation of this ratio allows different populations to be compared on a common basis (Wetzel & Likens 2000). Production to biomass ratios, in biological studies, have been used to identify physiological and external environmental factors that influence rates of production, as discussed further, below.

2.2.1 Food Chains

2.14 Each step in the food chain may be referred to as a trophic level. Autotrophs are usually assigned a trophic level of one. The trophic level of a consumer is one above that of the species it consumes. A generalised schematic of the different trophic levels in a typical food chain is illustrated in Figure 1. Such a schematic is very simplified and does not contain trophic groups such as omnivores, parasites and detritivores, nor can it illustrate that an organism may feed at more than one trophic level (as many heterotrophs do).

2.15 The amount of energy available to each trophic level is underpinned by net primary productivity and the efficiencies with which food energy is converted to biomass in each link of the food chain. At each step in a food chain, carbon and energy are lost as the consumer does not assimilate all the organic matter ingested (some material is excreted) and energy is used to respire, reproduce and support other biological processes. As efficiencies are never 100%, each trophic level after level 1 has less energy and organic matter available to it than the preceding level. **Trophic efficiency** is a measure of the efficiency of energy transfer from one trophic level to the next. The trophic efficiency of organisms feeding on primary producers equals the percentage of the net primary production that is converted to their production. Similarly the production of a third level carnivore equals the percentage of the production of the second level carnivores that it converts to production. Determining values for trophic transfer efficiencies is difficult however and they have been found to vary greatly depending on the behaviour or physiology of the organism (Chapman & Reiss, 1999). Zooplankton feeding on phytoplankton have assimilation efficiencies of 50 to 90% but assimilation efficiencies of deposit feeders feeding on poor quality material with low organic content can be much lower (Barnes & Hughes, 1999).

2.16 The pyramid shape, illustrates some basic properties of food chain (these are general principles and some exceptions may be found);

- The abundance and total biomass of organisms decreases as the trophic level increases. This means that the total biomass of organisms that feed at higher trophic levels will be lower than the total biomass of lower trophic levels. This fact was noted by Elton (1927), who coined the term the ‘pyramid of numbers’ to refer to the decreasing abundance of organisms at each trophic level. For example he noted, that there are many small insects in a wood, a smaller number of small birds that feed on these and only a few hawks; and
- The pyramid diagram can also be interpreted as a representation of the energy flow between different trophic levels. Energy is lost from the system at every trophic level, primarily as heat energy.

2.17 Although the total biomass generally declines at higher levels of the food chain, the average size (biomass) of species within a population tends to increase. This is based on feeding relationships, e.g. consumers need to be larger than their prey to consume it. When biomass rather than abundance is used as a value, however, inverted pyramids may occur in some parts of the ecosystem. For example, at certain times of the year, phytoplankton may support a higher biomass of zooplankton (the next trophic level), (Whittaker, 1975). Similarly in a seabed habitat where the organic input is dominated by the input of large fish or mammal carcasses, inverted food webs dominated by scavengers can occur.

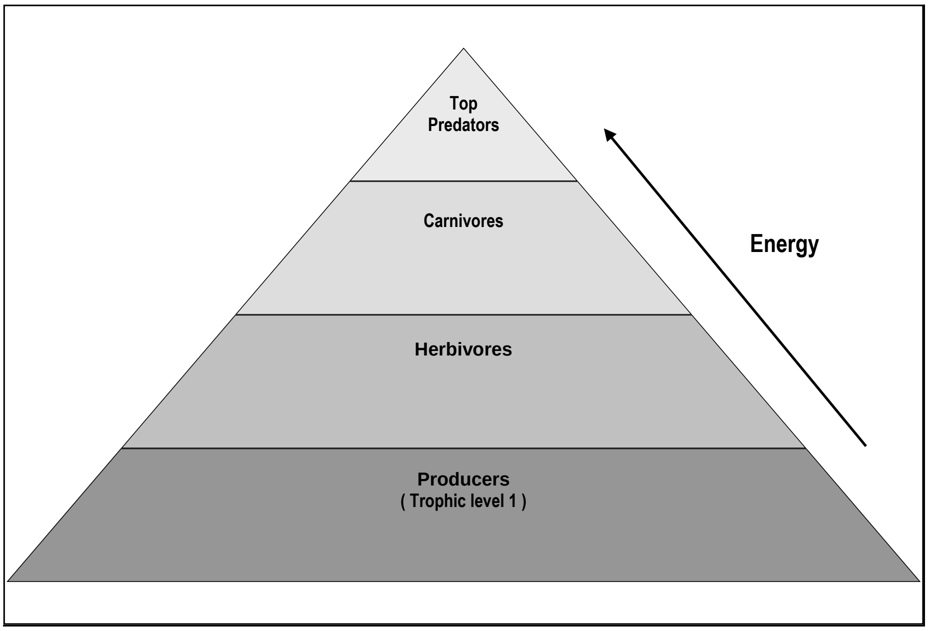


Figure 1: Simplified diagram of the trophic levels within an ecosystem (decomposition pathways not included)

2.2.2 Factors Influencing Production and Productivity

2.18 The growth of an organism (production) is determined by integral, physiological characteristics and environmental, physical and chemical factors and by interactions with other species (biotic factors). The growth of an individual or population will be better in an optimal location (habitat), where the resources that the species requires e.g. food and space are present and where conditions are within the species physiological tolerance range i.e. the organism is not stressed. Environmental variables such as sediment type, depth, current flow and temperature influence production/productivity through effects on food supply and metabolism and hence growth. Growth rates (productivity) will also be higher where predation, competition and parasitism do not kill, stress or divert resources.

2.19 In this section important factors that influence production/productivity are outlined briefly.

2.2.3 Metabolic Rates

2.20 Metabolism is the set of chemical reactions that occur in living organisms that maintain life. The metabolic rate of an organism determines the amount of energy it requires per unit time and hence influences the amount of food required. Metabolic rate is frequently measured as the basal metabolic rate, which is the energy required by a resting organism, in a temperately neutral environment to maintain vital life functions. Metabolic rates vary by size, life style and phylogeny.

2.21 In general, larger organisms require more energy each day and therefore more food. However, metabolic rates are not directly proportional to body mass, an organism that is ten times larger than another, does not require ten times as much energy, for example. Consistent relationships between metabolic rates and other life history characteristics and the size (body mass) of organisms and have been uncovered (Huxley, 1932, Peters, 1983) and these influence rates of production (Waters, 1979, Dickie *et al,* 1987). The lifestyle of a species is also an important factor, animals that are very mobile have high energy requirements and species such as seals and whales have been shown to have very high metabolic rates. Similarly, mobile invertebrate predators have higher metabolic rates than sedentary species that filter feed. Phylogeny is also a factor in differences in metabolic rates, partly as different phyla exhibit different life strategies.

2.2.4 Biotic Factors: Size, Age, Feeding Guild

2.22 The use of P:$\overline{B}$ ratios, provides a useful measure to compare species and populations in different locations. Species with a high P:$\overline{B}$ ratio are generally fast growing with small body mass (Brey, 1999a). In contrast large species with a long life span display low annual P:$\overline{B}$ ratios (molluscs, echinoderms). Larger species live longer, grow slower and have lower annual reproductive output (Brey, 1999a). As a result animals that are larger have lower production rates in relation to their size (Brey, 1999a). Species that live in colder and deeper waters display these characteristics often achieving a greater size and living longer than similar temperate and tropical organisms or those living in shallower waters, hence these have a lower P:$\overline{B}$ ratio.

2.23 Proportionally, large individuals within a species, use more energy for respiration than for growth, so that somatic P:$\overline{B}$ ratios decrease with age/body mass and are high in populations dominated by young cohorts (Warwick & Uncles, 1980, Sarda *et al,* 2000). Thus within a population, younger cohorts are predicted to be more productive as they invest more energy in growth (growth rates are higher in younger stages than older ones) while older individuals invest more in reproduction (reproductive production rather than somatic production). Noda (1997), found that the secondary production of a subtidal sand snail population was highly variable (over a 6 year period). Annual production was high when young individuals dominated the population.

2.24 A recent meta-study found that molluscs had higher production values than other taxa and that in an analysis of feeding guilds, filter feeders and grazers had high production values and omnivores, deposit feeders and predators had low production values (Cusson & Bourget, 2005). The P:B ratios tend to show an inverse pattern with arthropods exhibiting the highest P:B ratios, followed by annelids, molluscs and echinoderms. High P:B ratios were found for omnivores and predators and low P:B ratio values were observed for filter and deposit feeders and grazers. High P:B ratios were found from soft-substrata. The P:B ratios of mobile species were higher than non-motile ones (mobile species smaller) (Cusson & Bourget, 2005).

2.2.5 External Biotic Factors

2.25 Marine organisms in estuaries and brackish water areas will have lower productivity due to the sub-optimal conditions. Production therefore differs between populations of the same species, in different locations. High rates of inter and intra specific competition will also alter the production/productivity of individuals and populations.

2.26 Parasites can reduce the productivity of their host by diverting resources to themselves and can alter the energy flow between trophic levels (Hudson *et al*, 2006). Studies have shown that the green crab *Carcinus maenas* becomes larger and more abundant when it moves into new habitats where parasites are less abundant (Lafferty & Kuris, 1996, Torchin *et al,* 2001).

