IS LONG-TERM ECOLOGICAL FUNCTIONING STABLE: 
THE CASE OF THE MARINE BENTHOS?

C.L.J. Frid* and B.A. Caswell
School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, UK.

*Email: cljfrid@liverpool.ac.uk, Tel: +441517954382.

ABSTRACT

It is widely acknowledged that human activities are contributing to substantial biodiversity loss and that this threatens ecological processes underpinning human exploitation of ‘ecosystem services’ (defined by the Millennium Ecosystem Assessment as ‘the benefits people obtain from ecosystems’). In the present study we consider three ‘intermediate ecosystem services’ in both contemporary and ancient marine systems and although ‘ecosystem services’ per se did not exist in the Jurassic our study seeks to consider the future provision of these services and so the term is retained. We consider the temporal patterns in benthic marine ecosystems: (1) spanning four decades at two offshore stations in the North Sea, UK; and (2) over millennial scales in Late Jurassic UK palaeocommunities. Biological traits analysis is used to link changes in taxonomic composition to variations in ecological functioning and the potential supply of three ‘intermediate’ ecosystem services: the ability to provide food to fish and other predators, benthic nutrient regeneration and carbon cycling. We examine whether changes in taxonomic composition drive temporal variation in functioning, whether this variation increases over time and the extent to which species turnover is comparable in contemporary and
ancient systems. Taxonomic variability was of a similar magnitude in all three systems and there was evidence for changes in functioning linked to changes in several (key or rivet) taxa. During other periods resilience maintained functioning in the face of taxonomic change. These results suggest that in these benthic systems the Biodiversity–Ecosystem Functioning relationship is idiosyncratic, but a degree of temporal stability in functioning is maintained such that the ecosystem services they underpin would also be stable during decadal and longer-term changes.

Key words: Dove Time Series, ecosystem services, nutrient regeneration, food supply; Jurassic; Kimmeridge Clay Formation; biological traits analysis; long-term.

INTRODUCTION

Global biodiversity loss is one of the most marked changes that the biosphere is experiencing in response to anthropogenic activities. Biodiversity loss has been observed in terrestrial, freshwater and marine ecosystems and the IUCN lists 22,103 species, of the 1.73 million species described, as being ‘threatened’. The proportion of total global biodiversity that this represents has not yet been accurately ascertained as only 4% of the total species described have been evaluated (IUCN, 2014) and because true global biodiversity is currently unknown (although it is estimated at ~19 million species).

Biodiversity loss is predicted to continue to increase (Cheung et al., 2009, Perreira et al., 2010) for example, the bioclimate envelope models of Cheung et al. (2009) predict a 60% turnover of marine biodiversity from present levels by 2050. Biodiversity loss has severe impacts on the way that ecosystems
function (e.g. Cardinale et al., 2012) and thus is often cited as a significant threat to the delivery of the ecosystem services that underly human well-being and livelihoods (United Nations, 2005). Marine ecosystems provide many important ecosystem services such as providing ~15% of our dietary animal protein, natural sea defences, waste treatment and recreational services and high diversity systems consistently provide more ecosystem services with less variability in delivery (Worm et al., 2006, Beaumont et al., 2007).

Most studies of the ecological functions, that underpin the delivery of ecosystem services, are of short duration (<5 years) and small scale. Research on small temporal and spatial scales may grossly underestimate the affects of diversity loss on ecosystem functioning because diversity effects increase in both time and space (Cardinale et al., 2012) therefore the results of small scale short term studies cannot simply be scaled up and used to inform management decisions (Worm et al., 2006). Understanding the temporal patterns of ecosystem service delivery is important because it has clear management implications when considering the recovery and restoration of habitats that have been compromised by human activities (LaPeyre et al., 2014). For example, La Peyre et al. (2014) followed variations in three ecosystem functions of restored oyster reefs over four years, these functions were: improving water quality, stabilising the shoreline and enhancing estuarine habitat for fish and invertebrates. La Peyre et al. (2014) found that each of the three ecological functions were delivered by the restored reefs but restoration of functioning followed very different trajectories. There was no
simple relationship between the time since restoration and the recovery of functioning and therefore ecosystem service provision by the oyster reefs.

