CHALLENGES TO MARINE ECOSYSTEMS

Incorporating ecological functioning into the designation and management of marine protected areas

C. L. J. Frid · O. A. L. Paramor · S. Brockington · J. Bremner

© Springer Science+Business Media B.V. 2008

Abstract Marine protected areas are generally designed and managed on the basis of the presence and extent of specific habitat types or the habitats of important species. However, it has become clear that in addition to including these 'structural' elements of marine systems, management strategies should incorporate a consideration of the functional aspects of the ecosystems. Biological traits analysis (BTA) has been successfully used to describe ecological functioning in marine benthic systems. BTA uses a number of biological characteristics expressed by the taxa present as indicators of key ecosystem functions. Two expert workshops were used to examine the potential for the application of BTA in the

Guest editors: J. Davenport, G. Burnell, T. Cross, M. Emmerson, R. McAllen, R. Ramsay & E. Rogan Challenges to Marine Ecosystems

C. L. J. Frid (⊠) · O. A. L. Paramor · J. Bremner School of Biological Sciences, Biosciences Building, University of Liverpool, Crown Street, Liverpool L69 7ZB, UK e-mail: C.L.J.Frid@liverpool.ac.uk

S. Brockington English Nature, Northminster House, Peterborough PE1 1UA, UK

Present Address:

J. Bremner Section of Marine Biology and Limnology, Department of Biology, University of Oslo, P.B. 1064, Blindern, Oslo 0316, Norway designation and management of MPAs. They concluded that BTA represented the best tool currently available for quantifying ecological functioning and agreed on 10-key ecological functions delivered by marine benthic communities. Twenty-four biological traits were also identified by the workshops as indices of these ten functions. In order to demonstrate the practical utility of the approach, BTA using these traits, was applied to a dataset covering benthos from within and around the proposed Eddystone Special Area of Conservation (SW England). The case study demonstrated that with the type of data normally available from conservation assessment type surveys, and a knowledge of the relevant biological traits, it is possible to use a consideration of ecological functioning to set boundaries for the MPA and to inform the site management objectives. The use of structure and function information to inform the designation process and subsequent management of marine protected areas is discussed.

Keywords Ecological services · Biological traits analysis · Conservation objectives · Benthos

Introduction

A variety of international conventions (e.g. RAM-SAR, ASCOBANS), as well national legislation (EC,

1992; Australian Fish Resources Management Act, 1994; US Magnuson-Stevens Fishery Conservation and Management Act, 1996; Canadian Ocean's Act, 1997; EC, 2004), require the protection of sites for nature conservation purposes. It is now recognised that protection of the habitat, and its associated functional processes, is a key element of ensuring ecological sustainability and is therefore a key element of the application of the 'ecosystem approach' (Frid et al., 2005, 2006). Until recently, sites have been selected for protection based on the presence of specific habitats or species. However, a growing number of legislative agreements, including the Convention on Biological Diversity (United Nations, 1992), the European Marine Strategy Directive (EC, 2005) and the Habitats Directive (EC, 1992), require management schemes to address the functioning of ecosystems.

Consideration of functioning in the designation process has been difficult in the past due to the lack of science to support such an approach. A number of studies have recently sought to describe the delivery of 'ecological goods and services' from the marine ecosystem (Chapin et al., 1997; Snelgrove et al., 1997; Lasiak, 1998; Beaumont & Tinch, 2003; Frid & Paramor, 2006). Most of these have been descriptive accounts, or focussed on only one aspect (say fisheries resources or nutrient regeneration), and presented their analysis in units appropriate to that function. However, application of an ecosystem approach requires the integration of ecosystem components, and so requires a multivariate, multifunction, approach. Recent advances in data handling have made this possible and one approach that has been applied with some success is biological traits analysis (BTA). It uses the biological traits of taxa as indicators of key aspects of functioning. BTA was initiated in lentic systems (Statzner et al., 1994), and developed for application to marine ecosystems (Frid et al., 2000; Bremner et al., 2003, 2005, 2006a). It focuses on the behaviour and attributes of biological entities that contribute to the maintenance of ecosystem processes and differs from previous trait-based approaches (e.g. trophic or functional groups (Pearson & Rosenberg, 1986; Snelgrove & Butman, 1994; Grall & Glemarec, 1997; Whitlatch et al., 1997; Clarke & Warwick, 1998; Dauwe et al., 1998; Telesh et al., 1999; Herrando-Pérez & Frid, 2001)) as it utilises a wider range of information on organism functional traits. It can be applied to any taxonomic level and can incorporate indicators of several different aspects of functioning. Furthermore, BTA can be used in a 'fuzzy coding' mode where a species is not allocated to a single code for each trait but can be dispersed over a number of code classes to reflect its biology, or our uncertainty of its biology. For example in classic functional group analysis an organism might be scored as either a predator or a scavenger. However, many such taxa exhibit both feeding modes. Under a fuzzy coding approach the organism can be scored 0.5 to each, or if predominantly a carnivore then, may be, 0.8 carnivore and 0.2 scavenger. The use of fuzzy coding complicates the subsequent analysis but allows for a much more realistic representation on the functional biology of the assemblage.