2.2.6 Food Supply

2.27 Production, in basic terms, is a measure of the growth of individuals/populations/ or assemblages, so it is clear the supply of food material is a critical factor influencing productivity (the amount and rate of growth).

2.28 Photosynthetic autotrophs can live only in or on the sediment where the photic zone extends down to the substratum. The infralittoral zone is defined by the dominance of photosynthetic organisms, and is limited by depth and water clarity. Autochthonous (*in situ*) production is therefore limited to the zone where primary production can occur. Within the infralittoral zone, consumers are, of course, present and secondary production will also occur.

2.29 At greater depths, or where water turbidity limits light penetration, benthic communities are animal (consumer) dominated and secondary production is the dominant form of production. Secondary production is dependent on primary production so that rates of benthic secondary production are influenced by (i) rates of primary production on the seafloor, which depend on light penetration, which is affected by turbidity and depth, and (ii) by the supply of phytoplankton and organic matter (such as zooplankton faeces) from primary production in the water column or inputs of other allochthonous matter (these are more important in estuaries and coastal areas which are influenced by the adjacent terrestrial environments and receive riverine inputs).In addition dissolved organic matter is utilised by some benthic animals (Stephens, 1968, Southward & Southward, 1982). The importance of the different types of food supply will vary between habitats.

2.30 Depth is also a factor determining the quality and amount of food reaching the seabed as in deeper waters organic matter may be consumed in the water column or the food value of organic matter may be degraded by microbial decomposition in the water column before it reaches the seabed. The proximity of other supplies of nutrients and organic detritus e.g. coastal saltmarshes and estuarine discharges (Barnes & Hughes, 1999) also influence both primary and secondary productivity. Planktonic food availability is also related to these variables and water currents near the seabed partially determine the amounts that become available to suspension feeders.

2.31 Currents and associated bottom shear stress also influence food availability and hence benthic secondary production (Warwick & Uncles, 1980, Wildish & Peer, 1983, Loo & Rosenberg, 1996). Water movements supply food and in many cases sedentary filter feeders rely on currents to renew food supplies. At high current velocities, however, feeding activity can be inhibited and strong currents can scour and remove substrata. Emerson (1989), for example, found that productivity was negatively correlated with wind-stress and elevated bottom current speeds.

2.2.7 Environmental Factors (Habitats)

2.32 In a meta-analysis of production rates and the variables influencing these, Cusson & Bourget (2005) found that depth and temperature explained some of the variation in production for some taxonomic groups and temperature explained a small part of the variance in P:B ratios. Depth explained 5% of amphipod and polychaete P:B ratio variances. Temperature explained 23% and 5% of the P:B ratio variance for echinoderms and polychaetes, respectively. Edgar (1990) found that invertebrate production nearly doubled for every doubling of temperature (^{o}C), which is due to the influence of temperature on metabolic rates (Gillooly *et al,* 2002).

2.33 Habitat related differences in secondary production were found in the meta-analysis by (Cusson & Bourget, 2005). Production was higher in areas with algae and higher on hard than soft-sediments. Macroalgae may increase larval settlement, increase sediment stability and protect organisms against disturbance (Paterson & Black, 1999), resulting in lower juvenile mortality, high growth rate and high P:B ratios (e.g. annelids, mainly deposit feeders, omnivores). Other vegetation also enhances production rates, production in shallow-seagrass beds is higher, for example, and differs significantly from the production of unvegetated inter-tidal and soft-bottom populations (Tumbiolo & Downing, 1994).

3. Potential Value and Use of Productivity Datalayer

3.1 The use of benthic, secondary production as an indicator of the condition of ecosystems has not been widely adopted by marine environmental managers but has a number of potential applications, as it represents one of the fundamental properties of marine ecosystems. Somatic production is a measure of the amount of matter/energy that is potentially available as food for the next trophic level (Brey, 2001). In terms of secondary production, therefore, benthic invertebrates represent an important link in the energy flow from primary producers to fish (Crisp, 1984). The production of benthic invertebrates, therefore, underpins the economic value of marine ecosystems by supporting the supply of goods, such as commercially exploited fish and invertebrates such as Dublin Bay prawns (*Nephrops norvegicus*) and brown crab (*Cancer pagurus*) (Crisp, 1984, Brey, 1990). For example, between 1975-1980, 40% of the production of cod in Kiel Bay was estimated to depend on the clam, *Arctica islandica* (Brey *et al*, 1990).

3.2 Productivity has been used in studies as a measure of the condition or health of an ecosystem (Valentine-Rose *et al*., 2007), as it represents a quantitative measure of ecosystem function (Benke, 1993). Secondary production integrates the output of ecosystem processes such as energy flow, organic matter cycling and food web interactions (Crisp, 1984, Morin *et al,* 1987, Tumbiolo & Downing, 1994).

3.3 Recovery of productivity levels has also been used to evaluate the success of restoration projects (Peterson *et al,* 2003, Cardoso *et al,* 2005).

3.4 The designation of MPAs that take into account productivity patterns would aid the implementation of ecosystem-based management in the marine environment and the achievement of governmental targets for the marine environment (Elliott *et al*, 2006). A productivity datalayer would potentially also be useful to implement Marine Spatial Planning policy as part of the Marine and Coastal Access Bill and equivalent provisions elsewhere in the UK.

3.5 Aside from primary production, the quantitative measurement of the production/productivity of benthic assemblages, which consist of a number of species, requires a large amount of data and analysis. The aim of this study was therefore to review the existing approaches, including those that use surrogate measures such as biomass, and to identify the strengths and weaknesses of these for the construction of a UK-wide GIS datalayer on benthic productivity.

4. Adopted Approach

4.1 In order to fulfil the aims and objectives of this project, the project team completed a systematic literature review, to identify the different methodologies that could be used to assess benthic productivity. The literature database ‘Scopus’ was used to identify and locate journal papers relevant to productivity. Other relevant literature was sourced from books, the ‘grey literature’, including reports commissioned by the conservation agencies and from internet searches.

4.2 A one-day workshop was executed in January 2009, where experts from research and other institutions were invited to discuss the issues around mapping benthic productivity. The remit of the workshop was to invite experts to contribute to this draft review. Specifically opinions and feedback were sought on the approaches that could be used to construct a productivity datalayer and the use of this to deliver management objectives. The notes from this meeting are presented in Appendix 1.

4.3 The workshop also acted as a form of peer-review to complement the research and reporting undertaken by ABPmer. Details of the Workshop including a list of attendees, which included academic institutions and the conservation agencies, can be found in Appendix 1.

5. Review of Secondary Production and Methods of Assessment - Outcomes

5.1 Methods of Estimating Secondary Production

5.1 The four main approaches (Table 1) that have been used to estimate secondary productivity and P:B ratios for marine populations are:

1. Cohort Methods
2. Size Class Methods
3. Empirical Models
4. Expert Judgement/ Relative scaling of productivity

Table 1: Approaches to assessing benthic productivity

Approach	Methods	Data	Comments
Cohort Methods	Allen Curve	A series of subsequent samples of abundance and mean individual body mass of a cohort during the period of investigation.	These methods are equivalent; the Allen curve uses a graphical approach based on the same formulae as the Increment Summation method.
	Increment Summation		
	Removal Summation		Evaluates production for a single-species cohort as the sum of mean individual biomass multiplied by the change in abundance for each sample interval. These are summed to evaluate production (P).
	Instantaneous Growth		Assumes growth is continuous
Size Class Methods	Size Frequency Method	Sample data on size of individuals, biomass of individuals and information on individual growth parameters.	Assumes linear growth rate
	Mass Specific Growth Rate		Requires a growth function
Empirical Models	Models based on allometric equations or multivariate regressions	Data on production and biomass and parameters that influence these.	These include the derivation of P or P:B values from life history parameters and the use of P:B values from literature sources to assess productivity and identify influential factors.
Expert Judgement/ Relative Scaling	Comparative approach to produce qualitative scaling of productivity	Data on factors that are known to influence productivity, such as temperature, depth and/or expert judgement	Develops conceptual models based on the relationship between productivity and environmental factors, to produce a qualitative ranking of areas or locations.

5.2 Cohort and Size Class Methods

5.2.1 Measuring Somatic Production of an Individual Animal

5.2 In Section 2, secondary production was defined as somatic production- the amount of organic matter, taken in by an organism that was assimilated and turned into matter (part of the assimilated matter is used for respiration and reproduction). Secondary production is therefore a measure of growth, so that, production is measured as the change in biomass over time:

Production P = Δ biomass/ time

5.3 The production of a single animal over a time period is the body mass of the animal at the end of the time period (M_2) minus the body mass at the start of the time period (M_1). Therefore:

$P = M_2 - M_1$

5.4 Estimating the production of an individual is therefore straightforward and requires data for one variable- mass- over a time period. Production can be measured for any time period, e.g. daily, monthly, annually.

5.2.2 Measuring Somatic Production of a Group of Animals

5.5 To calculate the somatic production of a group of animals of the same species, such as an age class (cohort), is less straightforward than measuring individual production, as biomass is added to the cohort over time, through growth, but is also lost as individuals die or are removed (e.g. by predators). Therefore the individual growth and mortality rate of every individual of the cohort determines the amount of production.

