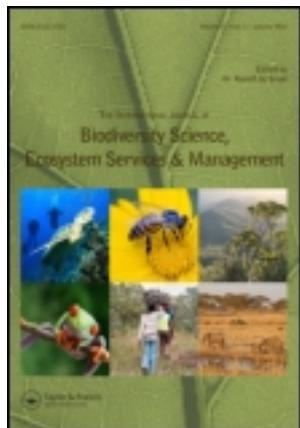


This article was downloaded by: [Colmex]

On: 11 April 2013, At: 17:03

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



International Journal of Biodiversity Science, Ecosystem Services & Management

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/tbsm21>

Incorporating indirect ecosystem services into marine protected area planning and management

Siân E. Rees^a, Melanie C. Austen^b, Martin J. Attrill^a & Lynda D. Rodwell^a

^a Marine Institute, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK

^b Plymouth Marine Laboratory, Plymouth, UK

Version of record first published: 23 Apr 2012.

To cite this article: Siân E. Rees, Melanie C. Austen, Martin J. Attrill & Lynda D. Rodwell (2012): Incorporating indirect ecosystem services into marine protected area planning and management, *International Journal of Biodiversity Science, Ecosystem Services & Management*, 8:3, 273-285

To link to this article: <http://dx.doi.org/10.1080/21513732.2012.680500>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Incorporating indirect ecosystem services into marine protected area planning and management

Siân E. Rees^{a*}, Melanie C. Austen^b, Martin J. Attrill^a and Lynda D. Rodwell^a

^aMarine Institute, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK; ^bPlymouth Marine Laboratory, Plymouth, UK

Marine Protected Areas (MPAs) are recognised as being the mechanism through which marine ecosystem services may be conserved to benefit human well-being. Planning and decision-making can be supported by the quantification and valuation of ecosystem services. To inform the development and management of MPAs a ‘service-orientated’ framework has been developed to use available data to spatially map and explore the pathways between ecosystem services, processes and the ecological functioning of benthic species for indirect ecosystem service provision within a case study area. The framework demonstrates that ecosystem service delivery is functionally interlinked and ecological function cannot be clearly mapped onto individual ecosystem services. The methodology developed here enables decision-makers to understand the links between benthic species, ecological function and indirect ecosystem services. There is currently no measure to quantify *how much* function is required to maintain human well-being. This lack of a measure, coupled with a large amount of uncertainty surrounding the links between ecosystem function and ecosystem service provision in marine systems, demonstrates that the inclusion of percentage targets for the conservation of broad-scale habitats in MPA planning and management should be considered within a precautionary approach to maintain the delivery of indirect ecosystem services.

Keywords: biological traits analysis; ecosystem function; MPA; marine spatial planning; service-orientated framework

Introduction

Marine ecosystems provide a number of essential ecosystem services, such as the provision of food and climate regulation, which underpin life on earth. These ecosystem services form the constituent parts (e.g. food, shelter, clean water) that are essential to maintain human well-being (Millennium Ecosystem Assessment 2005; Beaumont et al. 2007; Austen et al. 2011). As such, these services are of value to humankind.

Widespread and intensive human activity in the world’s oceans and the subsequent loss of marine populations and species are believed to be impairing the ability of marine ecosystems to provide the essential ecosystem services that contribute to human well-being (Chapin et al. 2000; Hooper et al. 2005; Worm et al. 2006; Halpern et al. 2008). Marine Protected Areas (MPAs), designated through a system of marine spatial planning, are recognised as being the mechanism through which marine ecosystem services may be conserved as ‘they are the only approach to marine resource management specifically designed to protect the integrity of marine ecosystems and preserve intact portions and examples of them’ (Sobel and Dahlgren 2004, p. 20).

In response to international and European drivers for MPAs (European Community Council Directive 1992; OSPAR Convention 2002; Secretariat of the Convention on Biological Diversity 2004), the UK administrations are tasked to substantially complete an ecologically coherent network of MPAs by 2012 (HM Government 2011). To support the UK Government in meeting these international and European commitments and to achieve the government’s aim of ‘clean, healthy, safe, productive and

biologically diverse oceans and seas’ (Department for Environment, Food and Rural Affairs 2002) the development of the Marine and Coastal Access Act (MCAA) (HM Government 2009), the Marine (Scotland) Act (2010) and the forthcoming Northern Ireland Marine Bill (2012) provides the legal frameworks to develop Marine Plans (guided at a national level by the Marine Policy Statement (HM Government 2011)). The development of Marine Plans is led by the UK Marine Management Organisation (MMO). Two planning areas on the east coast of the United Kingdom are the first areas in England to be selected for marine planning. It is the role of the MMO to approve each plan for consultation and adoption. The MCAA, the Marine (Scotland) Act (2010) and the forthcoming Northern Ireland Marine Bill will also enable the designation of a new type of MPA called a marine conservation zone (MCZ). These commitments are underpinned by a requirement to adopt management measures to enable the functioning of marine ecosystems to be maintained (OSPAR Commission 2006; European Parliament and Council 2008; HM Government 2011).

Decision-making, especially where the natural environment is concerned, is inherently exposed to high conflict potential (McShane et al. 2011; Minter and Miller 2011) thereby necessitating a methodology for capturing the complex context of ecosystem function and service provision (Salafski et al. 2001). The development of descriptors (Beaumont et al. 2007) to translate the complexity of marine ecosystem functions into marine ecosystem services has broadened the inclusion of this range of values into decision-making for marine nature conservation. As a

*Corresponding author. Email: sian.rees@plymouth.ac.uk

result, the consideration of economic, social and ecological values in decision-making (the ecosystem approach) through defining ecosystem services has therefore become integral to marine conservation planning and policy in the United Kingdom (OSPAR Commission 2006; European Parliament and Council 2008; HM Government 2009, 2011).

To inform the development of an ecosystem services framework and its application in marine conservation planning and management, research is gathering pace on projects to spatially map and value 'direct uses' of the marine environment, for example, recreation and fisheries (Klein et al. 2008; Rees SE, Rodwell LD, et al. 2010). There has been less focus on ecological function particularly for indirect ecosystem service provision which is defined as those benefits which are 'derived from the environment without the intervention of man' (Pearce and Turner 1990; Beaumont et al. 2007). These services have not been measured directly in previous research for marine planning as their delivery is considered to be functionally interlinked by both biotic and abiotic processes (Hiscock et al. 2006; Petchey and Gaston 2006; Bremner 2008). This research therefore attempts to focus on the indirect regulating and supporting services in relation to biodiversity in a case study area to inform marine planning.

There are variations on the definitions of indirect services (Constanza et al. 1997; De Groot et al. 2002; Millennium Ecosystem Assessment 2005; Haines-Young et al. 2007a; The Economics of Ecosystems and Biodiversity 2010). This research applies the definitions of indirect ecosystem services for the marine environment following Beaumont et al. (2007) and Beaumont et al. (2006):

- gas and climate regulation (a regulating service): the balance and maintenance of the chemical composition of the atmosphere and oceans by marine living organisms;
- bioremediation of waste (a regulating service): the removal of pollutants through storage, burial and recycling; and
- nutrient cycling (a supporting service): the storage, cycling and maintenance of nutrients by living marine organisms.

To define the importance (or value) of ecosystem functions in relation to ecosystem services previous research shows that the functional characteristics of species strongly influences ecosystem processes (Hooper et al. 2005). Biological traits analysis (BTA) is a method which has been proposed to assess ecosystem function in marine benthic environments (Bremner et al. 2003, 2006a). BTA uses a series of behavioural (e.g. feeding), life history (e.g. age) and morphological characteristics (e.g. body size) of species to define ecological function (Bremner et al. 2006b). The ecological function of a species is then used to infer an aspect of ecosystem function (Lavorel and Garnier 2002; Bremner 2008).