The initial stages of BTA involve the identification of key aspects of functioning (e.g. the processes involved in energy/carbon/nutrient cycling) and the functional traits that can be used as indicators of these (e.g. feeding traits as indicators of carbon transport between the pelagos and benthos).

In this article, we investigate how BTA might be used to aid designation and management of MPAs by providing a wider ecosystem approach than traditional models of MPA management. In order to do this we: (i) establish what are the most important, or key, ecological functions delivered by marine benthic systems, and consider the biological traits that organisms possess that underpin delivery of these functions and (ii) consider how this information might be used in MPA management. As a case study to assess the feasibility of this, we apply our approach, includes consideration of species' identities and ecological functioning, to a UK-proposed Special Area of Conservation (SAC).

How can ecological functioning be used in MPA management

Delivery of the ecological functioning of a healthy ecosystem can be incorporated in the designation of MPA management in two ways. First, in setting the boundary of the MPA to ensure key functions are protected by the MPA designation, and second, in setting the management objectives for the site, so that performance of the management regime can be assessed against them.

Setting boundaries

As MPAs do not exist in ecological isolation, but exchange resources with a much larger area, there is an argument to extend the boundaries of the protected area beyond the physical extent of the habitat/feature being targeted. However, since the spatial and temporal scales of processes that need to be considered in order to protect the structure and functioning of the habitat/feature are considerable, a more pragmatic approach is to protect those areas close to the feature that exhibit similar ecological functioning. Thus, regions of rapid change in the multivariate descriptor of the biological traits (and hence ecological functions performed) might be considered as possible boundaries for the MPA.

Conservation objectives

Designating an area on the basis of the presence of a feature/habitat or even the spatial distribution of functions, is only the beginning of effective management. Current management approaches focus on the delivery of defined objectives (objective-based management). Traditionally, conservation objectives have either been set in broad terms, e.g. maintain habitat x in a good condition, or have focussed on key or indicator taxa, e.g. provide habitat for 5% of the regional population of species y. With the availability of tools that provide quantitative metrics of ecosystem functioning, either in total/aggregate form or by individual functions, it is possible to set conservation objectives for function delivery. BTA allows the species delivering any given function to be identified and so changes in functions can be traced back to changes in the biota and hence back to impacting activities that can be controlled by management measures.

Methods

Identification of the ecological functions and the traits that map them

The selection of the key functions and the traits to that can be used to measure them was supported by two international workshops, one in London and one in Plymouth. At each workshop around 10 experts in various aspects of marine benthic ecology and ecosystem functioning, were asked to develop a list of key ecosystem functions delivered by marine benthic systems. They were then asked to consider whether BTA was a suitable means of measuring the functioning, and if so, which traits of the biota would be the most useful proxies. This included a consideration of practicality, which included information availability.

This was achieved in a workshop format using a semi-structured, round-table, discussion approach. The results of the discussions were consolidated and, after a period for reflection, were re-presented to the groups for review. The two workshops were run independently with the aim of using the degree of congruency of the outputs as an indication of the robustness of the conclusions.

The workshops identified 10 aspects of benthic marine system functioning which were seen as their key functions (Table 1). There was complete agreement in the composition of this list between the two workshops. The two workshops considered that 24 biological traits that could be used as indicators of the contribution of the biota to delivery of the key functions (Table 2). The two workshops independently came up with the same 20 traits and the remaining three were identified by only one of the workshops, this difference being a reflection of the specialisms of the experts present

A full explanation of the links between traits and key aspects of functioning are given in Bremner et al. (2006b).