5.6 All the biomass added by growth to the cohort is eventually lost through mortality. When every individual of the cohort has been removed, the total somatic production (addition of new biomass by growth) that was gained is equivalent to the loss of biomass due to mortality. Therefore the somatic production of the cohort over a time period, can be measured using information on increase in biomass (growth) and loss of biomass (elimination).

5.7 To calculate the somatic production of a population, two main approaches have been developed, cohort and size based methods. Cohort and size based methods are based on similar principles to estimating production. For each method the species population is divided into groups, based on either age (cohort) or size-classes (size-based methods). The production of these groups is estimated and then the groups are summed to estimate the production of the population. These approaches are outlined below.

5.8 A cohort is an age class of a population e.g. for animals that reproduce once a year with synchronised reproductive cycles there will be one cohort of recruits to a population. For animals that reproduce twice annually there will be two cohorts formed per year. Some benthic invertebrate species can be aged on the basis of growth markers e.g. growth bands on bivalve molluscs and growth lines in echinoid tests, so that populations are suitable for cohort analysis of productivity. Other species can be separated into cohorts based on size, this approach tends to be more suitable for species with short life-spans and distinct reproductive episodes (Wetzel & Likens, 2000).

5.9 If reproductive cycles are continuous and hence there are no distinct age classes within a population, then cohort based methods cannot be used. For some species distinct age classes may be identifiable for young stages but for mature stages an asymptotic size may be reached and age classes merge and are indistinguishable (Wetzel & Likens, 2000).

5.2.3 Cohort Methods

5.10 Prior to production analysis the individuals within a sample are sorted into cohorts, based on the age of every individual, or the age of those in a representative sub-sample of sufficient size so that the age can be extrapolated to the whole sample based on size-at-age. If age cannot be estimated then a representative size-frequency distribution can be split into cohorts, this technique is useful for benthic invertebrates where individuals cannot be aged. However this technique requires a representative sample of a population that consists of distinct cohorts which differ in average size and where growth is fast in relation to the accuracy of size measurement (Brey, 2001). In some cases different cohorts can be separated by eye from size frequency histograms (see Elliott & Taylor, 1989) but separation into cohorts may require statistical analysis (Brey, 2001).

5.11 To compute the production of one cohort for a period of time, the change in numbers of the population and the mean individual body mass of the cohort during the period are tracked. If the population consists of several cohorts then these data are obtained for all cohorts. The standard cohort methods for estimating production are the Allen Curve and the Increment Summation method, these methods are equivalent (Brey, 2001). The Allen Curve (Allen, 1950) is a graphical approach to estimating production that plots abundance against mean individual body mass. The same data are used for the Increment Summation Method and entered into a series of equations to calculate production using mortality (change in abundance)- the removal summation method and growth increment summation.

5.2.4 Allen Curve/Increment Summation

5.12 The Allen Curve Method and increment Summation method are based on the same data and are equivalent. The Allen Curve method (Allen, 1950) is a graphical approach and uses a plot of the relationship between mortality (abundance) and biomass of a cohort over a life cycle to estimate production. For a unit area the number of individuals is plotted against the mean weight of individuals. Production is estimated as the area under the resulting curve.

5.13 The Increment summation method uses the same data as the Allen curve approach (abundance and mean individual biomass for a series of subsequent samples over a time period). The production of the cohort for a sampling interval is computed by multiplying the mean abundance of individuals by the change in individual biomass over the time period. The loss of production by mortality (elimination E) for each time interval is calculated as the mean change in individual biomass (M) multiplied by the change in abundance (N). So that:

$P = (N_1+N_2)/2 * (M_2 - M_1)$

$E = (M_1 + M_2)/2 * (N_1 - N_2)$

5.2.5 Removal-Summation Method and Growth Increment Summation

5.14 The removal summation method calculates the amount of biomass lost through mortality, at intervals, through the life of a single cohort. As the biomass lost through mortality is equivalent to the biomass gained through growth, the productivity of the cohort can be calculated by summing these changes in biomass.

5.15 For each time interval the production of the cohort is calculated as:

$P = \overline{B}\ \Delta N$

5.16 The Production of the cohort over its lifespan is calculated by:

$P=\Sigma\overline{B}\ \Delta N$

5.17 Where $\overline{B}$ = mean individual mass and N = abundance.

5.18 This method is based on the same population statistics as the growth increment summation method, based on the same population statistics, where production is equal to the sum of mean numbers multiplied by the change in mean individual biomass, for each sample interval, so that production is calculated as:

$P= \Sigma\overline{N}\ \Delta\ \overline{B}$

5.2.6 Instantaneous Growth

5.19 The production rate for each interval for a cohort is calculated by multiplying the instantaneous rate of growth by mean biomass during the time interval:

$P = G\overline{B}$

5.20 Examples of the use of cohort-based methods in the scientific literature can be found for amphipod species (Wildish & Peer, 1981, Collie, 1985, Dolbeth *et al*, 2005), the isopod *Cyathura arinata* (Cruz *et al*, 2003, Dolbeth *et al,* 2005), molluscs, including the mud snail *Hydrobia ulvae* (Dolbeth *et al,* 2005, Cardoso *et al,* 2005), the bivalve *Scrobicularia plana* (Dolbeth *et al,* 2005) and *Arctica islandica* (Brey *et al,* 1990).

5.2.7 Size Class Methods

5.21 In many population studies cohorts (age class) cannot be separated because individuals cannot be aged using available methods, or a size-frequency distribution cannot be split into cohorts, or there are no cohorts (Brey, 2001). To overcome this size class based methods may be used. These estimate the production of an assemblage from the sizes of the animals occurring. First the size structure of the assemblage is described and from this, production is estimated.

5.22 The data that are required to estimate production are representative size-frequency data (SFD), average body mass per size class and information on individual growth rates.

5.23 Production of a population is a measure of changes in biomass and abundance over time. It is therefore dependent on the growth and mortality rate within the population that describe changes in body mass and numbers with time. This means that the SFD information on changes in numbers and body mass with size need to be translated into time 'age' (Brey, 2001). Methods of doing this are i) size frequency methods, which assume that individual growth is linear, and ii) mass specific growth rates that require a growth function, and (iii) separate estimation of growth.

5.24 Hynes & Coleman (1968) introduced Size Frequency Methods for estimating production of aquatic insect larvae. The data required are a representative size-frequency sample of the population, average body mass size per class and an estimate of maximum lifespan. Production is calculated via elimination (mass loss) of the average cohort between two subsequent size classes (see Krueger & Martin, 1980), using the same formula that is used to compute elimination between sampling dates by the cohort-based Increment Summation Method.

5.25 Hermsen *et al* (2003) used this method of direct estimation of production for the most abundant animals in their study, however the assumption of linear growth throughout the lifespan of an individual leads to errors in the production calculation (Wildish & Peer, 1981, Morin *et al*, 1987). Organisms do not grow linearly throughout life, as discussed above. Growth and therefore production declines with age. Brey (2001) suggests, therefore, that where possible other methods should, therefore be used to estimate production.

5.3 Empirical Models

5.26 Estimating production through cohort and size class methods requires the collection of large amounts of data and time-consuming analysis and is therefore costly. These methods are therefore not suitable for the estimation of production for assemblages, which consist of many species.

5.27 In theory if there are consistent relationships between P:B ratios and size/biomass spectra for an entire sample/assemblage, irrespective of the identities of the taxa, then in production/productivity estimates could be obtained from empirical models based on biomass. Robertson (1979) demonstrated such a relationship by relating the P:B ratio to the life-span of populations and thus providing an estimate of marine macrobenthos production.

5.28 Empirical models based on easily obtained parameters offer a less time-consuming and more cost-effective method of obtaining production estimates for assemblages than the direct approaches described above. Empirical modelling approaches estimate production based on modelled relationships between population characteristics (life span, maximum individual weight, mean individual weight, mean biomass) and/or environmental parameters (temperature, depth). Models are discussed below starting with the simpler models that describe the relationship between production and size/mass that underpin the multivariable, predictive models.

5.3.1 Allometric Equations

5.29 A common feature of empirical models is the allometric relationship between secondary production (P) and body size (M) of an organism that is usually expressed in power-law form:

$$P = a\,BM^{b}$$

5.30 Where the constant, a, is determined by the ecological type of the organisms, B is the average biomass and b is the scaling exponent.

5.31 If production (P) can be related to the biomass (B) already present, then an estimate of productivity can be obtained. The recognition that P:B ratios are related to life-span allows the productivity of populations of known biomass and life-span to be estimated (Robertson, 1979).

5.3.2 Estimating Productivity from Biomass and Size

5.32 The simplest models used to estimate macrobenthic secondary production use one variable related to P:B, either lifespan or adult body mass. The lifespan of benthic invertebrates can be difficult to determine and may vary due to predation or other factors (Nichols, 1975) so that the method developed by Robertson (1979) may be difficult to apply or inaccurate. To counter these difficulties, simpler models have been developed for terrestrial and aquatic invertebrates, which relate P:B to the adult mean body mass (Banse & Mosher, 1980, Schwinghamer *et al*, 1986) which is easier to measure and less variable than life-span.

5.33 Models with two population parameters; mean annual biomass and mean individual body mass, have been developed (Brey, 1990, Edgar, 1990). Edgar (1990) developed allometric equations relating daily macrobenthic production to biomass values (ash-free dry weight) and temperature from published studies on 41 marine invertebrate species. Production was also estimated for adults and juveniles within populations.