In previous research relating to the marine environment BTA has been used to illustrate how ecosystems function in relation to the biological assemblages (Bremner et al. 2006b; Frid et al. 2008) and in relation to time (Frid 2011). BTA has also proved useful as a tool to show how changes in species composition caused by anthropogenic impacts affect ecosystem functioning (Tillin et al. 2006; Hewitt et al. 2008). These studies have applied BTA to infer that the ecological function of benthic species contributes to the delivery of *all* ecosystem services. However, issues arise with this approach as marine managers, when working with stakeholders, may need to make trade-offs between different ecosystem services when decisions are made on the use of marine area (Kremen 2005). Managers will therefore need a more detailed understanding of how ecological function is linked to these services and how they can be defined and valued at a local to regional scale (Loreau et al. 2001; Chan et al. 2006).

In this research a 'service-orientated' approach was developed as this is most likely to translate across the science-policy interface (Kremen 2005; Raffaelli 2006). The development of a framework for this research follows the 'ecosystem cascade' theory developed by Haines-Young and Potschin (2007b) where the relationship between biodiversity, ecosystem function and human well-being is described in a simple linear framework. The complex concepts of ecosystem processes, functions and benefits act as prompts by which the complexities of ecosystem functioning, linked to services and human well-being, can be visualised to help understand a problem (Haines-Young et al. 2007b). For a given case study area the services of interest are identified, followed by the identification of the processes and functions that affect the delivery of those services linked to the ecology of the case study marine area. Here, the framework was applied to Lyme Bay in south-west England. To inform ongoing debate regarding marine planning, conservation and the long-term delivery of ecosystem services the described research aims to (1) define the spatial area over which benthic species operate for the delivery of the indirect services of nutrient cycling, gas and climate regulation and the bioremediation of waste in a case study area; (2) link the provision of services with current conservation policy; and (3) make recommendations for the inclusion of indirect service provision in marine spatial planning policy.

Materials and methods

Case study area

Lyme Bay was chosen as it is a data-rich case study area. The offshore reef areas have been identified as a draft Special Area of Conservation under the European Union's Habitats Directive (92/43/EEC) for the Annex 1 habitat criteria for reefs. Additionally, there is currently a 206 km² statutory MPA within the bay. This closure was designated on 11 July 2008 by the UK Department for Environment, Food and Rural Affairs to protect the marine biodiversity

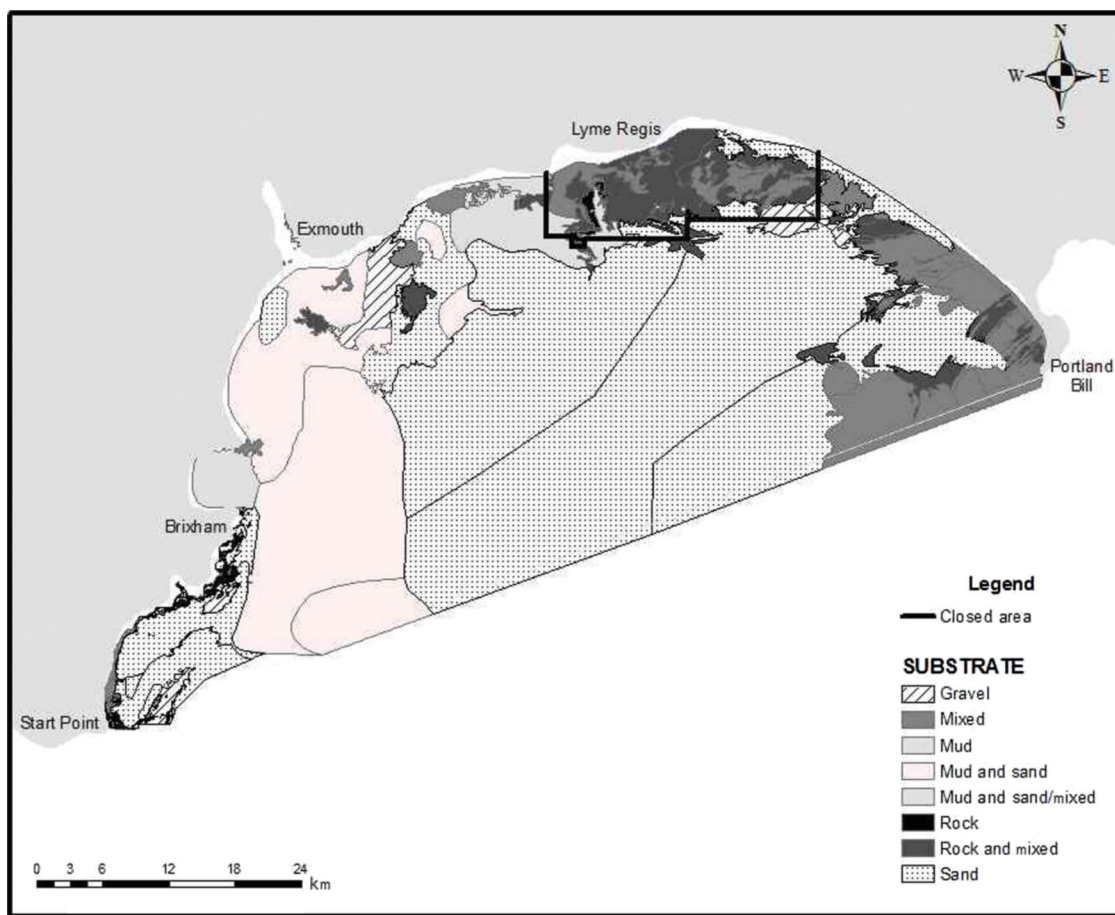


Figure 1. The Lyme Bay case study area showing the 2008 closed area and substrate. Source of substrate data: Devon Biodiversity Records Centre.

of the reefs from the impact of fishing with dredges and other towed gear.

The Lyme Bay study area is approximately 2460 km² and is defined as the sea area which is enclosed by a line drawn between Portland Bill in Dorset and Start Point in Devon (Figure 1). This study focused on the benthic habitats which comprise of sublittoral rocky reefs (defined as areas of rock and mixed ground in the northern section; mixed ground is defined as seabed consisting of combinations of sand, gravel, pebbles, cobbles and boulders (Black 2007)), extending to soft sediment areas as the depth increases offshore. Lyme Bay has been identified as a 'marine biodiversity hotspot' (Hiscock and Breckels 2007). These are identified as areas of high species richness that include rare and threatened species. The benthic habitats of Lyme Bay have been much studied (Rees SE, Attrill MJ, et al. 2010). To inform both statutory and non-statutory marine spatial planning processes, extensive survey work to produce detailed biotope and substrate maps of Lyme Bay was commissioned by the Devon Wildlife Trust in 2005 (Ambios 2006). These maps were further refined by Stevens et al. (2007). There is a large amount of available data relating to benthic assemblages. Any conclusions that can be drawn from these data sets can be used to inform

ongoing conservation planning activity both locally and regionally.

Data selection

Species distribution data (presence only) across 464 survey sites (Figure 2) were extracted from three data sets, made available by Devon Biodiversity Records Centre, Data Archive for Seabed Species and Habitats (www.dassh.ac.uk) and the University of Plymouth:

- sea search dive surveys (Wood 2007);
- grab sample and drop video surveys undertaken by Ambios Ltd on behalf of the Devon Wildlife Trust (Ambios 2006); and
- University of Plymouth drop video surveys (Stevens et al. 2007).

These surveys were undertaken to quantify patterns of marine biodiversity at a scale relevant to marine spatial planning within the case study area of Lyme Bay (Stevens et al. 2007). These data are typical of the data available to conservation planners and managers to inform their decision-making process.