Some of the traits identified may be of greater practical use than others because they are indicators of more than one aspect of functioning. However, the workshop participants decided not to rank traits by importance, as this was considered too subjective and difficult to apply to different sites. Participants concluded that all the listed traits should be included in the analysis, with the condition that particular traits could be further considered in isolation, if this was considered appropriate for a particular site, for example because a particular function was seen to be of great importance (i.e. food resources for birds, breeding habitat for species of high conservation importance). Process property or activity

72

riocess, property of activity		
1.	Energy and elemental cycling (carbon, nitrogen, phosphorus, sulphur)	
2.	Silicon cycling	
3.	Calcium carbonate cycling	
4.	Food supply/export	
5.	Productivity	
6.	Habitat/refugia provision	
7.	Temporal pattern (population variability, community resistance and resilience)	
8.	Propagule supply/export	
9.	Adult immigration/emigration	

 Table 1 Key aspects of functioning identified during two international workshops (Bremner et al. 2006a)

A case study: the Eddystone Reef, Cornwall

Modification of physical processes

Data source

10.

As no contemporary data were available we used a historical dataset for the site to demonstrate the feasibility of the approach. The Holme's 'scoop sample' dataset from soft sediment habitats in the area of Eddystone Reef (Holme, 1953) considers all macrofauna obtained from sieving a sample of sediment retrieved from the seabed in a 'scoop' sampler. Holme's sampler was similar to what might now be known as a pipe or anchor dredge, thus samples are not strictly quantitative but as the same

Table 2Biological traitsidentified as indicators ofkey aspects of functioningin potential MPAs(Bremner et al. 2006a)

transect running north-south and data used here cover
three transects and an additional station located close
to the Eddystone Reef (see station locations in
Fig. 4). All Holmes transects lie to the east of the
Eddystone and so cover only the eastern portion of
the proposed SAC which is centred on the reef itself.
Data analysis

method was applied at each site they are comparable.

Holme sampled stations arranged on a series of

Ecological structure

Centred (covariance) PCA (Gower & Hand, 1996) was used to examine differences in ecological structure at stations on and around the potential SAC features. Unlike non-parametric procedures, like MDS, PCA produces scores for each station and these scores can be used as a measure of how different the communities are in terms of their ecological structure (stations with similar scores contain communities with similar ecological structure). The first and second set of scores produced by the analysis (axes 1 and 2 scores) can, therefore, be used to generate an ordination plot that allows the differences between the communities to be visualised and quantified.

Where the resulting ordinations contained outlying stations that compromised the ability of an analysis to describe emergent patterns in the data, the abundance dataset was transformed (double root) and the

1.	Maximum size	15.	Resource capture method
2.	Maximum growth rate	16.	Food type
3.	Longevity	17.	Energy transfer efficiency
4.	Time to maturity	18.	Tissue components
5.	Reproductive method	19.	Defence strategy
6.	Fecundity	20.	Movement method
7.	Propagule dispersal	21.	Mobility
8.	Body design	22.	Water column migration
9.	Living habit	23.	Horizontal migration
10.	Living location/environmental position	24.	Intra-specific sociability
11.	Exposure potential	25.	Predictability of dynamics
12.	Degree of flexibility	26.	Recruitment variability/success
13.	Degree of attachment	27.	Biogenic habitat provision
14.	Strength of attachment	28.	Scale of habitat provision

analysis repeated. If transformation of the abundance data did not prove sufficient to reduce the influence of outliers, these stations were removed and the dataset re-analysed.

Ecological functioning

Co-inertia analysis (Doledec & Chessel, 1994) was utilised to examine differences in ecological functioning over the sampling stations. Co-inertia analysis assesses the co-structure between two data tables by simultaneously ordinating them, maximising both the variance from the individual tables and the correlation between them (Doledec & Chessel, 1994). This analysis produces scores for the stations that can be used as a measure of how different the communities are, in the same way as PCA, but because they incorporate information on both the abundance of taxa at a station and the biological traits they exhibit (Doledec et al., 1999), these scores describe how different the communities are in terms of their ecological functioning. The coinertia scores can also be plotted on an ordination map, with each point on the map representing the abundance-weighted 'biological trait composition' of an individual station. Interpretation of the contoured structure and functioning maps required reference back to the results of the biological ordinations.