5.34 Using these equations, production was calculated for different size classes of animals (based on retention on sieves of different mesh sizes). Edgar (1990) used this method to estimate productivity in three different habitats, intertidal sand flats, artificial algal habitats and eel-grass beds. This method was utilised by Robinson *et al*, (2004) in the North Sea, using data on infaunal and epifaunal macroinvertebrates.

5.35 The Brey (1990) model was developed from 337 datasets and relates production to mean annual biomass and mean individual mass. The modelled equation provides a method of estimating production from these two variables. This approach has been used to determine human impacts on benthic production rates by Jennings *et al* (2001). In this study the effects of fishing, using trawled gears, on benthic productivity was investigated by describing changes in size-spectra (all animals assigned to $\log_2$ body size categories) between sites subjected to different levels of fishing effort. Production and P:B ratios were predicted using allometric relationships based on body size. The data for parameterising these models were sourced from Brey (1990, 1999b).

5.3.3 Meta-analyses of Large Production Datasets

5.36 Recent studies have attempted to identify patterns in production using meta-analyses of a number of population production studies (Tumbiolo & Downing, 1994, Cusson & Bourget, 2005). These metanalyses have assessed the validity of empirical models for assessing production and helped clarify the relationship between size, production and P:B ratios. Patterns in production have been identified that relate to taxonomic and functional groups and environmental parameters, such as oxygen concentration, food availability and temperature (Tumbiolo & Downing 1994).

5.37 Tumbiolo & Downing (1994) performed a meta-analysis on 125 populations of marine benthic invertebrates from 34 different sites testing the Brey (1990) empirical model and one developed for freshwater invertebrates, against direct estimates of production. The study found that the Brey model performed well and correctly estimated the influence of biomass and body mass on productivity. As in previous studies larger species were found to have lower P:B ratios than smaller species. However there were large errors, systematically correlated with environmental conditions, indicating that models of secondary production should take the environment into account. To address this, multivariate regression equations were fitted to the data and these showed that including temperature as a variable improved model fit and that depth also explained some variation in production (Tumbiolo & Downing 1994).

5.4 Estimating Production Using Multivariable Models

5.38 Cusson & Bourget (2005) extended the meta analysis of Tumbiolo & Downing (1994) to 170 study sites and 207 macrobenthic populations, with additional information in relation to depth, habitats and feeding groups. They collected papers from 15 journals that provided direct estimates of annual somatic production (details of papers used are given in the electronic appendix of that paper). Multivariable regression modelling was conducted for production and P:B ratios using a number of population, habitat and environmental explanatory variables. These regression models explained a significant percentage of the amount of variance of benthic production, (92%) and P:B ratios (50-86%).

5.39 Brey *et al.* (1996) used artificial neural networks to estimate P:B ratios from a number of variables including body mass, taxon, living mode (guild), water temperature and depth. Further empirical models were developed (Brey, 2001) using multiple linear regressions with 11 parameters, including mean energy content of the organism (kJ), depth (m), temperature (^{o}C), motility and phyla to estimate production. The latest models are available on a website and are updated regularly[3] as new studies become available. A number of studies have supported the use of this model to estimate production (Cusson & Bourget, 2005, Dolbeth, et al. 2005). In a comparative study of empirical models Dolbeth *et al* (2005) found that the modelled estimates of production from the empirical Brey (2001) model most closely matched the production estimates from the more accurate cohort based model.

5.40 The size-spectra models developed by Duplisea *et al* (2002) use a number of model variables to predict the size-based distribution of benthic assemblages, these were originally used to investigate trawling impacts. As productivity is related to size these models can also be used to predict the productivity of an assemblage. The model was parameterised using data collected in six replicate dredges from each of seven sites in the Silver Pit area in the North Sea. All free-living infaunal individuals were weighed and assigned to $\log_2$ body size categories. Mean biomass by size class were reported as the mean for the six replicates and the biomass size-spectra were normalised by dividing the biomass in a given body mass class interval by the width of that interval. For existing data sets, the average size of a species within an assemblage could be used to back-predict production.

5.4.1 Model Development

5.41 The Duplisea *et al*, (2002) model was developed as a difference model using 37 state variables that relate to the size groups of three faunal groups:

1. Meiofauna (MEIO, five size-classes);
2. Soft-bodied macrofauna (SOFT, sixteen-size classes); and
3. Hard-bodied macrofauna (HARD, sixteen size-classes).

5.42 The growth of population biomass in each body-size organism type component was modelled using a modified Lotka-Volterra competition equation, with the following variables:

- Total wet weight;

[3] http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html

- Carrying capacity (set at a fixed level for all three compartments and reduced by competition);
- Growth rates (modelled using von Bertalanffy growth curves);
- Natural mortality (calculated from growth using the equation in Brey (1999a);
- The direct mortality resulting from the passage of a single beam trawl (estimated from literature values, see Duplisea *et al*, 2002);
- Competition (estimated using modified Lotka-Volterra competition equations. SOFT and HARD organisms were assumed to be in competition but MEIO were assumed not to compete with another group. Values for the Lotka-Volterra competition were derived using a prey overlap index for soft and hard body benthos from an ECOPATH model (Pauly *et al*, 2000) of the Celtic Sea in conjunction with growth rates).

5.43 The Duplisea *et al.* (2002) model developed using North Sea data was used as the basis to model production in Welsh coastal waters. The model was re-parameterised to account for local environmental conditions and bottom trawling disturbance (Hiddink, 2006). The interaction between habitat type and trawling effects was modelled by including relationships such as the sediment type on trawling mortality, the effect of bed shear stress on population growth rate, the remote sensed chlorophyll a content of the surface waters on carrying capacity and the effects of sediment erosion on mortality.

5.44 The study predicted that coastal areas were the most productive and that bottom trawling reduced production in a non-linear fashion.

5.5 Dynamic Models: Ecopath with Ecosim

5.45 The Ecopath with Ecosim approach combines different types of models, parameterised using information on production, to model energy flows between different trophic groups or pools. Ecopath is a static, mass-balanced model of the resources in an ecosystem and their interactions represented by trophically linked biomass pools. Ecopath require production data, which is sourced from the literature or stock assessments etc. to parameterise the biomass pool. Although the models are useful for exploring interactions, and potential changes under different management scenarios, they are parameterised using data related to production, rather than providing estimated production values. With current data availability this approach would not be useful in supporting development of a benthic production datalayer.

5.6 Expert Judgement and Proxy Measures of Productivity

5.46 At higher spatial levels it is clear that some areas are more productive than others. Shallow shelf seas are more productive than deep oceans and gyre areas due to the upwelling of cold nutrient rich currents and organic matter inputs from adjacent land masses. At a smaller scale the use of empirical models has identified a number of environmental variables, as discussed in Section 2, that are related to productivity. In addition there are some variables that have not generally been included as parameters in models but which are likely to influence production, such as the level of chlorophyll a in surface waters (Table 3).

5.47 To provide a qualitative assessment of productivity, environmental variables that are known to influence productivity can be used to construct a qualitative ranking scale. So that, for example, habitats that have higher productivity may be selected in an area, but the actual amount of production/productivity is not quantified.

5.48 These approaches require that general relationships have been established between selected variables and productivity. Selection of these is informed by previous studies and also expert judgement. In previous studies these results have then been validated using a productivity measure.

5.6.1 Habitat Type

5.49 An important factor determining productivity is food supply and net primary productivity which underpins food chains (as the source of food for consumers), has been demonstrated to vary between habitat types (see Table 2).

Table 2: A net primary productivity (as accumulation of dry organic matter per m^2 per year) in major aquatic habitat types (from Whittaker, 1975)

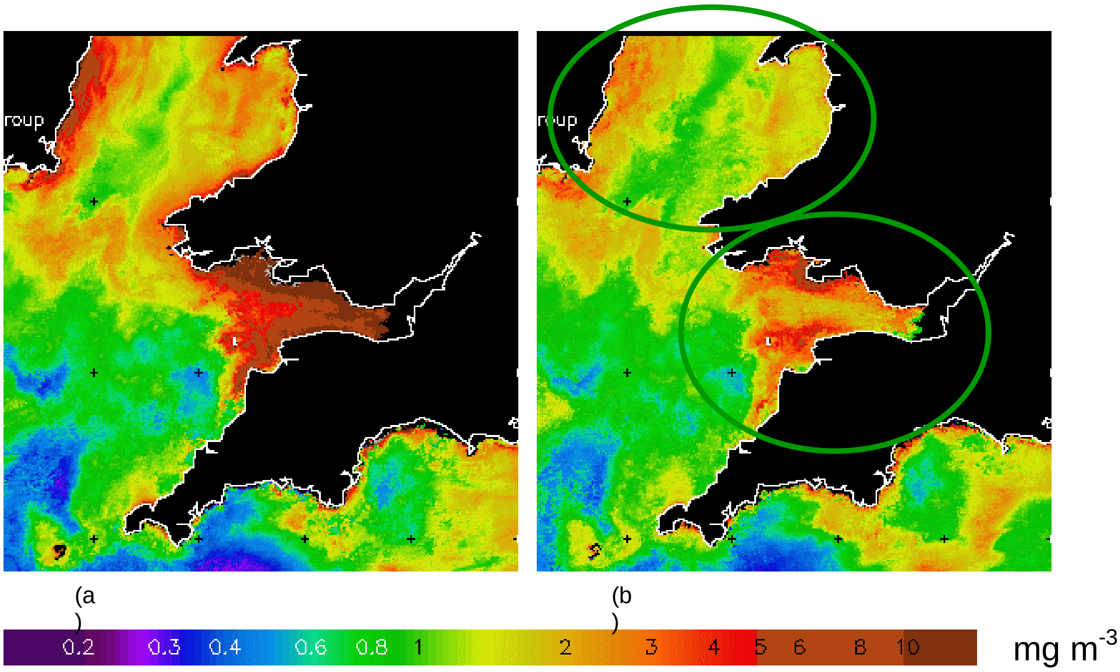
Habitat Type	Net Primary Productivity (dry g/m²/yr)	
	Mean	**Range**
Swamp and marsh	2000	800-3500
Algal beds/reefs/estuaries	1800	500-4000
Continental shelf	250	200-1000
Open ocean	125	2-400

5.6.2 Temperature and Food Supply

5.50 Temperature has been shown to influence rates of production due to effects on metabolism) and information on this combined with current, seafront and, chlorophyll a content of the surface water layer, may be informative as proxies for underlying benthic productivity (availability of food supply).