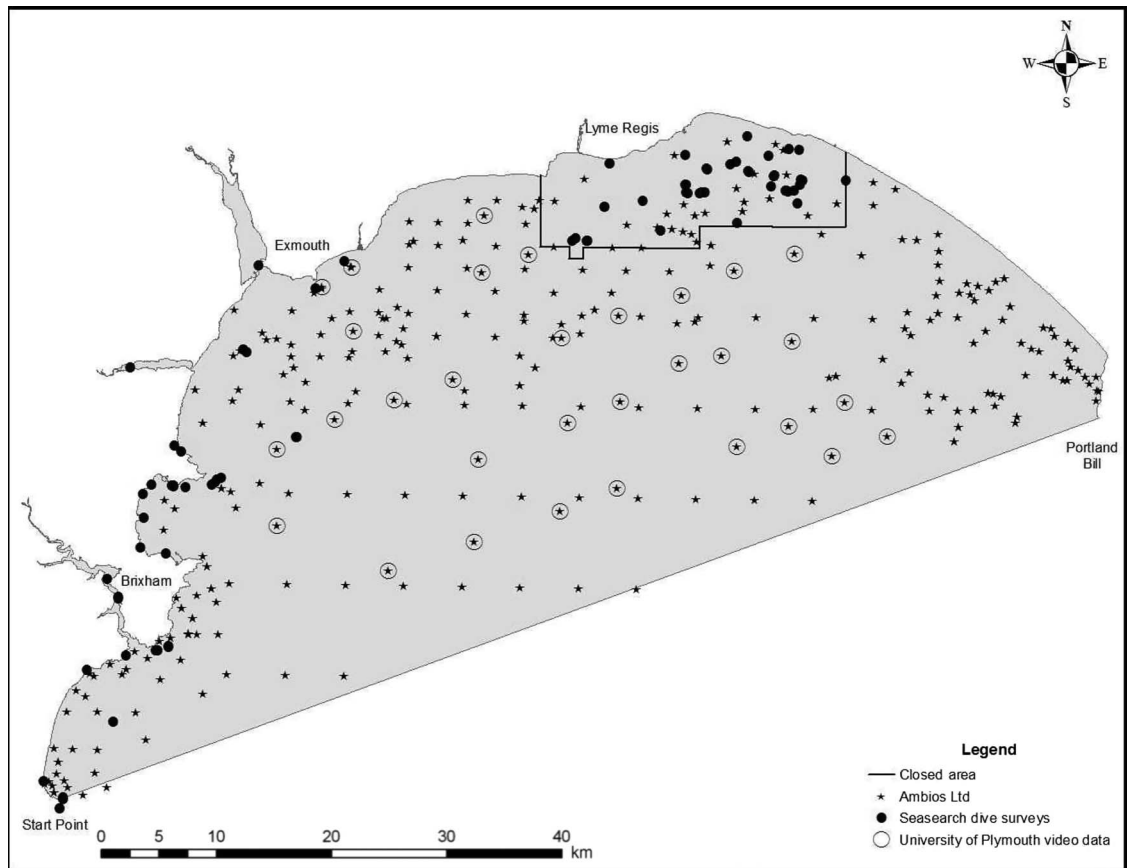


Figure 2. Survey sites in Lyme Bay.

A service-orientated framework and BTA

The services of interest were identified, followed by the identification of the processes and functions that affect the delivery of those services linked to the ecology of Lyme Bay. The three ecosystem services selected for study were nutrient cycling, gas and climate regulation and the bioremediation of waste. Nutrient cycling supports the other two regulatory services but, in addition, these three services are highly interlinked in the marine environment through the functional roles performed by benthic species (Snelgrove 1998). Three ecosystem processes were selected which collectively and in combination largely enable delivery of the three services, namely energy fixation, energy transfer and the burial and enhancement of microbial decomposition. Each of these processes can be partially mapped onto the delivery of the three services (Table 1).

A multi-trait approach was adopted that included as many traits as possible that are closely linked to these ecosystem processes. The aim of a multi-trait approach is to provide the most complete description of how the ecology functions in the case study marine area (Bremner et al. 2006b; Bremner 2008). Species can be sorted into groups of effect traits that represent a functional role or that contribute to a process (Lavorel and Garnier 2002; Giller et al. 2004; Bremner et al. 2006a) (Table 1).

Fourteen biological traits that relate directly to the ecosystem processes (Table 1) were chosen from a list of 248 traits listed in the Biological Traits Information Catalogue (BIOTIC) (MarLIN 2006).

In order to comprehensively capture the function of species in the case study area, multiple traits were selected and therefore several traits overlap within the same process (this is because not all records within BIOTIC are complete). For example, a species may be referenced in BIOTIC as being a 'crawler' under 'movement type' (therefore exhibiting some bioturbator potential) but not referenced as a 'bioturbator' under the category of 'bioturbation'. The inclusion of multiple traits ensured that the role of each species would be included in the data analysis. If the species is recorded in BIOTIC as both a crawler and a bioturbator then it was only scored once within the process. Epifaunal and epibenthic species were only counted in the burial and enhancement of microbial decomposition if they also expressed relevant traits under the movement, habit and bioturbation category.

The BIOTIC (MarLIN 2006, www.marlin.ac.uk/biotic) was used to determine the attribution of relevant biological traits for species found in the study area. Of the total of 452 species identified from the survey data 383 species were successfully matched via the BIOTIC database.

Table 1. A service-orientated framework linking the provision of the ecosystem services of nutrient cycling, gas and climate regulation and the bioremediation of waste to functions that are influenced by the biological traits of benthic marine organisms.

Ecosystem service	Process	Description	Function	References	Trait category	Trait
Nutrient cycling	Energy fixation	The respiration of gases and the assimilation of carbon and nutrients by primary producers to create biomass	– Carbon fixation	Bremner et al. (2006a), Hiscock et al. (2006)	Environmental position	Epifloral
			– Nutrient cycling			
Gas and climate regulation	Energy transfer	The respiration of gases, the excretion of organic matter, the assimilation of carbon and nutrients and the metabolising of pollutants by secondary producers operating at the water column/surface interface	– Respiration of gases	Kristensen and Blackburn (1987); Snelgrove (1997, 1998), Bremner et al. (2006a, 2006b)	Environmental position	Epifaunal/epibenthic
			– Consumption of pollutants			
Bioremediation of waste	Enhancement of microbial decomposition	The role of secondary producers in the burial of organic matter and supply of nutrients and oxygen via bioturbation activities which enhance the microbial decomposition process at the surface/subsurface interface	– Nutrient cycling	Kristensen and Blackburn (1987), Snelgrove (1997, 1998), Petersen et al. (1998), Pearson (2001), Austen et al. (2002), Bremner et al. (2006a, 2006b)	Environmental position	Epifaunal/epibenthic
			– Respiration of gases			
Bioremediation of waste	Enhancement of microbial decomposition	The role of secondary producers in the burial of organic matter and supply of nutrients and oxygen via bioturbation activities which enhance the microbial decomposition process at the surface/subsurface interface	– Resuspension of organic matter	Kristensen and Blackburn (1987), Snelgrove (1997, 1998), Petersen et al. (1998), Pearson (2001), Austen et al. (2002), Bremner et al. (2006a, 2006b)	Environmental position	Epifaunal/epibenthic
			– Decomposition of organic matter			
Bioremediation of waste	Enhancement of microbial decomposition	The role of secondary producers in the burial of organic matter and supply of nutrients and oxygen via bioturbation activities which enhance the microbial decomposition process at the surface/subsurface interface	– Movement	Kristensen and Blackburn (1987), Snelgrove (1997, 1998), Petersen et al. (1998), Pearson (2001), Austen et al. (2002), Bremner et al. (2006a, 2006b)	Environmental position	Epifaunal/epibenthic
			– Consumption			
Bioremediation of waste	Enhancement of microbial decomposition	The role of secondary producers in the burial of organic matter and supply of nutrients and oxygen via bioturbation activities which enhance the microbial decomposition process at the surface/subsurface interface	– Burial (sequestration)	Kristensen and Blackburn (1987), Snelgrove (1997, 1998), Petersen et al. (1998), Pearson (2001), Austen et al. (2002), Bremner et al. (2006a, 2006b)	Movement	Burrower
			– Detoxification			
Bioremediation of waste	Enhancement of microbial decomposition	The role of secondary producers in the burial of organic matter and supply of nutrients and oxygen via bioturbation activities which enhance the microbial decomposition process at the surface/subsurface interface	– Cycling of organic materials and nutrients into and out of the sediment	Kristensen and Blackburn (1987), Snelgrove (1997, 1998), Petersen et al. (1998), Pearson (2001), Austen et al. (2002), Bremner et al. (2006a, 2006b)	Habit	Tubicolous
			– Resuspension of organic matter			
Bioremediation of waste	Enhancement of microbial decomposition	The role of secondary producers in the burial of organic matter and supply of nutrients and oxygen via bioturbation activities which enhance the microbial decomposition process at the surface/subsurface interface	– Resuspension of organic matter	Kristensen and Blackburn (1987), Snelgrove (1997, 1998), Petersen et al. (1998), Pearson (2001), Austen et al. (2002), Bremner et al. (2006a, 2006b)	Bioturbation	Burrow dweller
			– Decomposition of organic matter			
Bioremediation of waste	Enhancement of microbial decomposition	The role of secondary producers in the burial of organic matter and supply of nutrients and oxygen via bioturbation activities which enhance the microbial decomposition process at the surface/subsurface interface	– Resuspension of organic matter	Kristensen and Blackburn (1987), Snelgrove (1997, 1998), Petersen et al. (1998), Pearson (2001), Austen et al. (2002), Bremner et al. (2006a, 2006b)	Bioturbation	Bioturbator
			– Decomposition of organic matter			