The biological processes associated with sea floor ecosystems contribute to a number of important ecological functions and in turn key ecosystem services, including food production (fish and shellfish), genetic resources (including pharmaceutically active compounds), climate regulation, natural hazard protection, and maintenance of water and sediment quality (Beaumont et al., 2007). It is becoming increasingly clear that biodiversity underpins a range of critical ecosystem services and that changes in the composition and abundance of species, genes and habitats can have effects ranging from small scale (local) to major, cascading, impacts on global processes, such as the biogeochemical cycles of nutrients and carbon (Naeem et al., 2012).

Understanding the effects of these biodiversity changes requires both the classic reductionist experimental approaches to understanding the biodiversity – ecosystem function relationships and large scale (temporal and spatial) investigation of patterns of ecological and functional change (Raffaelli and White, 2013).

While populations show spatial and temporal variability in their abundance such that communities appear to undergo changes over time, if the net result of these changes is that individuals of one taxa are substituted (in the simplest terms) by those of another species with similar biological attributes the impact of this species turnover on the functioning of the system may be small. This extension of the ‘redundancy model’ of Biodiversity-Ecosystem Functioning
(BEF; Walker, 1992) leads us to propose the following hypotheses; (i) ecosystem functioning will show less temporal variation than species composition, and (ii) that longer time series will show greater variation in functional composition that short time series. Furthermore, we can ask whether the degree of species level change that does cause a change in functioning is similar in contemporary communities to those in the deep past. We examine these three assertions by drawing on two recent studies (Caswell and Frid, 2013; Frid, 2011) that have considered the temporal variations in ecosystem functioning to understand the potential of benthic systems to deliver ecosystem services in the face of long-term variations in the environment. We consider data for a contemporary shelf sea system in which species composition is known to vary on decadal and inter-annual time scales in response to varying food input, and a palaeocommunity from a shelf sea ecosystem subject to fluctuating periods of deoxygenation. Gogina et al. (2014) have shown that contemporary benthic systems subject to hypoxia have reduced diversity and they hypothesised, but were unable to confirm that this led to a decreased ability of the system to maintain functioning through compensatory mechanisms. Here we consider derived measures of ecological functioning and proxies for ‘intermediate ecosystem services’, where intermediate services are benefits derived from the ecosystem but which are not directly traded in a market (sensu Norris, 2012), so ‘food for fish’ underpins the ‘final’ service of food (fish) production.
METHODS

Decadal Scale Change: The Dove Benthic time series

Three multi-decadal time-series are collected off the northeast coast of England in the central-west North Sea (Clark and Frid, 2001; Fig. 1a-b).

Originally established by staff from the University of Newcastle’s Dove Marine Laboratory, data collection continues using the same methods as when the time series commenced (Clark and Frid, 2001). One series considers mesozooplankton and is not considered further. The other series are of benthic macrofauna at two offshore stations located in areas away from local river discharges.

Station P (55° 07' N, 01° 15' W) lies 18.5 km off the northeast coast of England in 80 m water depth (Fig. 1a-b). The sediments at Station P are silty-sand with a greater than 50% silt-clay content, of which approximately 20% consists of faecal pellets. The benthic community at Station P is the Brissopsis lyrifera-Amphiura chiajei variant of the Amphiura filiformis community type (Petersen and Boysen-Jensen, 1911). The station was initially sampled in January 1971 and the dataset analysed here covers samples taken in January/February of each year from 1971 to 2006. In 1998 no samples were collected as the weather and operational constraints prevented sampling.

The second station M1 (55° 07' N, 01° 20' W) lies some 10.5 km off of the Northumberland coast (Fig. 1b). The station has a predominantly sandy sediment, with a 20% silt-clay content and lies in 55 m of water (Frid et al., 1996, Frid et al., 1999). Benthic sampling commenced in September 1972
and the dataset analysed here covers samples taken in March of each year between September 1973 and 2005. No samples were collected, due to weather or operational constraints, in March 1998.