The analysis utilised both the dataset of taxon abundance used previously to examine ecological structure over the sampling stations, and the biological traits tables prepared for each of the four datasets examined. First, separate ordinations of the individual data tables were carried out. As before, centred PCA was used to investigate the ecological structure of the stations. However, for this analysis the table was transposed so that the taxa were in rows. Fuzzy correspondence analysis was used to assess the biological traits table. This is a form of correspondence analysis used when the categories of variables are fuzzy coded (Chevenet et al., 1994).

Co-inertia analysis was then carried out using both ordinations and the significance of the resulting costructure was examined with a random permutation test (Doledec & Chessel, 1994). This test randomly permuted the rows of the co-inertia table and recalculated the inertia statistics 100 times. The observed co-inertia value was then compared to the frequency distribution of the randomly permuted values to assess if it was significantly larger.

The co-inertia analysis was initially applied to the four datasets in-full, irrespective of whether outlying stations had been removed from any of these datasets for the purposes of describing ecological structure. This is because several taxa can exhibit the same traits; therefore extreme differences in abundance of particular taxa at a station may not necessarily translate into extreme differences in trait composition. However, if outlying stations were noted on the resulting co-inertia ordination plots, the datasets were transformed and stations removed as appropriate.

Boundary mapping

As a result of the way they are calculated, the first set of station scores (axis 1 scores) generated by both the PCA and co-inertia analysis contain the greatest amount of information on the variability in ecological structure or functioning among the sampling stations, making them useful variables for summarising differences among the communities. These axis 1 PCA and co-inertia analysis scores were plotted over maps of the Eddystone Reef survey area, to provide a visualisation of how the structure and functioning varied over the region and to identify the areas of greatest change.

The ecological structure and functioning scores were grouped into appropriate categories using the mapping package ArcGIS 9 (ESRI, California, USA) and coloured labels assigned to the categories to ease interpretation of the maps. The co-ordinates of the sample stations were plotted and overlaid with the ecological structure and functioning scores. The structure and functioning scores information was then contoured using a Triangular Irregular Network (TIN), see the caption for Fig. 4 for a full explanation. TINs were utilised, in this case, as they were found to best reflect the patterns in the data from the Holmes' (1953) Eddystone Reef surveys.

This allowed species and functions causing data clusters and regions of rapid change on the map to be identified.

munities sampled by Holme (1953) in the area of Eddystone Reef					
Ordination axis	Eigenvalue	Relative inertia (%)	Cumulative inertia (%)		
Ecological stru	icture (PCA)				
1	11.600	29.11	29.11		
2	5.773	14.49	43.59		

50.01

17.14

50.01

67.15

Table 3 Multivariate analysis of the ecological structure (PCA) and functioning (co-inertia analysis) of benthic communities sampled by Holme (1953) in the area of Eddystone Reef

Results

1

2

Benthic structure and function at Eddystone

Ecological functioning (co-inertia analysis)

0.202

0.069

Ecological structure

Analysis of untransformed data resulted in station A2 (a 'very fine muddy sand' area to the far north of Eddystone) as an extreme outlier on the ordination plot. Square-root transformation of the abundance data did not help to reveal the patterns in ecological structure over the remaining stations, so A2 was removed from the analysis. PCA of the remaining stations described approximately 43% of the variability in the dataset (Table 3).

Samples from 'clean sand' habitats (also the unclassified stations C5 and C6 from the sandy grounds) showed some degree of grouping on the plot, however, there was insufficient replication of the other habitat types to determine how strongly stations grouped together based on habitat type (Table 4, Fig. 1).

The variable distribution of *Phaxas pellucidus* (Pennant) and *Lumberineris* sp. (de Blainville) caused the separation of stations along the first axis. Station C6 (to the south-east of Eddystone) and, to a lesser extent the 'clean sand' stations (Fig. 1), had relatively high abundance of both taxa, while they were not recorded (except for four *Lumbrineris* sp. found in A4) in stations C1, B2, A4 and A5. These stations contained a variety of substrate types (Table 4). Station C1 was differentiated from the latter stations by markedly higher abundance of *Echinocyamus pusillus* (OF Müller) and indeterminate polychaetes.