5.51 Phytoplankton production has been closely correlated with carnivorous fish and squid production in seasonally stratified waters (Iverson, 1990). In off-shore areas phytoplankton is the main food source for benthic invertebrates and this food supply may be episodic and related to sedimentation periods following phytoplankton blooms (Smetacek, 1980). The relationship between the level of primary production and food supply to the benthos is not clear and the results of studies are contradictory. Hargrave (1973) suggested that when primary productivity levels were high the amounts reaching the benthos were low, although Wassman (1990) found that increased primary production led to higher exports. Studies in the Barents Sea have found a high degree of pelagic-benthic coupling, with a positive link between the quality of food reaching the benthos and benthic activity (Morata & Renaud, 2008). Organic matter decomposes as it sinks so that food quality and supply may decrease with increasing depth (Pomeroy *et al*, 1984) although other studies have found that the degree of decomposition is seasonal (Morata & Renaud, 2008). Estuarine and nearshore areas will have less episodic inputs of organic matter as detritus, although the role of outflowing organic matter to the coast is poorly known.

5.52 Chlorophyll-*a* content of the surface layer could be used as a proxy of underlying benthic productivity (availability of food supply). There are identified problems with using SeaWiFS/Aqua satellite data in coastal areas due to turbidity, tidal re-suspension and disturbance. However, several algorithms have been proposed to tackle this problem: the empirical OC5 algorithm (Gohin *et al,* 2002) corrected the chlorophyll-*a* signal by estimating and removing the radiance contribution from suspended sediment, significantly reducing these errors in turbid water (see figure below). Plymouth marine Laboratory (PML) has developed systems enabling the processing of long time-series of satellite chlorophyll-*a* data, including the OC5 algorithm that permits usage within potentially turbid shelf seas. These data have been proposed for use as a datalayer for biodiversity hotspots (one of the tasks within the MPA package) (Figure 2) (P. Miller pers comm.).



(a) Standard NASA OC3 algorithm

(b) Turbid water OC5 algorithm, with rings indicating areas where errors due to suspended sediment were significantly reduced

Figure 2: Illustration of improvement to chlorophyll-a estimation in turbid shelf-seas using OC5 algorithm. Aqua-MODIS 7-day chlorophyll-a maps for UK southwest region on 12 June 2008 (Source P. Miller, PML)

5.53 Valavanis *et al*, (2004) estimated production from environmental variables, A GIS model based on sea surface temperature (SST) and Sea-viewing Wide Field-of view Sensor (SeaWiFS) chlorophyll-*a* concentrations were used to identify pelagic productivity ‘hot spots’. Data were analysed for anomalous distribution in these parameters to identify areas where chlorophyll levels were high and sea surface temperatures were persistently low, indicating the upwelling of cold, nutrient rich oceanic waters that stimulate production. These data were then validated using fisheries catch data on small pelagic fish and pelagic cephalopods, which were predicted to aggregate where primary productivity was high.

5.6.3 Benthic Biomass

5.54 The production of a species or population is equivalent to growth. Biomass may therefore be used as a proxy measure of productivity. Areas/habitats with a higher biomass of benthic organisms can be assumed to have higher production than areas with benthic assemblages consisting of a few, small species. Given, however, that productivity depends on the size and age of an individual and the age structure and mean lifespan of a population, some drawbacks to the use of this variable as a proxy for productivity is apparent. Assemblages consisting of small, fast growing, short lived populations will, theoretically, be more productive than assemblages where the dominant organisms are long-lived and have already reached maturity.

5.55 Data coverage of the UKCS will also be limited as the results from surveys conducted using different methodologies e.g. gear type and sampling effort, will not be directly comparable.

Table 3: Possible parameters to include in assessments of relative productivity

Parameter	Influence on Productivity	Rationale for Inclusion
Temperature/ Sea surface temperature	Influences metabolic rates, may be used to identify currents carrying nutrients.	Influences benthic productivity through metabolism and food supply
Depth	Influences fall-out rates of phytoplankton, that support production, and quality of food reaching the benthos	Influences benthic productivity through the quality of food supply from the water column.
Sediment	Relates to organic matter content, e.g. muds contain more organic matter than sands and hence food supply. Also reflects prevailing hydrodynamic conditions e.g. bottom current speeds, which influence food supply and production.	Reflects food supply for the benthos.
Chlorophyll levels	Food source that underpins benthic productivity	Influences benthic productivity through food supply
Habitat type (based on physical, chemical and biological components)	Productivity varies between habitat types	Some habitats can be a priori associated with relative production values.
Benthic biomass	Biomass is a measure of secondary production (growth), and productivity is a measure of the amount of biomass produced over a time period.	Biomass may be considered as a proxy indicator of productivity.

6. Strengths and Weaknesses of the Approaches to Measuring Productivity

6.1 Table 4 provides a summary of the strengths and weaknesses of different methods for developing a secondary production datalayer. Table 5 considers the strengths and weaknesses of the factors identified in Section 5 as potentially suitable for use as proxy indicators of production/productivity.

Table 4: Strengths and weaknesses of different approaches to map productivity

Approach	Data Requirements	Data Availability	Assumptions	Accuracy of Estimate	Cost	Weaknesses	Strengths
Cohort Based Measures	A series of subsequent samples of an identifiable cohort including measurements of abundance and mean individual body mass	Not available at a spatial scale to produce UK datalayer.	Some assumptions such as continuous growth are not biologically realistic.	If sufficient data can be collected this provides a rigorous method to assess production..	Estimation requires costly fieldwork and laboratory analysis.	Data requirements are prohibitive. Can only be applied to certain species. Measures suitable for single populations not assemblages. Estimates from a population growing under a local range of conditions may not be applicable in different locations, e.g. where food supply is different	Provides an accurate estimate of production. Could be useful to estimate production in habitats which are dominated by one or two species.
Size Class Measures	Size frequency data Average body mass per size class Information on individual growth	Not available at a spatial scale to produce UK datalayer.	Require growth functions to relate biomass to production				
Empirical Models	Production and biomass values and parameters that influence these	Data used to parameterise model may not be available to provide consistent spatial coverage	Fits a function to existing data, cannot identify causal factors.	Predictive accuracy of derived allometric relationships varies. Multivariable models not extensively validated.	Varies by model and available data. Cost lower than direct methods but some approaches e.g. Brey (1990) model require sample data.	Require data on production and biomass, otherwise extrapolate from existing models.	Useful for identifying parameters that relate to productivity
Expert Judgement	Requires expert knowledge on the productivity of key species and habitats, to rank areas in terms of productivity.	Depends on expert availability and knowledge, some aspects of marine systems little studied and currently poorly understood.	That there is sufficient information and understanding of system dynamics	Not known	Costs of convening workshops and conducting literature reviews.	Not repeatable and validation may be problematic. More fundamentally rates of productivity for some species and habitats may be unknown, and coverage of areas./habitat types may be patchy. Known differences in productivity rates may not be enough to meaningfully rank species/habitats/areas	Pragmatic approach based on current understanding.
Relative Scaling	Relative scaling of production rates, estimated using selected factors that affect productivity . The strengths and weaknesses of each factor are considered below (Table 5).						