On each sampling occasion at least five 0.1 m² grab samples were collected, and each was gently sieved over a 0.5 mm mesh and the residue fixed in 4% buffered formalin. All organisms were identified to species level, where possible and enumerated. Buchanan and Warwick (1974) and Buchanan and Moore (1986) describe the methods of sampling in detail.

The macro-infaunal data are originally recorded to species or the lowest practical taxon, but for this study the data were aggregated to genera (data at lower taxonomic resolution remain unchanged) to give total abundance of genera per 1 m² based on five (or more) replicate samples. This approach reduced any problems due to misidentification at the species level and changes in taxonomy leading to problems with homonyms. Genera richness and total abundance of individuals are based on the entire ‘genera aggregated’ data set.

For multivariate analyses of community composition the dataset was reduced to make computation manageable and reduce any influence of very rare or under-sampled taxa. For the more diverse M1 station, only those genera representing more than 0.1% of the individuals recorded (i.e. more than 15 individuals found during the entire survey period) were included in these analyses, leaving 89 genera in the ordination at M1. At station P the original
dataset included 262 taxa, which was reduced to 173 genera (or higher taxa) all of which were included. For multivariate analyses of the community composition the dataset was transformed \((\log (x+1))\) to reduce the influence of common taxa.

**Millennial Scale: The Kimmeridge Clay Formation Series**

The palaeocommunity data comprise the benthic species composition and abundance data (number, expressed as percentage, per 0.2 m\(^3\) of rock sampled) collected by Wignall (1989, 1990) from coastal exposures of the Kimmeridge Clay Formation (KCF), Kimmeridge, UK (Fig. 1a and c). Wignall (1990) classified these data into 21 unique associations, hereafter refer to as palaeocommunities. The 21 palaeocommunities spanned between 0.05 m–24.4 m of vertical rock and had an average thickness of 0.90 m equivalent to an average temporal duration of ~7000 years based on the cyclostratigraphic timescale of Weedon et al. (2004).

The links between changes in the palaeoenvironment and benthic community functioning were investigated using geochemical proxy data, measured from bulk rock samples, collected from the KCF exposed on the coast (i.e. the same facies as those from which the palaeontological data were collected) and two nearby boreholes sections (Fig. 1a and c). The KCF represents the longest period (~8 million years; Weedon et al., 2004) of organic carbon accumulation during the Mesozoic (Jenkyns et al., 2002) although not the most severe (cf. Caswell and Coe, 2013), and was deposited under fluctuating levels of oxygenation (Pearce et al., 2010) that ranged from
hypoxic (low dissolved oxygen, 1-30% of saturation) to anoxic (the absence of oxygen) to euxinic (oxygen absent and toxic H2S present).

**Biological traits and ecosystem functioning**

Biological traits analysis (BTA) replaces biological identities with a profile of biological traits, such as feeding mode, degree of locomotion, longevity etc. BTA has previously been shown to provide a sensitive measure of changes in the system (Charvet et al., 1998, Doledec et al., 1999, Usseglio-Polatera et al., 2000a, Charvet et al., 2000). Each trait has a number of modalities associated with it, i.e. for feeding trait the modalities represented different feeding types. Each taxon in the database was scored for its affinity to each trait modality using a scale of 0 to 1 (0 = no affinity to 1 = high affinity). Scores were given using the ‘fuzzy scoring’ method which allows the taxa to exhibit more than one modality for any given trait, but the total score per trait always had a value of one (Bremner et al., 2003).