Table 4 Substrate types at stations sampled by Holme (1953)in the area of Eddystone Reef

Substrate type	Stations
Very fine muddy sand	A2
Clean medium grade sand/mixed muddy sand and gravel	A3
Muddy sand with small stones and shell fragments	A4
Shell gravel	A5
Clean sand	A6, A7, B5, B6, B7, C4
Fine muddy sand with small stones	B2
Slightly muddy fine sand	B4
Fine gravel of shell fragments and small stones	C1
Muddy sand with a few stones	C2, C3
Unclassified (sandy grounds)	C5, C6



Fig. 1 PCA ordination of the stations analysed during investigation of ecological structure of benthic communities sampled by Holme (1953) in the area of Eddystone Reef. Information on substrate type for each station is given in Table 4. 'Clean sand' and 'unclassified' stations sampled from the sandy grounds are highlighted

Ecological functioning

Analysis of ecological functioning was based on a square-root transformation of the abundance data. Removal of station A2 was not necessary for this analysis, as it was not portrayed as an outlier in the ordination.

However, interpretation of the analysis was impaired by one-trait category, 'regular-seasonal/ reproductive water column migration'. This trait category was so separated from all the others on the trait ordination plot that further interpretation of the results was not possible. This trait was only expressed by one taxon in the dataset (indeterminate polychaetes), and then only to a low degree (only a very small number of polychaetes undertake regular water column migrations, for reproductive purposes). For this reason, the analysis was repeated after exclusion of the category 'regular-seasonal/reproductive water column migration'.

The co-inertia analysis accounted for 67% of the variability in ecological functioning over the stations (Table 3). The 'clean sand' stations separated out from the other stations in terms of their trait compositions (Table 4, Fig. 2), although they were not as tightly grouped in general as they had been in the ordination of ecological structure (Fig. 1).

The traits most important for determining differences between stations were body design, living habit, exposure potential, degree of flexibility,



Fig. 2 Co-inertia ordination of the stations analysed during investigation of ecological functioning of benthic communities sampled by Holme (1953) in the area of Eddystone Reef. Information on substrate type for each station is given in Table 4. 'Clean sand' and 'unclassified' stations sampled from the sandy grounds are highlighted

horizontal and water column migrations and habitat provision (Table 5). Stations A4 and A2 ('muddy sand with small stones and shell fragments' and 'very fine muddy sand' stations to the north of Eddystone) were characterised by tube-dwelling organisms, those with high exposure potential and taxa forming habitat by the accretion of sediments (Fig. 2). Stations A6, B7 and C4, all 'clean sand' stations to the south (A6, B7) and east (C4) of Eddystone, were characterised by shelled organisms and taxa undertaking irregular or single horizontal migrations.

Stations in the lower left quadrant of the ordination plot, principally B4 but including the remaining 'clean sand' stations and the unclassified stations from the sandy grounds (C5 and C6), were characterised by flexible taxa (>45°), organisms inhabiting temporary burrows and those making irregular or seasonal water-column migrations (Fig. 2). The random permutation test indicated a lack of costructure between the taxon abundance and biological traits tables (P = 0.15).

Boundary mapping

The depth contours around Eddystone Reef are shown in Fig. 3. The physical feature of the reef itself is clearly demarcated. The stations sampled by Holmes (1953) were all to the east of the Eddystone complex, on a well-dispersed grid. A few rapid changes in ecological structure were observed among the data points (Fig. 4), although this may have been due to the dispersed pattern of the sampling stations.

 Table 5
 Trait categories contributing most to differences in ecological functioning over stations sampled by Holme (1953) in the area of Eddystone Reef

Trait	Trait category
Body design	Hard-shell
Living habit	Tube
	Temporary burrow
Exposure potential	High (erect surface/interface dwelling)
Degree of flexibility	>45°
Horizontal migration	Irregular/single
Water column migration	Irregular/single
Habitat provision	Action-sediment accretion



Fig. 3 The depth contours around the Eddystone Reef complex (adapted from Axelsson et al. 2006)

Figure 5 shows the functional changes across the survey area. The ecological functioning data shows a pattern distinct to that of the species composition

dataset and, therefore, provides an additional information to the ecological structure analysis. However, it too is affected by edge effects due to the restricted nature of the sampling programme.

Delineation of the Eddystone Reef SAC would currently be limited to the physical extent of the reef feature as data were not available, at the time of analysis, on which to undertake a comprehensive assessment of gradients of change in the ecological structure and functioning of the reef and surrounding areas.