Table 5: Strengths and weaknesses of utilising proxy indicators of productivity, as variables, in relative scaling approaches. For some factors, e.g. habitat type, expert judgement may be utilised

Approach	Data Requirements	Data Availability	Assumptions	Accuracy of Estimate	Cost	Weaknesses	Strengths
Temperature	A number of available measures may be biologically relevant, surface temperatures, sea bottom temperatures.	Interpolated data available on a UK wide scale.	Temperature has an effect on metabolic rates of organisms and may reflect food supply to benthos where temperature is related to colder, nutrient rich currents	Estimate based on qualitative scale	Data on temperature readily available, therefore low cost.	Temperature influences production through metabolic rates. Strength of the relationship would require validation.	Pragmatic, cost-effective approach if it can be demonstrated to provide an estimate of production/ productivity.
Depth	Depth of water column	Depth data available for most locations/ regions.	Assumes relationship between depth and productivity in the benthos.	Estimate based on qualitative scale	Data on depth readily available, therefore low cost.	Influence on production relates to food supply and temperature. Use of this variable as a proxy indicator would require validation.	Pragmatic, cost-effective approach if it can be demonstrated to provide an estimate of production/ productivity.
Chlorophyll concentration	Levels of chlorophyll in water layers.	Remotely sensed (SeaWiFS) chlorophyll data available for UK waters	Assumes that the level of chlorophyll in surface waters reflects food supply to benthos.	Estimate based on qualitative scale.	Data readily available	Chlorophyll levels in seawater may not reflect transfer rates to seabed	Relates directly to food supply, a key factor influencing production. Data should be relatively straightforward to obtain.
Habitat Type	Data on the locations of different habitat types and estimates of production rates associated with these.	Landscape/habitat maps available for some regions but classification schemes and availability vary.	Assumes that production rates are similar in habitats of the same type. In some cases habitats are predicted from other variables.	Estimate based on qualitative scale.	Data available but resolution/classification patchy. Off-shore data may consist only of substratum type interpolated from BGS survey.	Data on off-shore habitat types limited. Production values for habitat types are limited	Pragmatic approach that integrates a number of variables if habitat classification is based on physical, chemical and biological information.
Benthic Biomass	Either quantitative sampling or qualitative expert judgment.	A number of benthic datasets are available but these are not collected using comparative methodologies. Coverage of offshore areas is poor.	Assumes that biomass is a good proxy for production/ productivity.	Estimate based on quantitative/qualitative scale. Data limitations will determine the accuracy of the estimate of biomass.	Depends on whether approach is qualitative (expert judgement based) or requires more quantitative data (e.g. sampling program)	Benthic species that are large and long-lived may have very low annual production rates once mature. Hence a mussel bed of mature individuals may not have high levels of secondary production, despite having high biomass. Lack of comparative, quantitative data.	Intuitive measure relating to production that is easy to understand for stakeholders Qualitative ranking could be based on available survey data and expert judgement.

6.1 Strengths and Weaknesses of Approaches to Construct A UK Productivity Datalayer

6.1.1 Direct Methods (Cohort and Size Class Based Methods)

6.2 Based on the data requirements and the need for time-consuming analysis direct methods of estimating production are not suitable for the development of a UK CS wide benthic productivity layer.

6.1.2 Empirical Models

6.3 Empirical models are potentially useful for the development of a UK CS datalayer and a number of models have been developed to estimate production from variables that are relatively easy to measure or obtain..

6.4 Simple empirical models such as those developed by Brey (1990) and Edgar (1990) estimate production from two variables (biomass and mean individual weight) and have been used to estimate production from sampled benthic assemblages that have been divided into size groups. These method require less information and data processing and hence have more potential for developing a productivity datalayer.

6.5 Multivariable regression models (e.g. Brey et al., 1996, Brey, 1999b) estimate production from biomass and life history and environmental variables (temperature and depth) which can be readily obtained for the UK CS. Empirical models such as those developed by Jan Hiddink (School of Ocean Sciences, University of Wales, Bangor) to predict secondary production, use physical drivers and assemblage characteristics e.g. competition (Hiddink *et al,* 2006). Participants at the workshop identified these types of approaches as useful for the development of a UK CS productivity datalayer.

6.6 Both model types can be easily tested and refined. Validation data could be sought from holders and stakeholder confidence could inform how much validation is required.

6.1.3 Proxy Indicators/Expert judgement

6.7 Based on knowledge held by experts and information from the literature, estimated productivities of benthic assemblages/habitats could also be used to develop a qualitative ranking scale. The drawback of approaches based on expert judgement is that they are unrepeatable and may be rejected by stakeholders on the grounds of it’s the subjectivity of the approach.

6.8 Expert judgement cannot compensate for datagaps, for example, information on rates of secondary productivity for many species and habitat types is limited. As with the use of proxy measures the use of expert judgement for broad scale data i.e. at a regional level, may be too coarse to designate sites, or account for small-scale differences: e.g. it is not clear that different areas of mud are more or less productive.

6.9 The approach also depends on the availability of experts and the knowledge available is likely to be patchy in distribution. For example some areas/habitat types are likely to be comparatively poorly studied, whereas others have been subject to greater research effort.

6.10 The relationship between surface chlorophyll levels and benthic productivity would need to be demonstrated and this relationship may vary temporally and spatially Although the datalayer construction process might rely on some large assumptions, attendees at the workshop felt this was acceptable as long as the process was transparent. This also allows prioritisation of effort. Some of the data layers that are being developed for other parts of the project may be informative and could be used. The advantage of using these are that they already incorporate information for the project area (the UK Continental Shelf [UKCS]).

6.11 The drawbacks of such an approach are that it would rely on large assumptions about the correlation between selected environmental variables and benthic productivity. As with the modelled approaches validation of such approaches would be required. If the approach can be demonstrated to rank areas/habitats based on production then the approach would have value for the cost effective production of a UKCS wide production datalayer.

6.1.4 Mapping Productivity Scale and Resolution

6.12 Estimates and/or ranking of productivity could be tied in with MESH & EUNIS habitat maps, although consideration should be given to the scale selected and whether the resolution of the datalayer should vary. That is whether productivity for some areas would be based on the EUNIS Level 3 broad habitat coverage (which provides coverage for the entire UKCS) but with added detail provided based on biotope types where the data was available. Data availability on the distribution of biotope/habitat types is likely to vary regionally and depends on survey effort. For example not all habitats defined as ‘mud habitat ‘ by *sediment* are likely to have the same productivity. The quality of predictions in this case will vary across the datalayer, so there is a requirement to weight attendant confidence and uncertainty.

7. Discussion on Use and Development of a Benthic Productivity Layer

7.1 Recommended Method to Construct Productivity Datalayer

7.1 Direct methods of assessing production (cohort and size based) have onerous data requirements, requiring information (e.g. life-span) that is not available for some species and time-consuming laboratory processing of samples and desk-based calculations. At the workshop it was concluded therefore that, based on data requirements and processing/calculation costs direct methods are unlikely to be of practical use to construct a datalayer of secondary production of assemblages. At the workshop delegates also felt that expert judgement alone would not be an appropriate method of producing a datalayer as the approach could not be validated or repeated and this approach was rejected. However, expert judgement that was based on selected and tested proxy indicators may be a useful approach.

7.2 Empirical models that estimate productivity from more readily available sample characteristics e.g. biomass and size spectra were considered to have potential, particularly if these methods were used to ground truth the results from other suitable approaches for broad-scale productivity mapping, such as the use of proxy indicators and predictive models.

7.3 Therefore three approaches were identified as potentially useful to construct the datalayer. These were:

- The multivariable regression modelling approach, developed by Thomas Brey (1999b), which are parameterised using environmental variables and mass energy values from a benthic invertebrate sample;
- The models developed by Jan Hiddink (School of Ocean Sciences, University of Wales, Bangor) to predict secondary production, that use physical drivers and assemblage characteristics e.g. competition (Hiddink *et al,* 2006); or
- Relative scaling (ranking) approaches using proxy environmental variables such as chlorophyll a levels, depth, sediment and habitat type.

7.4 It was not possible to source any comparative studies on the performance of these approaches. It is therefore recommended that a small-scale pilot-study would be a useful exercise to trial the above approaches and identify what is achievable and the limitations of each approach.

7.2 Management Uses of a Secondary Production Datalayer

7.5 Secondary production is not widely used to inform marine management and as such the data and methodological development in this area are limited. This is particularly true of hard substrata, as most of the work to date has concentrated on the productivity of soft-sediment benthic communities. Although the review process identified research that is being undertaken to develop methods of evaluating epifaunal productivity, these are at an early stage and will not report in the near future (M. Kaiser pers comm.).

7.6 Despite these difficulties, the development of a productivity datalayer would provide useful information on ecosystem function (carbon cycling and energy flow are fundamental ecosystem processes). Hence the datalayer would have relevance to spatial planning to support ecosystem function and potentially the conservation of species and habitats and in particular, fisheries conservation (as benthic secondary production supports fish populations). In one model test, productivity is reported to have been a good predictor of diversity on the Welsh coast. The models developed by Jan Hiddink (Hiddink, 2006) have successfully predicted the occurrence of unexpected areas of high diversity (M. Kaiser pers comm.). Expert judgement alone, it was thought, would not have selected these areas as potentially highly diverse. This illustrates that a productivity datalayer, may have the potential to be a useful spatial planning tool. This would of course require testing to evaluate performance.

7.7 Measuring productivity could be useful to support delivery of the requirements of the European Marine Strategy Framework Directive. One of the indicators of Good Environmental Status (GES) refers to the status of marine food webs and hence a measure of food availability (benthic secondary production/productivity) would potentially be informative to achieve this indicator. (These indicators are currently at the development stage, so this application is speculative).

7.8 A productivity datalayer could also have value in measuring the overall performance of Marine Conservation Zones. Productivity encapsulates ecosystem processes such as organic matter cycling and energy flow so that it incorporates more information about the ecosystem than single, structural metrics. This means that there is also a longer term, monitoring value, to developing this datalayer. For example, a monitoring programmes may detect a change in ecosystem structure within an MCZ e.g. a change in of abundance of a single species, or a change in a measure of assemblage structure (e.g. diversity). If the MCZ objective was to conserve the species or the diversity of the assemblage then it would be clear that the MCZ had not performed as hoped. However, if MCZ performance has regard to wider ecosystem function then these changes may be interpreted in terms of ecosystem function. A change in structure may not be reflected in a change in function, for example different species may perform similar roles, so that processes such as production may be maintained.