For the Dove Benthic Series five trait categories (size, trophic role, burrow depth, bioturbation capacity, and longevity) (Table 1) were used. For each taxa identified, by SIMPER, as being a major contributor to the between period shifts in assemblage composition the biological traits profile was determined (Frid, 2011). Trait information was derived from the University of Liverpool’s trait database (Frid et al. unpub.), the BIOTIC database maintained by the Marine Biological Association UK (http://www.marlin.ac.uk/biotic/) and by targeted literature searches to fill any gaps.
For the Kimmeridge Clay Formation eight biological traits were selected to represent aspects of the organisms morphology, life habit, feeding patterns and life histories (Table 2). Each trait comprised five modalities, except for sociability that comprised only three (Table 2). This assignment was based on published accounts of the palaeobiology of each species and information from The Treatise of Invertebrate Palaeontology (Geological Society of America Inc., 1953-2009), The Palaeobiology Database (http://palaeodb.org), and for extant taxa the BIOTIC database (http://www.marlin.ac.uk/biotic/). When information was not available at the species level data used were based on accounts of other members of the genera or, more rarely, the family. When no information on a particular trait was available for a taxon, zero values were entered for each category and, therefore, the taxon did not contribute to the trait weightings.

The frequency of each trait modality in the two datasets was calculated by weighting the category scores by the abundance of each taxon exhibiting that modality (Charvet et al., 1998). This resulted in a sample by trait table showing the abundance of biological traits for each palaeocommunity/assemblage over the interval studied.

The composition of the assemblage in terms of the abundance of each of the trait modalities (Table 1, Table 2) present was analyzed for all the scored traits by non-metric MDS and then for combinations of traits that mapped on to the principle intermediate ecosystem services carbon cycling, provision of food for fish and nutrient cycling/regeneration. The traits were deemed to be
associated with ecological functions (Frid et al., 2008), and the ecological functions in turn were deemed to support intermediate ecosystem service provision (Hussain et al., 2010). For example, ecological processes that contribute to sediment turnover are assumed to underpin organic matter breakdown and nutrient regeneration. The intermediate ecosystem service, nutrient regeneration, in the modern ocean underpins our use of the seas as a repository and treatment option for organic waste. High carbon cycling was associated with small body size and thus short longevity, high value as a food source for fish with a large body size, and a surface or shallow burrowing habit whilst nutrient cycling/regeneration was indexed by high or moderate bioturbation, deep burrowing and a deposit feeding habit.

Similarity between each pair of palaeocommunities was calculated using the Bray-Curtis index (after a log (x+1) transformation of the abundance data to reduce the influence of dominant species) and a dendrogram of similarity of species composition of the palaeocommunities was produced. All multivariate analyses were carried out using the statistical software PRIMER v. 6 (PRIMER-e, Plymouth, UK; Clarke and Warwick 1994) and univariate comparisons were made using SPSS v. 20 (IBM, Ltd).

RESULTS
The species composition and ecology of the three systems has been described extensively elsewhere (see Frid, 2011, Frid et al., 2009b, Frid et al., 2009a and references therein) but the following summary is offered to provide context for the subsequent analyses and their interpretation. A total of 516 taxa, from 327 genera, have been recorded at the Dove benthic station.
M1 (Frid et al., 2009b). The macro-infaunal assemblage may be considered a variant of the classical Petersen *Amphiura filiformis* benthic community (Petersen, 1913), except that it is often dominated by small-bodied polychaetes with *Prionospio fallax* (Söderström) being the top-ranked species in most years (Table 3; Frid et al., 1996). During the period 1973–2005, the total abundance of infauna at M1 in March, the seasonal low, averaged 380 individuals per 0.1m$^2$ (Table 3; range 104–720 per 0.1m$^2$) whilst genera richness ranged from 63–124 genera (with a mean of 94). Throughout the time-series the top ten genera, comprised four taxa of polychaete worms, one phoronid worm, four bivalve molluscs and one brittlestar and together accounted for approximately 43% of all the individuals observed (Table 3).

At the Dove benthic station P, the ten most abundant genera accounted for ~70% of the individuals present, and in total 173 genera (or higher taxa) were recorded (Table 3). The polychaete *Heteromastus* accounted for nearly 30% of all the individuals recorded in the time series, and over the 36 year period *Heteromastus* was the dominant taxon every year except between 1973 and 1977 when the polychaete *Levinsenia* was dominant. Although polychaetes dominated the benthos, the top ten taxa also included nemerteans, an amphipod, a bivalve mollusc and an ophiuroid (Table 3).