Discussion

This study has demonstrated a means by which ecological survey data can be used in the delimitation of boundaries for marine protected areas through the explicit consideration of the ecological structure (biological diversity) and functioning of the systems. Until now, delimiting nature conservation sites has either been done with reference to the spatial



Fig. 4 The ecological structure to the east of Eddystone Reef, based on PCA scores of the biological communities sampled by Holme (1953) (see Fig. 1). These scores explain 29.1% of the variability in the data. A triangulated irregular network (TIN) was used to spatially contour the data. TINs are based on a set of adjacent, non-overlapping triangles with x, y coordinates and z vertical elevations for their vertices, with topological relationships between the triangles and their adjacent

neighbours. The contour lines produced can therefore be read as a landscape map, with lines close together indicating areas of greatest change and lines further apart indicating areas of similarity. Each data point was categorised and labelled with a different colour to allow points of similarity to be identified. The box enclosing some of the sites represents the boundaries of the sampling area selected by the survey contractors (Axelsson et al. 2006) Fig. 5 The ecological functioning to the east of Eddystone Reef, based on co-inertia scores of the biological communities sampled by Holme (1953) (see Fig. 2). These scores explain 50% of the variability in the data. A triangulated irregular network (TIN) was used to spatially contour the data. See Fig. 4 caption for an explanation of TINs. The box enclosing some of the sites represents the boundaries of the sampling area selected by the survey contractors (Axelsson et al. 2006)



distribution of 'key' species or the extent of specific types of physical environment, i.e. the physical habitat. Marine systems are dynamic and, ecologically, open. This means that ecological processes extend across physical habitat boundaries and the health of the biological assemblage in a habitat may be dependent on processes occurring elsewhere. The approach developed and demonstrated here addresses these issues by explicit consideration of biological diversity and ecological functioning using BTA.

BTA has several potential uses with regards to SAC designation and management. First, BTA can be used as a tool to assist in boundary setting. A strict interpretation of the Habitats Directive requires SAC boundaries to follow the edge of the distribution of the species or habitat of concern. However, the Convention on Biological Diversity (United Nations, 1992) and subsequent treaty undertakings (e.g. World Summit on Sustainable Development, Johannesburg, 2002) require explicit conservation of ecological functioning. One can, therefore, envisage the application of BTA to delimit areas that function as Annex 1 habitats, even if our perception of them is that they are a different type of habitat. For example, conservation of offshore sandbanks less than 20-m deep is required under the Habitats Directive (EC, 1992). These areas deliver a range of ecological functions, so this delivery must, logically, also be protected. If an area adjacent to the banks is also delivering the same functions, but is, say, 24-m deep, then given the open nature of marine systems, it seems reasonable to include this as part of the bank system and incorporate it within the SAC boundaries.

Second, BTA allows the identification of both the ecological functions strongly expressed in a habitat (or unique to it), and the species delivering them. This information can then be used in the setting of conservation objectives for the site. For example, at Eddystone, body design, living habit, exposure potential, flexibility, migrations and habitat provision were the ecological traits that were most important in distinguishing among the stations.

In addition to its use for describing ecological functioning across a potential SAC site, the ability of the approach to identify whether communities in similar habitats but different geographic locations function in the same way (Bremner et al., 2006a), means it can provide information on differences or similarities in functioning between sites proposed for inclusion in SAC series. This information will be useful in the process of identifying sites for protection, because two sites with similar Annex I habitat types may not necessarily function in the same way.

The expert workshops reviewed the approaches available for providing information on ecological functioning and concluded that BTA was the most practical approach available at this time. In order to apply BTA requires two things, a knowledge of what are the important functions to include in consideration and secondly what traits can be used to index those functions in the biota. The workshops, with special reference to offshore sandbanks and subtidal reefs, identified a list of 10-key ecological functions (Table 1) and 24 biological indicator traits that could be used to index them (Table 2). It is reassuring that the combined expertise available to the two workshops should firstly agree on the list of functions and secondly that that lists of functions, and the linked traits, are not so long as to be impractical to apply using BTA. In order to examine the practical application of this conclusion we used these traits for the basis of the analysis presented here for the Eddystone Reef area.