7.9 While the scope of this project has investigated secondary production, primary production is also an important contributor to overall benthic production where light penetration is sufficient, e.g. macroalgae, microalgae and seagrasses. While it is theoretically possible to assess primary production this has not been considered within this study, and as such future work should consider addressing this parameter.

7.10 Data availability will ultimately determine the practicality of constructing a datalayer for the UKCS and will constrain the spatial resolution of mapped outputs. Data availability (environmental variables, assemblage sampling, mapping of habitats) would be expected to be highest for coastal areas and this is likely to be where productivity varies the most (due to habitat diversity). This allows the highest spatial resolution of production to be achieved where it is required. To produce a UKCS wide datalayer a number of datasets have been identified as potentially useful including the coastal models held by the oceanographic research institutes (e.g. PML, POL), the North Sea Benthic Surveys co-ordinated by ICES and other environmental and biological datasets collected and held by institutions. These would be useful to develop a datalayer of point (station) production values. Alternatively if production can be related to habitat types then the UK SeaMap landscapes (??) may be used to interpolate secondary production values to habitat types for greater spatial coverage.

7.3 Pilot Study

7.11 A small-scale quantitative pilot study is recommended to identify the most cost effective approach for producing a datalayer. The study will compare the performance of small-scale datalayers based on proxy indicators of productivity and empirical modelling approaches using existing data. Results from proxy indicators of productivity such as; chlorophyll-a levels in surface waters, depth, temperature etc. can be tested for correlation with empirical modelling approaches that have already been developed (Brey et al., 1996, Brey 1999b, Hiddink, 2006, Hiddink, *et al*, 2006). This would be useful to evaluate the sensitivity of different approaches that have differing data requirements.

7.12 There is a potential option to use sample data from other studies where production has already been estimated by one of the chosen methods. Cefas have nearly completed a Defra funded project (ME3112) where they sampled 155 offshore stations around the UK. This dataset was selected as time-consuming cohort analysis has already been undertaken for the samples. Although other datasets may contain more sites, we were unable to identify other datasets that contained the required information. Secondary production estimates were derived using the Brey multiple regression model, so that for each station there is an estimated total production value and mean community P:B ratio. A number of environmental measures and/or samples were also taken at each station so that other modelling approaches (e.g. Hiddink *et al*, 2006) and the use of proxy indicators could be trialled to evaluate alternate methods of assessing productivity.

7.13 This pilot study will identify whether 1) approaches based on the use of simple indicators/expert judgement perform sufficiently well (against two types of empirical model) to be adopted or if 2) Quantitative empirical models are required (data requirements may mean these are too costly to employ). The study would therefore be informative on the approaches, issues and effort required to produce a datalayer for the entire UKCS. This is required to understand whether the development of a productivity datalayer for the entire UKCS is feasible. If a proxy/expert judgement approach is adopted, based on this study, the pilot will have provided an initial validation of the approach against a quantitative estimate of production.

7.14 The tasks involved in the pilot study are presented in Table 6. These costs represent an initial estimate of the effort required to develop the pilot study that will compare the three selected approaches to assessing secondary production. This pilot study will allow us to select an approach for developing a UKCS secondary production datalayer and to estimate the costs of producing this. The outputs of this study will be:

- A comparative trial of the three suitable approaches for estimating secondary production;
- Identification of the strengths and limitations, with particular regard to estimates and data gaps, of these approaches in relation to producing a UKCS wide productivity datalayer;
- Recommendations on the most appropriate approach to estimate secondary production;
- An outline of data availability; and
- An estimated cost for producing a UKCS wide datalayer based on the selected approach.

Table 6: Breakdown of tasks involved in the pilot study

Task	Sub-tasks	Timeline
Collation of datasets	Define study area. Collation of key datasets.	July 2009
Environmental Variable Model Trial	Generate predictions of productivity based on proxy indicators including: • Chlorophyll-a levels in surface waters • Depth • Temperature	August 2009
Duplisea/Hiddink model test	The environmental and biological data collected as part of the CEFAS survey will be used to generate predictions of benthic productivity using the empirical model developed by Hiddink.	
Productivity evaluation Brey Model	Extract benthic productivity data from CEFAS survey results for sample locations within the study area. Extraction of relevant variables for proxy indicators and Duplisea/Hiddink model test.	
Reporting	Review relative performance of each model type. Assess suitability of each model type for developing a benthic productivity layer for the entire UKCS. Provide an indication of data availability and costs for producing datalayer using the recommended approach.	30th September 2009
Project Management	Overall project management. Quality Assurance. Meetings.	Ongoing throughout project

8. Conclusions

8.1 Historically secondary production has not been widely used to inform marine management. There are, however, a number of benefits that can be derived and such information may help inform the selection of suitable areas for MPAs. A number of approaches exist that could be employed to generate a map of benthic productivity, each of which has a number of advantages and disadvantages.

8.2 A workshop was convened to evaluate different approaches to assessing production/productivity and a draft report was circulated to independent experts. The most accurate methods of assessing productivity in benthic assemblages are the direct methods, based on population analyses using age and biomass. To derive the data requires time-consuming laboratory analysis on many species from repeated benthic samples. These methods are therefore too costly and time-consuming to produce a UK-wide productivity datalayer.

8.3 This required that other methods be considered. The data requirements and the complexity of empirical modelling approaches varies considerably. One broad group of models estimates productivity based on the derivation on P:B ratios from size-spectra analysis of a sample. (These approaches still require that sampling is undertaken and that these samples are sorted into size-spectra to estimate productivity (from biomass).

8.4 Empirical models that estimate production from environmental variables (with variables that account for impacts on productivity by human activities) have been developed. These largely circumvent the need for benthic sampling, although ground-truthing should be considered. Potentially this approach is a suitable, cost-effective method for producing a UK wide datalayer.

8.5 Another, potentially useful, alternate approach is to develop proxy indicators of productivity, which could perhaps be combined with expert judgement, to rank production by benthic habitats and to apply this ranking to benthic habitats found in the UK continental shelf. If a proxy/expert judgement based approach can be shown to discriminate between the productivity of habitats to an acceptable degree, then this approach could be selected to produce a UK-wide datalayer.

8.6 To identify a suitable approach, the performance of the Duplisea *et al*, (2002) empirical model and the proxy indicator approach require testing, to assess and compare the fitness of these for purpose. It was therefore recommended that the approaches should be tested against a simple empirical model based approach. The chosen approach uses estimated productivity derived using the Brey model from sample data. It was not possible to source any comparative studies on the performance of these different approaches. It was therefore recommended that a small-scale comparative pilot-study be undertaken to identify what is achievable and the limitations of each approach for the production of a UK wide benthic productivity datalayer. Predicted results from these methods need to be validated (ground-truthed) against productivity estimates, derived from a method, which stakeholders and managers can be confident provides an accurate measure of productivity. In this instance the results from the Brey multiple regression model will provide a validation of the results of the Duplisea *et al*, 2002 model and the proxy indicator approach. Direct measures of assessing productivity (cohort and size-class methods) would be most desirable as the validation data, but the cost and time scale of producing these is prohibitive.

8.7 The recommended pilot study will therefore evaluate the performance of the Duplisea *et al.* (2002) model and expert/proxy approaches against quantitative estimates of productivity obtained using the methods developed by Thomas Brey (Brey *et al*, 1996, Brey, 1999b. This comparative approach will indicate whether proxy indicators/expert judgement have potential value for the production of the datalayer or whether they should be rejected in favour of either of the empirical models. The results of this study will indicate whether it is feasible to develop a productivity datalayer and the likely cost of this (the cost will depend on the approach selected).

Abbreviations

ABPmer	ABP Marine Environmental Research Ltd
BMR	Basal Metabolic Rate
CCW	Countryside Council for Wales
Cefas	Centre for Environment, Fisheries and Aquaculture Science
Defra	Department for Environment Food and Rural Affairs
DOENI	Department of Environment (Northern Ireland)
EUNIS	European Nature Information System
IOM	Isle of Man
JNCC	Joint nature Conservation Committee
MarLIN	Marine Life Information Network
MESH	Mapping European Seabed Habitats
MCZ	Marine Conservation Zones
MPA	Marine Protected Areas
NE	Natural England
OSPAR	Oslo Paris Convention
$P:\overline{B}$	Production:Biomass Ratio
PML	Plymouth Marine Laboratory
POL	Proudman Oceanographic Laboratory
RMR	Resting Metabolic Rate
TTE	Trophic Transfer Efficiency
SAC	Special Area of Conservation (EC Habitats Directive)
SFD	Size frequency data
SG	Scottish Government
SPA	Special Protection Areas (EC Birds Directive)
UKCS	UK Continental Shelf

Definitions

Assimilation Efficiency:	The percentage of energy that an organism ingests that is assimilated rather than egested.
Basal Metabolic Rate:	Is the amount of energy expended by an organism while at rest in a neutrally temperate environment, in the post absorptive state (digestive system inactive). The release of energy in this state is sufficient only for the functioning of vital organs. A more common measurement used under less strict conditions is resting metabolic rate (RMR).
Biomass:	The weight of living material (usually measured as energy per unit area)
Gonad Production:	The amount of matter assimilated that is used in reproductive processes e.g. to produce eggs and sperm.
Gross Productivity:	The amount of energy assimilated in organic matter at a given tropic level over a time period.
Metabolic Rate (of an organism):	The amount of energy needed per unit time. Basal metabolic rate refers to the amount of energy required to maintain vital functions only.
Net Productivity:	The amount of energy held in organic matter at a given trophic level, minus the respiration of organisms at that level. Net productivity usually refers to primary producers.
$P:\overline{B}$	Production:Biomass ratio - the overbar indicates that this value represents mean biomass. The $P:\overline{B}$ will usually refer to a specific time period, e.g. annual $P:\overline{B}$
Primary Production:	The synthesis of complex organic molecules by autotrophs, the main route for this is photosynthesis using light energy, but other routes include chemosynthesis using the energy of organic compounds.
Primary Productivity:	The rate at which biomass is produced per unit by plants (Begon *et al*, 1996).