The KCF assemblage included a total of 99 taxa, mostly true species, with taxa richness of individual assemblages varying between seven and 42. The dominant taxa were bivalve molluscs, followed by gastropods, and brachiopods (Table 4). The bivalves *Protocardia morinica*, *Isocyprina*...
minuscula and Corbulomima suprajuresnis accounted for ~70% of all specimens found (Table 4) and together dominated 16 of the 21 palaeocommunities. The species composition of two assemblages (E6 and E9) were highly distinct (Bray-Curtis similarity <5%) from each other and all the other samples and so were omitted from the cluster analysis and ordinations of the taxonomic composition because they were sufficiently distinct as to cause the remaining samples to ordinate in one tight cluster making it impossible to distinguish patterns.

Ecosystem functioning will show less temporal variation than species composition

The species composition at station M1 showed a high degree of consistency between years with successive years (i.e. 1972 to 1973) having a Bray-Curtis similarity of >80% (Fig. 2a). The exceptions to this pattern have been used to define periods of change in species composition and generally resulted in a shift to a ‘new configuration’ of species in the assemblage that persisted for a number of years before undergoing a further shift. These patterns were observable from both the pairwise similarities (Fig. 2a) and the non-Metric Multidimensional Scaling ordinations (nMDS; Fig. 3a). For the station M1 samples collected in March there were four main taxonomic groups (with a Bray-Curtis similarity >77%; Figs 2a and 3a) these were 1973-1985, 1986-87, 1988-1991, and 1992-2005. There were more minor shifts between 1997-1999 (1998 missing) and between 2002-2003 (Fig. 2a).

At station P Bray-Curtis similarity between successive years was generally >70% (Fig. 2c) except, as at M1, when the system under went a ‘shift' suggesting that the composition of species in the assemblage was quasi-
stable for a number of years before undergoing a change to a new configuration of species. This pattern is visible from both the pairwise similarities (Fig. 2c) and the nMDS ordinations (Fig. 3c). At station P the 'stable' periods with Bray-Curtis similarity > 69% (Fig. 2c and 3c were 1971-81 (plus 1987), 1982-1986, 1989-1991, 1992-1999 and 2000-2006 (1988 was an outlier).

At both station M1 and P the species composition of the macro-infaunal community exhibited periods of relatively high stability (Bray-Curtis similarity >~70%) in species composition that persisted for 4-14 years and then shifted to a different species composition. At station M1 the trait composition is more variable than the species composition with four groups being defined by a Bray-Curtis similarity of 70% (cf. 77% for taxonomy, Figs 2b and 3b) and with less congruency with the temporal separation of samples. At station P five groups of years (~65% similar, Fig. 2c) and a singleton with distinct taxonomic composition occur and for trait composition four groups and a singleton were identified (~75% similar, Fig. 2d). However, the temporal structure evident in the taxonomic clustering is not repeated in the trait composition based analysis (cf. Figs 2d and 3d). For example, the species composition at Station P was similar during 1982-86 (Figs 2a and 3a) whereas the trait composition for the same period differs (Figs 2b and 3b). The trait composition shows 1982, 1984 and 1986 clustered together but 1983 and 1985 occurred in different clusters to each other and the other three years (cf. Figs 2c and 2d).

Such patterns suggest that while changes in species composition were often minor, in terms of species abundance patterns, species changes often
resulted in certain trait modalities disappearing from or appearing in the
assemblage.

The Bray-Curtis similarity in species composition between the 21 KCF
palaeocommunities was lower than the similarity between the contemporary
communities at stations M1 and P, from the successive years, and Bray-
Curtis similarity was generally >60% between the KCF samples compared to
~70% in the two contemporary series. With the most extreme outliers (E6 and
E9) excluded the palaeocommunities formed three distinct groups that were
60% similar (A/E1, B1-B3; E2a and E5; B4, E2e, E4, and E7; and A1, E1a,
E1b, E2b, E2c, E3 with E8 being an outlier; Fig. 2d), these groupings were
less apparent in the nMDS ordination (Fig. 3d). The trait composition of the
21 palaeocommunities (NB all palaeocommunities included) had a Bray-Curtis
similarity of 45% and delimited three groups and two singletons (Fig. 2f). As
was found for the contemporary communities the grouping of
palaeocommunities by trait composition showed little similarity to that for the
taxonomic composition. For example, the two extreme outliers in the
taxonomic analysis (E6 and E9) ordinated in the largest cluster of trait
composition (Fig. 3e-f) while palaeocommunities A1 and B5, which had been
nested within groups in the taxonomic analysis, formed the singletons in the
traits based analysis (Fig. 2e-f).