Note: A definition of the traits can be accessed from BIOTIC (MarLIN 2006).

Data analysis

Each survey site was scored for the number of species which demonstrate traits defined within the ecosystem processes of energy fixation, energy transfer and the burial and enhancement of microbial decomposition. Where a species demonstrated traits in more than one process (e.g. a species may be both a suspension feeder (energy transfer) and a burrower (enhancement of microbial decomposition)) a score was given under each process. Where a species demonstrated two or more traits within the same process (e.g. a species recorded within the BIOTIC database as both a burrower and a burrow dweller) the species would only be scored once. The scores were summed over each survey site providing a 'process by site' matrix. To display the data spatially the 'process by site' matrix was imported into GIS (ArcMap version 9.3.1). Data were displayed using 'graduated symbols' where the size of the symbol indicated the relative score for each key process at each site. The relative score (excluding sites where 0 was recorded) was divided into five categories using Jenks optimisation method which classifies natural breaks in the data by reducing variance within groups but maximising variance between groups.

To enable an analysis of the three processes and the relationship with substrate, the 'process by site' matrix

data were joined spatially using the ESRI Arc GIS tool 'Spatial Join'. The spatially joined data were re-exported to Microsoft Excel to enable analysis of the data. To remove sampling bias in the data (e.g. there are more species which display biological traits in the rock substrate as there has been more sampling effort in this substrate type) the total for each key process within each substrate type was divided by the number of surveys undertaken, providing an average relative value for each key process within each substrate type.

Results

The BTA of species in Lyme Bay shows that the species which have traits that facilitate the key process of energy fixation are distinct from species which facilitate the key processes of energy transfer and the burial and enhancement of microbial decomposition within Lyme Bay. Many species possess traits which facilitate both energy transfer and the burial and enhancement of microbial decomposition.

The spatial results show (Figure 3) that the key process of energy fixation occurs in the inshore waters of Lyme Bay. This analysis represents the epiflora and photoautotrophs within Lyme Bay. Species which demonstrate



Figure 3. The delivery of the process of energy fixation facilitated by benthic species in the Lyme Bay case study area. Note: Data are displayed as graduated symbols (Jenks optimisation) where the size of the symbol indicates the count for the process at a survey site.

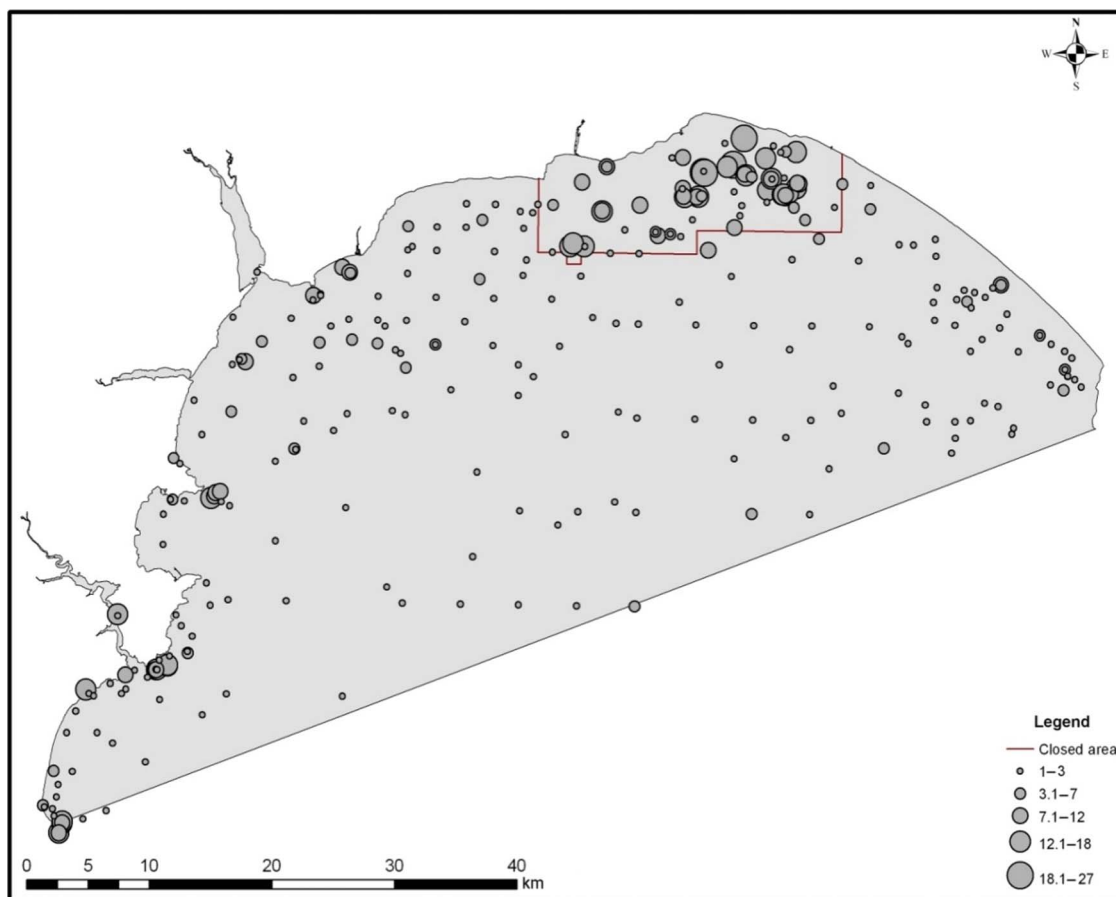


Figure 4. The delivery of the process of energy transfer facilitated by benthic species in the Lyme Bay case study area.

Note: Data are displayed as graduated symbols (Jenks optimisation) where the size of the symbol indicates the count for the process at a survey site.

traits that contribute towards the transfer of energy process can be seen within the protected (closed) area of Lyme Bay (Figure 4) and on the rock and mixed substrates along the coast from Brixham to Start Point. They include species such as *Alcyonium digitatum* (Linnaeus) and *Eunicella verrucosa* (Pallas). Benthic species which demonstrate the traits that contribute towards the process of enhancement of microbial decomposition were also found across all sites in Lyme Bay (Figure 5). Relevant activities include the burrowing of the bivalve mollusc *Abra alba* (Wood) and *Arenicola marina* (Linnaeus).