Our analysis has shown how the approach can be applied to both characterize the ecological functioning of the assemblages present in an area and to delimit areas of different ecological functioning. Furthermore, the output from the fuzzy coded BTA could be used as input to a GIS system. The GIS then allowed spatial contouring of ecological functioning and this could assist in the selection of boundary points for an MPA.

Given the complex interactions at each stage of the ecological chain that links environmental conditions to biological assemblage composition to ecological function delivery managing the system to deliver tight targets for functioning is unlikely to succeed. However, it is clear that changes in functioning could be an important element of any failure to deliver a healthy ecosystem. It therefore follows that, in addition to a role in delimiting MPA boundaries, monitoring programmes should be designed to allow changes in functioning, in space or time, to be detected with a high degree of confidence. This will aid managers in determining the effects of natural change and/or human activities in MPAs. BTA allows the links between function delivery and the taxa responsible to be explicitly linked. It is impossible to manage the marine ecosystem and it is equally impossible to manage ecological functioning of the system, however, by being able to link functions back to taxa, our knowledge of the vulnerability of specific taxa to various human activities will allow management schemes to be advanced that do provide explicit consideration for, and protection of, ecosystem functioning.

Acknowledgements This manuscript derives from a study on designation of offshore SACs commissioned by English Nature and we acknowledge their financial and material support. We would like to thank Dan Laffoley and Leigh Jones of English Nature for their input to the project. We also thank Silvana Birchenough, Erik Bonsdorff, Tasman Crowe, Jan Hiddink, Keith Hiscock, Kerry Howell, Stuart Jenkins, Charlie Marshall, Paul Somerfield, Harvey Tyler-Walters and Jack Sewell for participating in the Plymouth and London workshops. We are indebted to Jean-Luc Solandt of the Marine Conservation Society and Paul Robinson of the Joint Nature Conservation Committee for providing the Seasearch diver survey data and access to the Marine Recorder software (www.jncc.org.uk), Chris Cesar and Diane Jones for help with collating the Eddystone Reef datasets and Sarah King of the Zoological Society of London for providing assistance with the ArcGIS mapping programme.

References

- Australian Fish Resources Management Act, 1994. An Act relating to the management of fish resources, to repeal and amend certain Acts, and for related purposes. http://www. austlii.edu.au/au/legis/wa/consol_act/frma1994256/.
- Axelsson, M., S. Dewey, S. Chaddock & S. Duke, 2006. Survey of the reef habitat around Eddystone Reef, Plymouth. Report to English Nature. SeaStar Survey, Southampton. p601.
- Beaumont, N. J. & R. Tinch, 2003. Goods and services related to the marine benthic environment. CSERGE Working Paper ECM 03-14:12.
- Bremner, J., C. L. J. Frid & S. I. Rogers, 2005. Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? American Fisheries Society Symposium 41: 477–489.
- Bremner, J., S. I. Rogers & C. L. J. Frid, 2006a. Matching biological traits to environmental conditions in marine benthic ecosystems. Journal of Marine Systems 60: 302–316.
- Bremner, J., O. A. L. Paramor & C. L. J. Frid, 2006b. Developing a methodology for incorporating ecological structure and functioning into designation of Special Areas of Conservation (SAC) in the 0-12 nautical mile zone. A report to English Nature from University of Liverpool, Liverpool.
- Bremner, J., S. I. Rogers & C. L. J. Frid, 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Marine Ecology Progress Series 254: 11–25.
- Canadian Oceans Act 1997. Oceans Act 1996, c. 31O-2.4 [Assented to December 18th, 1996]. http://www.pac.dfompo.gc.ca/oceans/default_e.htm.
- Chapin, F., B. Walker, R. Hobbs, D. Hooper, J. Lawton & O. Saia, D. Tilman, 1997. Biotic control over the functioning of ecosystems. Science 277: 500–504.
- Chevenet, F., S. Doledec & D. Chessel, 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshwater Biology 31: 295–309.
- Clarke, K. R. & R. M. Warwick, 1998. Quantifying structural redundancy in ecological communities. Oecologia 113: 278–289.