Production :	The amount of assimilated organic matter incorporated as body mass by heterotrophic organisms. A distinction should be made between somatic production and gonad (reproductive) production.
Productivity	The *rate* of conversion of assimilated organic matter to biomass per unit area per unit time (Waide *et al*, 1999) (see also production and somatic and gonad production).
Reproductive production:	See gonad production
Production Efficiency:	The percentage of energy assimilated by an organism that becomes incorporated into new biomass.
Secondary Productivity:	The rate at which biomass is produced per unit area by heterotrophic organisms.
Somatic Production:	The amount of assimilated matter incorporated as body mass (usually measured for a unit area over time).
Trophic Transfer Efficiency:	The efficiency with which prey production is converted to predator production.
Voltinism:	Number of broods/generations year.

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Appendix 1. Meeting Notes

MPA Datalayers - Productivity Workshop

7th January 2009 10am-3pm

Attendance

Natalie Frost (NF)	(ABPmer);
Heidi Tillin (HT)	(ABPmer);
Stephen Hull (SH)	(ABPmer);
Beth Stoker (BS)	(JNCC);
Jen Ashworth (JA)	(NE);
Michel Kaiser (MK)	(University of Wales, Bangor);
Gwladys Lambert (GL)	(University of Wales, Bangor).

Post Workshop Notes

Introduction and Background

- Defra have contracted a consortium led by ABPmer to produce datalayers to aid MPA planning and spatial management in the marine environment.

- A datalayer based on productivity was identified in the project proposal as having the 'potential to be a useful tool for soft-sediment benthic invertebrate community selection'. There is therefore a need to;
  i) Review current approaches to assessing productivity
  ii) Identify the strengths and weaknesses of these approaches in terms of constructing a datalayer
  iii) Assess the value and use of a productivity datalayer.

- The remit of the workshop was to invite experts to contribute to this draft review. Specifically opinions and feedback were sought on the approaches that could be used to construct a productivity datalayer and the use of this to deliver management objectives.

1) Discussion on scope of project:

   - Productivity is not widely used to inform marine management so data and methodological development in this area is limited.

   - Although most work to date has concentrated on the productivity of soft-sediment benthic communities there is a requirement in the proposal scope to consider the productivity of soft and hard substrates. Currently GL is working on measuring the productivity of epifauna in hard substrate assemblages, although the results will not be available immediately.

- A productivity datalayer is essential to inform the conservation of species and habitats and as a useful tool for fisheries conservation .

- A productivity datalayer would have especial value in measuring the overall performance of MCZs. Productivity encapsulates ecosystem processes such as organic matter cycling and energy flow so that it incorporates more information about the ecosystem than single metrics. For example a change in the abundance of a single species or in an assemblage measure such as diversity does not allow understanding of why the character of an ecosystem/habitat/area has changed. This means that there is also a longer term, monitoring value, to developing this datalayer.

2) Discussion on methods of assessing productivity

   - ‘Direct methods’ Size and cohort based analysis of single populations

   - All present at the meeting concluded that direct methods are unlikely to be of practical application to construct a datalayer of secondary production of assemblages, due to the data requirements.

Modelling Approaches

- Modelling approaches are the only sensible option for datalayer construction .

- Empirical models such as those developed by Jan Hiddink (School of Ocean Sciences, University of Wales, Bangor) to predict secondary production, use physical drivers and assemblage characteristics e.g. competition (Hiddink *et al* 2006). These models can be easily tested and refined. The predictions from these models could be verified using data from different temperature and biogeographic zones. Validation data could be sought from holders and stakeholder confidence could inform how much validation is required.

- For the Hiddink models the scaling functions of carrying capacity and competitive interactions could be checked.

- Dynamic models such as Ecopath and bioclimate envelope and food web modelling should be included in review and considered as approaches to measuring productivity.

Proxy Measures of Productivity

Expert Judgement

- Information on relative rates of secondary production between habitat types is limited.

- Drawback of approaches based on expert judgement is that they are unrepeatable

- Use of expert judgement/broad scale data i.e. at a regional level, would be too coarse to designate sites, or account for small-scale differences: e.g. it is not clear that different areas of mud are more or less productive .

- Could use environmental variables that influence productivity rates to construct a qualitative ranking scale

- The ranking of productivity could be tied in with MESH & EUNIS habitat maps, although consideration should be given to the scale selected, or whether the resolution of the datalayer would vary i.e. some regions /areas of the datalayer would have finer scale resolution than others.

- Such an approach would rely on large assumptions about the correlation between selected environmental variables and benthic productivity.

Variables to Include in Datalayer

- Chlorophyll a content of surface layer to be used as a proxy of underlying benthic productivity (availability of food supply). There are problems with using SeaWiFS data in coastal areas due to turbidity, tidal re-suspension and disturbance (GL).

- The relationship between surface chlorophyll levels and benthic productivity would need to be demonstrated. This relationship may vary temporally and spatially.

- Current and seafront data may be informative.

- Temperature has been shown to influence rates of production (partly due to effects on metabolism).

- General feedback on measuring production

- Currently only limited information available on the relative productivities of different types of habitats.

- Natural productivity could be measured using a method: that predicts the expected productivity. To measure productivity and take pressures into account, then direct methods are required.

- Not clear what resolution of productivity of areas and habitats that could be achieved, this is likely to vary regionally depending on data variability. For example not all habitats defined as ‘mud habitat ‘ by sediment are likely to have the same productivity. An eel-grass muddy habitat may have much higher productivity levels than an off-shore mud habitat.

- The quality of predictions will vary across the datalayer so there is a requirement to weight attendant confidence and uncertainty.

- Although the datalayer construction process might rely on some large assumptions this is acceptable as long as the process is transparent. This also allows prioritisation of effort .

3) How a productivity datalayer could be used:

    - If production is a result of human activity e.g. trawling or nutrient enrichment then is this a potential drawback to protecting sites based on productivity for conservation purposes?

    - Measuring productivity could be useful within the requirements of the European Marine Strategy Directive.

    - In order for the datalayer to be useful as a management tool decision makers need to be able to respond to changes in outputs (adaptive management) in the longer-term i.e. act to change a designated area .

    - Productivity has been shown to be a good predictor of diversity. The models developed by Jan Hiddink have predicted the occurrence of areas of high diversity. Expert judgement alone would not have selected these areas as potentially highly diverse .

    - Data availability (environmental variables, assemblage sampling, mapping of habitats) highest for coastal areas and this is likely to be where productivity varies the most (due to habitat diversity). This allows the highest spatial resolution of production to be achieved where it is required. Area selection for higher resolution study could be based on environmental variables such as the depth contour.

    - Differentiation between habitats to select sites, need to be considered alongside socio-economic factors, to add weight to decisions made.

Other Issues

- Data availability – this will determine the practicality of constructing a datalayer for the UKCS, will influence the approach chosen and will constrain the spatial resolution of map.

- Overall Summary

- The use of empirical models to construct a productivity datalayer is the most practical and viable option.

- A productivity datalayer is potentially a highly valuable tool to select sites for MPA designation due to the correlation between productivity and diversity. This datalayer would also be valuable for long-term monitoring and to inform management

- The feasibility of a pilot study should be investigated, including data availability, to evaluate the performance of different approaches to measuring productivity.

- If appropriate a quantitative pilot study should be recommended to identify the approach most suitable for producing a datalayer. The study could compare the performance of small-scale datalayers based on proxy indicators of productivity and empirical modelling approaches. This study will identify whether simple models perform sufficiently well to be adopted. The study would be informative on the cost, time scales, issues and effort required to produce a datalayer for the entire UKCS.

- The pilot study would be highly valuable to identify whether the development of a productivity datalayer for the entire UKCS is feasible.

Recommendations

- A small comparative pilot study could be conducted to evaluate the sensitivity of different approaches that have differing data requirements. Results from proxy indicators of productivity such as; chlorophyll-a levels in surface waters, depth, temperature etc. can be tested for correlation with empirical modelling approaches that have already been developed (Brey, 1999, Hiddink, 2006, Hiddink *et al*, 2006). The models already exist and if the developers agree to run them for the study, results should be obtained relatively easily.

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Future Work Programme

- Circulation of workshop report and draft review for comment

- Draft Review submitted 1st February 2009

- Final review submitted May 2009