The substrates of mud, gravel and rock are the most favourable for the energy fixation process as the substrate hosts species such as *Zostera marina* (Linnaeus), *Laminaria hyperborea* (Gunnerus) and *Lithothamnion corallioides* (P & H Crouan). The mud and sand substrates are the least favourable for the presence of species which demonstrate traits that facilitate energy transfer processes in Lyme Bay (Figure 6). The soft substrates of mud and sand are more favourable for the enhancement of microbial decomposition than the harder substrates (Figure 6).

Discussion

The ecosystem processes which can contribute to the delivery of the indirect ecosystem services of nutrient cycling, gas and climate regulation and the bioremediation of waste are facilitated by the benthic flora and fauna across Lyme Bay. The main spatial differences are that the energy fixation process is inevitably limited to the shallow waters where light penetrates the water column enabling primary production in the benthos. Energy transfer and the enhancement of microbial action are distributed broadly across Lyme Bay with the former favouring the harder substrates and the latter favouring the soft substrates.

The results show that the MPA within Lyme Bay contains benthos which could potentially contribute to the delivery of the ecosystem services of gas and climate regulation, the bioremediation of waste and nutrient cycling. However, the processes of energy fixation, energy transfer and the burial and enhancement of microbial decomposition are also delivered by benthic species across the substrate types throughout Lyme Bay. This raises numerous points for discussion in relation to the practical application of this methodology and how the ecological function for

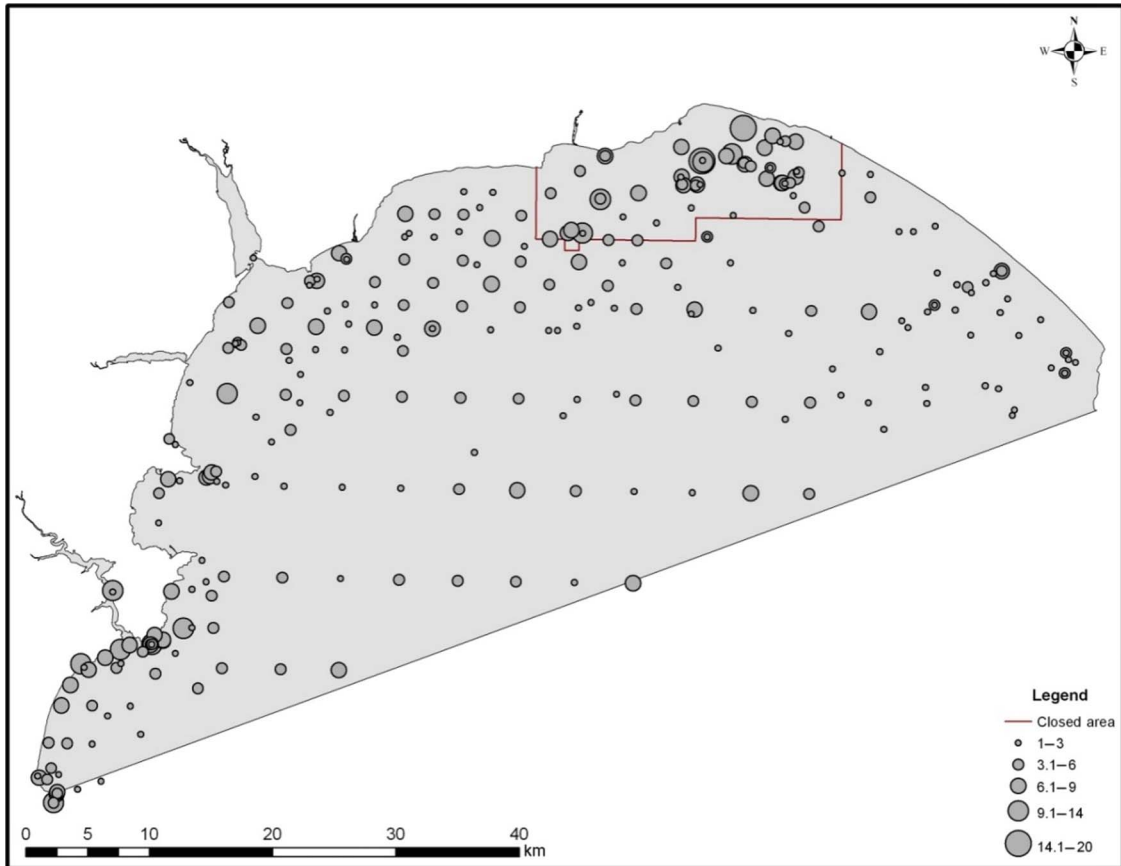


Figure 5. The delivery of the process of burial and enhancement of microbial decomposition facilitated by benthic species in the Lyme Bay case study area.
 Note: Data are displayed as graduated symbols (Jenks optimisation) where the size of the symbol indicates the count for the process at a survey site.

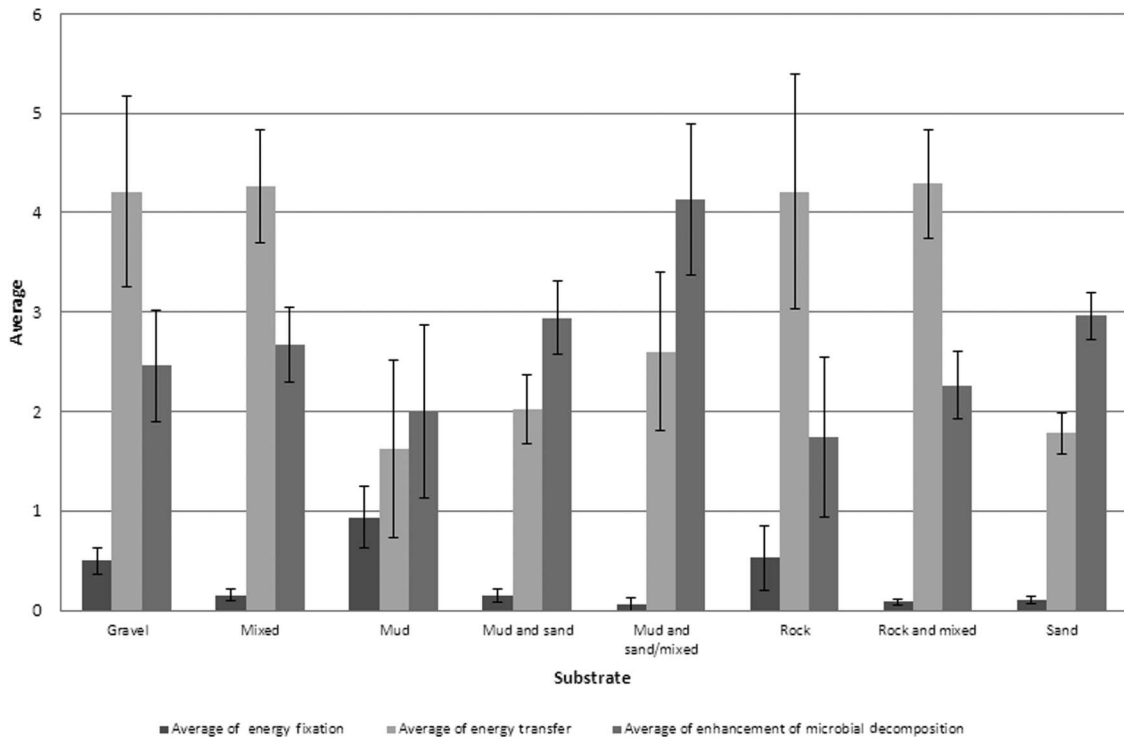


Figure 6. The relationship between substrate type and the delivery of the processes of energy fixation, energy transfer and the enhancement of microbial decomposition in the Lyme Bay case study area.
 Note: The standard error of the mean is shown for each process within each substrate type.

indirect ecosystem services can be quantified and valued as required for conservation planning and management.