- Dauwe, B., P. M. J. Herman, C. H. R. Heip, 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Marine Ecology-Progress Series 173: 67–83.
- Doledec, S. & D. Chessel, 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. Freshwater Biology 31: 277–294.
- Doledec, S., B. Statzner & M. Bournard, 1999. Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. Freshwater Biology 42: 737–758.
- EC, 1992. COUNCIL DIRECTIVE 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. European Commission, Brussels.
- EC, 2004. Council regulation no. 612/2004 of 22 March 2004 amending council regulation (EC) no. 850/98 as regards the protection of deep water coral reefs from the effects of trawling in an area north west of Scotland. European Commission, Brussels.
- EC, 2005. Proposal for a Directive of the European Parliament and the Council establishing a Framework of Community Action in the field of Marine Environmental Policy (Marine Strategy Directive) Brussels, 24.10.2005 COM (2005) 505 final 2005/0211 (COD).
- Frid, C. L. J., S. I. Rogers, M. Nicholson, J. R. Ellis & S. Freeman, 2000. Using biological characteristics to develop new indices of ecosystem health. 88th Annual ICES Science Conference; Mini-symposium on defining the role of ICES in supporting biodiversity conservation ICES CM Mini:02. ICES, Copenhagen.
- Frid, C. L. J., O. A. L. Paramor & C. L. Scott, 2005. Ecosystem-based fisheries management: progress in the NE Atlantic. Marine Policy 29: 461–469.
- Frid, C. L. J. & O. A. L. Paramor, 2006. Marine Biodiversity: The Rationale for Intervention. A Report to DEFRA. University of Liverpool, Liverpool.
- Frid, C. J. L., O. A. L. Paramor & C. L. Scott, 2006. Ecosystem-based management of fisheries: is science limiting? ICES Journal of Marine Science 63: 1567–1572.
- Gower, J. C. & D. J. Hand, 1996. Biplots, Vol. 54. Chapman & Hall, London.
- Grall, J. & M. Glemarec, 1997. Assessment of benthic structure in the Bay of Brest. Annales De L Institut Oceanographique 73: 7–16.

- Herrando-Pérez, S. & C. L. J. Frid, 2001. Recovery patterns of macrobenthos and sediment at a closed fly-ash dumpsite. Sarsia 86: 389–400.
- Holme, N. A., 1953. The biomass of the bottom fauna in the English Channel off Plymouth. Journal of the Marine Biological Association of the UK 32: 1–49.
- Lasiak, T., 1998. Multivariate comparisons of rocky infratidal macrofaunal assemblages from replicate exploited and non-exploited localities on the Transkei coast of South Africa. Marine Ecology-Progress Series 167: 15–23.
- Pearson, T. H. & R. Rosenberg, 1986. Feast and famine: structuring factors in marine benthic communities. In: Gee, J. H. R. & P. S. Giller (eds), Organization of Communities: Past and Present. Blackwell Scientific: 373–398.
- Snelgrove, P., T. Blackburn, P. Hutchings, D. Alongi, J. Grassle, H. Hummel, G. King, I. Koike, P. Larnbshead, N. Ramsing & V. Solis-Weiss, 1997. The importance of marine sediment biodiversity in ecosystem processes. Ambio 26: 578–583.
- Snelgrove, P. V. R. & C. A. Butman, 1994. Animal sediment relationships revisited—cause versus effect. Oceanography and Marine Biology 32: 111–177.
- Statzner, B., V. H. Resh & L. A. Roux, 1994. The synthesis of long-term ecological research in the context of concurrently developed ecological theory: design of a research strategy for the Upper Rhone River and it's floodplain. Freshwater Biology 31: 253–263.
- Telesh, I. V., A. F. Alimov, S. M. Golubkov, V. N. Nikulina & V. E. Panov, 1999. Response of aquatic communities to anthropogenic stress: a comparative study of Neva Bay and the eastern Gulf of Finland. Hydrobiologia 393: 95–105.
- United Nations, 1992. Convention on Biological Diversity. UN, New York.
- US Magnuson-Stevens Fishery Conservation and Management Act, 1996. An Act to provide for the conservation and management of the fisheries, and for other purposes. As amended through October 11, 1996. Public Law 94–265.
- Whitlatch, R. B., A. H. Hines, S. F. Thrush, J. E. Hewitt & V. Cummings, 1997. Benthic faunal responses to variations in patch density and patch size of a suspension-feeding bivalve. Journal of Experimental Marine Biology and Ecology 216: 171–189.

Copyright of Hydrobiologia is the property of Springer Science & Business Media B.V. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.