How much function is there (value)?

The use of BTA in this context enabled exploration of how the indirect services can be spatially visualised and the potential for the benthic species to deliver these services. This approach, however, does not enable the amount of functioning to be quantified and therefore a measure of how important these sites are in delivering the ecological functions and therefore a valuation of these ecosystem services is not possible to quantify.

Previous research has focused on species richness (species biodiversity) or the range of traits within biological assemblages (functional diversity) to indicate an amount of functioning and therefore the delivery of all ecosystem services. However, no clearly defined relationship between species diversity and ecosystem functioning has been demonstrated (Chapin et al. 2000; Schwartz et al. 2000; Ieno et al. 2006; Somerfield et al. 2008). Although functional diversity is considered to be the most relevant indicator of the link between function and ecosystem services there is no standardised metric (Petchey and Gaston 2006; Somerfield et al. 2008). For example, a species may provide an ecological function that contributes to the delivery of all services or just one service (Petchey and Gaston 2006). There is also considered to be significant functional redundancy within the marine environment (Snelgrove 1997). In other words, areas that are functionally diverse may not provide more ecosystem function. Furthermore, different scenarios of biodiversity loss will affect the ecological function of benthos in different ways (Solan et al. 2004). There is also a potential for species substitutions to maintain ecological function as the system changes over time (Frid 2011). This uncertainty makes it difficult to truly establish how subtle changes in biodiversity will affect ecosystem services (Snelgrove 1998; Raffaelli 2006).

It can be seen that the scientific foundations for valuation based on ecological function remain limited by a lack of a measure for how much function a habitat provides. Recent calls from scientists in relation to the Convention on Biological Diversity 2020 targets state that, although individual species have the capacity to provide a disproportionate amount of service within a habitat area, there is growing body of evidence that suggests that a measure of functional diversity would provide the best insurance for securing the delivery of ecosystem goods and services (Perrings et al. 2010). Future developments in this field of valuation may focus on making a case for functionally diverse habitats in conservation planning and policy.

How much function do we need?

At present, on a local level in Lyme Bay or regionally, there is no perception or evidence that maintenance of the global climate or the capacity of Lyme Bay to bioremediate waste

or the underpinning nutrient cycling is affected by human uses of the benthic environment. Unless an entire trophic type was removed from the system it is unlikely that any local effects would be noticed. For example, a local extinction of filter feeders might cause increased turbidity. Unlike some direct use ecosystem services such as food provision and recreation, which are experienced and managed across local or regional scales, indirect services are broad, large spatial-scale ecosystem services.

In the near future, as marine spatial planning is implemented, marine managers will be required to make decisions and trade-offs between spatially different ecosystem services (Kremen 2005). In determining 'how much function do we need?' managers will require an understanding of the potential contribution of all substrate types (and broad habitat types) to indirect service provision. They will also need to consider the impacts of human activities on the benthic environment and the sensitivity of some species to disturbance and how these in turn will affect service provision. Methodological approaches that can measure the delivery of ecosystem services in relation to indicators of human well-being, for example, health via the development of scenarios, may provide a more realistic picture of the delivery of these services and the impact on human well-being (Bohensky et al. 2011).

Other influences

The delivery of indirect ecosystem services is not solely linked to the ecological functions of benthic assemblages. Functioning is also affected by the physical and chemical properties of the system, for example, tidal currents and pH (Hiscock et al. 2006; Bremner 2008), as well as interactions between the pelagic and terrestrial systems. Analysis of the whole system remains impossible because of a lack of information on how these systems interact to provide these broad ecosystem services (Petchey and Gaston 2006).

Ecosystem functioning is also strongly linked to microbial groups present in the marine environment. For example, in coral reef systems it has been found that the bioremediation of waste requires a diverse microbial community (Nystrom and Folke 2001). Exactly how the larger macrobenthic organisms of this study impact upon microbial communities and hence impact upon microbially mediated ecosystem functions remains a research challenge (Petchey and Gaston 2006).

Can we plan for the long-term delivery of indirect services?

Integrating ecosystem services into conservation planning and management remains a key challenge (De Groot et al. 2010). However, the concept of ecosystem services is an example of where a framework developed by scientists has translated well into policy, but the development of methodologies to define and to value these ecosystem services has raised numerous issues in its practical application.

Conservation planning in the marine environment focuses on marine habitats and species and it has been demonstrated in this research that the delivery of indirect ecosystem services does not map neatly onto the presence of a particular species. Therefore, a consideration of the conservation of broader habitat types, for example, substrate as an insurance against the potential loss of these ecosystem services, may provide the best option for ensuring the long-term delivery of indirect services. The UK Joint Nature Conservation Council and Natural England (Ashworth and Stoker 2010) propose that a network of MCZs should include percentage targets for broad-scale habitats classified at the European Nature Information System level 3 and percentage targets for the inclusion of a select few species and habitats identified for protection in existing conservation legislation under the EU Habitats Directive, the UK Wildlife and Countryside Act (Biodiversity Action Plan species) and the Oslo Paris Convention (OSPAR). This policy proposal is an important step in recognising that all ecosystem services are not quantifiable and that conservation policy that focuses on biodiversity alone may result in areas which are functionally important but not biodiverse being left out of the planning process (Frid et al. 2008). The inclusion of percentage targets for broad-scale habitats in conservation is an essential precautionary approach to maintain the long-term delivery of indirect services.

Incorporating what we know into conservation management and planning

The use of BTA in the service-orientated framework demonstrates that the conservation of the reef habitat in Lyme Bay secures a level of ecological function (and therefore value) to ensure the delivery of indirect ecosystem services of gas and climate regulation and the bioremediation of waste and nutrient cycling. The provision of those services is not, however, exclusive to the MPA; they are provided by species and habitats across the bay.

This methodology provides an example of the practical application of current science to available data for the long-term delivery of indirect services. It demonstrates that these indirect services can be visualised but they cannot be valued. Valuations of ecosystems services remain central to the development of policy. The UK National Ecosystem Assessment, marine chapter, includes an economic analysis of the UK coastal margin and marine habitats (Beaumont et al. 2010). Economic valuations have also been provided for the required impact assessment to support the recommendations for a UK network of MCZs (Balanced Seas 2011; Irish Sea Conservation Zones 2011; Leiberknecht et al. 2011; Net Gain 2011). Such monetary valuations are important to maintain the importance of ecosystem services and human well-being in policy. Indeed, when applied spatially in a planning context they can show the relative economic importance of an activity. However, it is in its practical application for planning and management that caution must be exercised.

Decision-makers must be aware that if they focus on valuing the types of ecosystem services that are amenable to economic value then it is possible that they may end up only managing those economically valuable services at the expense of the rest (Robinson 2011).

In this study the use of BTA increased spatial awareness of where the links are between the ecological functions of benthic species and their potential to contribute towards the delivery of the ecosystem services of gas and climate regulation, bioremediation of waste and nutrient cycling. The fact that these services are functionally interlinked and cannot be directly mapped onto ecosystem service provision indicates that if indirect services are to be included in a cost-benefit or multi-criteria analysis for conservation planning and management then managers must be aware of the limitations of the available science to define and quantify (or value) ecosystem function in relation to the delivery of ecosystem services; they must also be aware that the linear nature of the service-orientated framework is a simplified model of ecosystem service delivery linked to biodiversity and that there are 'cascades' and feedbacks throughout the system (Haines-Young et al. 2007b). This is important particularly if trade-offs are to be considered. It should also be noted that the use of multiple traits to describe ecological function leads to a broad description of ecological functioning (Bremner et al. 2006b) as the 'real function' is not represented. What is represented by the framework is an indication of the potential of biodiversity to provide the ecosystem services. Therefore, with such a broad field of variables within the marine environment the selection of specific traits that are sensitive to those impacts relating to the management and conservation objectives for a marine site may help managers apply this tool to evaluate the effects of negative stressors (Elliott and Quintino 2007).

Conclusion – including indirect ecosystem services into MPA planning

We recognise that this study develops only a partial assessment of ecosystem functioning in relation to indirect service provision. Yet incorporating what is currently known about the basic roles that marine species have in the delivery of ecosystem services, using available data, can inform the progress of management and policy relating to the use and protection of the benthic natural resource. In this instance, the presence of species across Lyme Bay which contribute to the processes of energy transfer and the enhancement of microbial decomposition provides a strong argument for the incorporation of the OSPAR recommendations to include percentage targets for broad-scale habitats and to manage human activities within them. In response to the lack of information on ecosystem function, which species or habitats are critical for maintaining function and the delivery ecosystem services in the marine environment, there is a need to include 'precaution' and 'uncertainty' into the planning process (Balvanera et al. 2006; Bulling et al. 2010; Foley et al. 2010). A 'protect

a bit of everything' approach is largely precautionary and should remain open to the principles of adaptive management (Salafski et al. 2001) as our understanding of the links between ecology, divers for change, ecosystem function and the delivery of ecosystem services improves.

In terms of the development of research from the 'ecosystem services community' to support marine conservation planning and policy this research has shown that there is a need to further refine the BTA methodology so that ecological function can be quantified at a local to regional scale. In lieu of perfect ecosystem function models for the marine environment, research could support the development of a 'shortlist' of biological indicator traits that can provide a measure of the negative effect of environmental stressors. These indicators would be useful for managers to monitor the impact of activities in a marine area.

Acknowledgements

All substrate maps have been derived from data provided by Devon Biodiversity Records Centre, for which copyright belongs to a variety of organisations including UK Hydrographic Office and Devon Wildlife Trust and for which permission for use in this instance has been granted. No further copies may be made. This research has been enabled by funding from the Marine Institute at the University of Plymouth and the Devon Wildlife Trust as well as the NERC's Oceans 2025 programme. Thanks to Dr Tim Stevens, Griffith University, Australia, for providing the species matrix data; Dr Emma Jackson, Dr Olivia Langmead and Charlotte Marshall, University of Plymouth and MarLIN; and Dr Harvey Taylor-Walters, Marine Biological Association for advice on this research and Dan Lear and Becky Seeley, DASSH, for providing Seasearch data. We also thank the two anonymous reviewers for their valuable and constructive input.

References

Ambios. 2006. A technique for marine benthic biotope mapping in sedimentary environments. Lyme Bay (UK): Devon Wildlife Trust. Ambios Report.

Ashworth J, Stoker B. 2010. Delivering the Marine Protected Area Network. Ecological network guidance to regional stakeholder groups on identifying Marine Conservation Zones. Peterborough and Sheffield (UK): Natural England and the Joint Nature Conservation Committee. p. 24.

Austen MC, Lamshead PJD, Hutchings PA, Boucher G, Snelgrove PVR, Heip C, King G, Koike I, Smith C. 2002. Biodiversity links above and below the marine sediment-water interface that may influence community stability. *Biodivers Conserv*. 11(1):113–136.

Austen MC, Malcolm SJ, Frost M, Hattam C, Mangi S, Stentford G, Benjamins S, Burrows M, Butenschön M, Duck C, et al. 2011. Marine. Cambridge (UK): UNEP-WCMC. The UK National Ecosystem Assessment Technical Report.

Balanced Seas. 2011. Marine Conservation Zones Project. Final Recommendations. A report submitted by the Balanced Seas stakeholder project to Defra, the Joint Nature Conservation Committee and Natural England. p. 97. [cited 2012 Apr 16]. Available from: <http://www.balancedseas.org/gallery/download/1014.pdf>

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett*. 9(10):1146–1157.

Beaumont N, Hattam C, Mangi S, Moran D, Soest Dv, Jones L, Toberman M. 2010. National ecosystem assessment: economic analysis coastal margin and marine habitats. Final Report. UK NEA Economic Analysis Reports. p. 96. [cited 2012 Apr 16]. Available from: <http://uknea.unep-wcmc.org/Resources/tabid/82/Default.aspx>

Beaumont N, Townsend M, Mangi S, Austen MC. 2006. Marine biodiversity an economic valuation. Building the evidence base for a Marine Bill. London (UK): DEFRA. A DEFRA Report.

Beaumont NJ, Austen MC, Atkins JP, Burdon D, Degraer S, Dentinho TP, Deros S, Holm P, Horton T, Ierland Ev, et al. 2007. Identification, definition and quantification of goods and services provided by marine biodiversity: implications for the ecosystem approach. *Mar Pollut Bull*. 54(3): 253–265.

Black G. 2007. Lyme Bay Pink Sea Fan Survey 2006–2007. A report by Devon Biodiversity Records Centre. Devon (UK): DBRC. p. 33.

Bohensky E, Butler JRA, Costanza R, Bohnet I, Delisle A, Fabricius K, Gooch M, Kubiszewski I, Lukacs G, Pert P, et al. 2011. Future makers or future takers? A scenario analysis of climate change and the Great Barrier Reef. *Global Environ Change*. 21(3):876–893.

Bremner J. 2008. Species' traits and ecological functioning in marine conservation and management. *J Exp Mar Biol Ecol*. 366(1–2):37–47.

Bremner J, Rogers SI, Frid CLJ. 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Mar Ecol Prog Ser*. 254(2):11–25.

Bremner J, Rogers SI, Frid CLJ. 2006a. Matching biological traits to environmental conditions in marine benthic ecosystems. *J Mar Syst*. 60(3–4):302–316.

Bremner J, Rogers SI, Frid CLJ. 2006b. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecol Indic*. 6(3): 609–622.

Bulling MT, Hicks N, Murray L, Paterson DM, Raffaelli D, White PCL, Solan M. 2010. Marine biodiversity–ecosystem functions under uncertain environmental futures. *Philos Trans R Soc Ser B*. 365(1549):2107–2116.

Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC. 2006. Conservation planning for ecosystem services. *PLoS Biol*. 4(11):2138–2152.

Chapin III FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, et al. 2000. Consequences of changing biodiversity. *Nature*. 405(6783):234–242.

Constanza R, d'Arge R, de Groot RS, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature*. 387:253–260.

De Groot RS, Alkemade R, Braat L, Hein L, Willemsen L. 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecol Complexity*. 7(3):260–272.

De Groot RS, Wilson MA, Boumans RMJ. 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecol Econ*. 41(3): 393–408.

[DEFRA] Department for Environment, Food and Rural Affairs. 2002. Safeguarding our seas – a strategy for the conservation and sustainable development of our marine environment. London (UK): DEFRA.

[TEEB] The Economics of Ecosystems and Biodiversity. 2010. The Economics of Ecosystems and Biodiversity. Mainstreaming the economics of nature. A synthesis of the approach, conclusion and recommendations of TEEB. Villetta (Malta): Progress Press.

- Elliott M, Quintino V. 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Mar Pollut Bull.* 54(6):640–645.
- European Community Council Directive. 1992. Conservation of habitats and wild fauna and flora. EC 92/43/EEC. Brussels (Belgium): EC.
- European Parliament and Council. 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Brussels (Belgium): EC.
- Foley MM, Halpern BS, Micheli F, Armsby MH, Caldwell MR, Crain CM, Prahler E, Rohr N, Sivas D, Beck MW, et al. 2010. Guiding ecological principles for marine spatial planning. *Mar Policy.* 34(5):955–966.
- Frid CLJ. 2011. Temporal variability in the benthos: does the sea floor function differently over time? *J Exp Mar Biol Ecol.* 400(1–2):99–107.
- Frid CLJ, Paramor OAL, Brockington S, Bremner J. 2008. Incorporating ecological functioning into the designation and management of marine protected areas. *Hydrobiologia.* 606(1):69–79.
- Giller PS, Hillebrand H, Berninger U-G, Gessner MO, Hawkins S. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos.* 104(3):423–436.
- Haines-Young R, Potschin M. 2007a. The ecosystem approach and the identification of ecosystem goods and services in the English policy context. London (UK): DEFRA. Review Paper to DEFRA: Project Code NR010107.
- Haines-Young R, Potschin M. 2007b. The links between biodiversity, ecosystem services and human well-being. In: Raffaelli D, Frid C, editors. *Ecosystem ecology: a new synthesis.* Cambridge (UK): Cambridge University Press. p. 1–31.
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, et al. 2008. A global map of human impact on marine ecosystems. *Science.* 319(5865):948–952.
- Hewitt JE, Thrush SF, Dayton PD. 2008. Habitat variation, species diversity and ecological functioning in a marine system. *J Exp Mar Biol Ecol.* 366(1–2):116–122.
- Hiscock K, Breckels M. 2007. Marine biodiversity hotspots in the UK. A report identifying and protecting areas for marine biodiversity. Surrey (UK): WWF-UK.
- Hiscock K, Marshall C, Sewell J, Hawkins S. 2006. The structure and functioning of marine ecosystems: an environmental protection and management perspective. Peterborough (UK): English Nature.
- HM Government. 2009. Marine and Coastal Access Act. London (UK): Crown. p. 347.
- HM Government. 2011. UK Marine Policy Statement. London (UK): Crown. p. 47.
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr.* 75(1):3–35.
- Ieno EN, Solan M, Batty P, Pierce GJ. 2006. How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Mar Ecol Prog Ser.* 311(4):7.
- Irish Sea Conservation Zones. 2011. Final recommendations for marine conservation zones in the Irish Sea. Warrington (UK): Irish Sea Conservation Zones.
- Klein CJ, Chan A, Kircher L, Cundiff AJ, Gardner N, Hrovat Y, Scholz A, Kendall BE, Airama S. 2008. Striking a balance between biodiversity conservation and socioeconomic viability in the design of marine protected areas. *Conserv Biol.* 22(3):691–701.
- Kremen C. 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecol Lett.* 8(5): 468–479.
- Kristensen E, Blackburn TH. 1987. The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. *J Mar Res.* 45(1): 231–257.
- Lavorel S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol.* 16(5): 545–556.
- Leiberknecht LM, Hooper TEJ, Mullier TM, Murphy A, Neilly M, Carr H, Haines R, Lewin S, Hughes E. 2011. Finding sanctuary final report and recommendations. A report submitted by the Finding Sanctuary stakeholder project to Defra, the Joint Nature Conservation Committee and Natural England. p. 101. [cited 2012 Apr 16]. Available from: <http://www.finding-sanctuary.org/>.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science.* 294(5543): 804–808.
- [MarLIN] The Marine Life Information Network for Britain and Ireland. 2006. Database name edition ed. BIOTIC – Biological Traits Information Catalogue. Devon (UK): MarLIN.
- Marine (Scotland) Act. 2010. Crown copyright. p. 112.
- McShane TO, Hirsch PD, Trung TC, Songorwa AN, Kinzig A, Monteferrri B, Mutekanga D, Thang HV, Dammert JL, Pulgar-Vidal M, et al. 2011. Hard choices: making trade-offs between biodiversity conservation and human well-being. *Biol Conserv.* 144(3):966–972.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: synthesis.* Washington (DC): Island Press.
- Minteer BA, Miller TR. 2011. The new conservation debate: ethical foundations, strategic trade-offs, and policy opportunities. *Biol Conserv.* 144(3):945–947.
- Net Gain. 2011. Final recommendations. Submission to Natural England and JNCC. Hull (UK): Net Gain.
- Nystrom M, Folke C. 2001. Spatial resilience of coral reefs. *Ecosystems.* 4:406–417.
- OSPAR Convention. 2002. Convention for the protection of the marine environment of the North-East Atlantic. London (UK): OSPAR Commission.
- OSPAR Commission. 2006. Guidance on developing an ecologically coherent network of OSPAR marine protected areas (reference number 2006-3). OSPAR Convention for the Protection of the Marine Environment of the North East Atlantic; Oslo and Paris Commission 1992 May 9; Paris, France. London (UK): OSPAR Commission. p. 11.
- Pearce DW, Turner RK. 1990. *Economics of natural resources and the environment.* Hemel Hempstead (UK): Harvester Wheatsheaf.
- Pearson TH. 2001. Functional group ecology in soft sediment marine benthos: the role of bioturbation. Boca Raton (FL): Taylor & Francis.
- Perrings C, Naeem S, Ahrestani F, Bunker DE, Burkill P, Canziani G, Elmqvist T, Ferrati R, Fuhrman J, Jaksic F, et al. 2010. Ecosystem services for 2020. *Science.* 330(6002): 323–324.
- Petchey O, Gaston KJ. 2006. Functional diversity: back to basics and looking forward. *Ecol Lett.* 9(6):741–758.
- Petersen K, Kristensen E, Bjerregaard P. 1998. Influence of bioturbating animals on flux of cadmium into estuarine sediment. *Mar Environ Res.* 45(4–5):403–415.

- Raffaelli D. 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Mar Ecol Prog Ser.* 311(10):285–294.
- Rees SE, Attrill MJ, Austen MC, Mangi SC, Richards JP, Rodwell LD. 2010. Is there a win-win scenario for marine nature conservation? A case study of Lyme Bay, England. *Ocean Coastal Manage.* 53(3):135–145.
- Rees SE, Rodwell LD, Attrill MJ, Austen MC, Mangi SC. 2010. The value of marine biodiversity to the leisure and recreation industry and its application to marine spatial planning. *Mar Policy.* 34(5):868–875.
- Robinson JG. 2011. Ethical pluralism, pragmatism, and sustainability in conservation practice. *Biol Conserv.* 144(3): 958–965.
- Salafski N, Margoluis R, Redford K. 2001. Adaptive management: a tool for conservation practitioners. Washington (DC): Biodiversity Support Program.
- Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia.* 122(3):297–305.
- Secretariat of the Convention on Biological Diversity. 2004. Technical advice on the establishment and management of a national system of marine and coastal protected areas. Montreal (Canada): Secretariat of the Convention on Biological Diversity.
- Snelgrove PVR. 1997. The importance of marine sediment biodiversity in ecosystem processes. *Ambio.* 26(8):578–583.
- Snelgrove PVR. 1998. The biodiversity of macrofaunal organisms in marine sediments. *Biodivers Conserv.* 7(9): 1123–1132.
- Sobel J, Dahlgren C. 2004. Marine reserves. A guide to science, design and use. Washington (DC): Island Press.
- Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS. 2004. Extinction and ecosystem function in the marine benthos. *Science.* 306(5699):1177–1180.
- Somerfield PJ, Clarke KR, Warwick RM, Dulvy NK. 2008. Average functional distinctness as a measure of the composition of assemblages. *ICES J Mar Sci.* 65(8):1462–1468.
- Stevens T, Rodwell L, Beaumont K, Lewis T, Smith C, Stehfest K. 2007. Surveys for marine spatial planning in Lyme Bay. Report for Devon Wildlife Trust, under the EROCIIPS Project. Plymouth (UK): The Marine Institute, University of Plymouth. p. 87.
- Tillin HM, Hiddink JG, Jennings S, Kaiser MJ. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser.* 318:31–45.
- Wood C. 2007. Seasearch surveys in Lyme Bay. A report to Natural England. A report to Natural England, The Marine Conservation Society. Ross-on-Wye (UK): Marine Conservation Society. p. 26.
- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science.* 314(5800):787–790.