The main influence on the taxonomic composition of the two Dove time series
appears to be temporal with shifts in community composition occurring at,
approximately, decadal intervals with a major shift occurring in the late 1980’s
at both sites (Figs 3a and c). In the KCF data the main effect on taxonomic composition is the separation of sites with high total organic carbon (TOC; E1a, E2d, E2e, E4, E5, E6 and E9), indicative of deoxygenation, from the remainder (Figs 3e–f). Ordinations of the biological traits composition for the Dove time series (Figs 3b, d and f) showed samples were spread in a band across the centre of the ordination space (suggesting a trend rather than step wise changes). In comparison the KCF trait composition of the palaeocommunities from the deoxygenated periods (as indexed by TOC) differed significantly from the others (Pair wise ANOSIM, R = 0.449, p = 0.001).

In all three data sets the degree of variation in taxonomic composition and trait composition was similar (Fig. 2). However, it is also apparent that the variation in trait composition was not simply a reflection of the changing taxonomic composition, as in each case the patterns observed from cluster analysis were distinct from each other (Figs 2 and 3).

**Longer time series will show greater variation in functional composition than short-term series**

In both of the Dove series the decadal scale shifts in taxonomic composition suggest that longer time series show greater total variation in taxonomic composition than shorter time series. However, the intermingling of samples from across the time periods in the ordinations of trait composition (Figs 3b and d) points to the existence of a stabilising mechanism maintaining trait composition in the face of taxonomic change. For the KCF the relative distribution of palaeocommunities in taxonomic ordination space and trait
ordination space are distinct from each other, and both show a clear influence of deoxygenation (Figs 3 e and f; Caswell and Frid, 2013).

Is the degree of species level change that causes a change in functioning similar in contemporary and ancient benthic communities?

When considering the delivery of ecological functions, Dove station M1 showed the most variability in the amount of function delivered by the assemblage (Fig. 4a). This pattern is primarily driven by the inter-decadal patterns of total abundance: when there were more individuals in the community it delivered a greater amount of service. At Dove station P, the intermediate service ‘food for predators’ showed an increase in the latter part of the series, after the shifts in the late 1980’s (Fig. 4b), again associated with increased numbers of individuals of some taxa (Frid, 2011). However, the delivery of nutrient regeneration and carbon sequestration was remarkably consistent throughout the 33-35 years (Fig. 4b). This is also the case in the KCF where the delivery of the three intermediate ecosystem services varied little between the different levels of deoxgenation (Fig. 4c), in spite of large-scale changes in the taxonomic composition of the infauna.

DISCUSSION

The result of this study show that in two contemporary benthic time series and one ecologically comparable palaeoecological data set ‘background’ taxonomic turnover resulted in samples with a taxonomic composition that is ~70% similar. It is also clear that environmental drivers periodically caused larger scale changes in species composition (Caswell and Frid, 2013, Frid et al., 2009a, Frid et al., 2009b). Biological traits can be used to index the ecological functioning of assemblages and one might expect large-scale
changes in taxonomic composition to result in changes in trait composition and hence ecological functioning. Our data show that trait composition in the three data sets had comparable variability but critically the pattern of changes in trait composition did not match the changes in taxonomic composition. At times the trait composition, and hence ecological functioning, was maintained in the face of taxonomic changes, implying a degree of redundancy in the system. In other instances trait composition changed to a greater extent than taxonomic composition suggesting that ‘key’ taxa, i.e. those that were critical in supplying certain traits, changed. Thus, in both the long-term palaeoecological systems and the shorter (still multi-decadal) contemporary systems there is evidence of both ecological redundancy and the existence of key or rivet species (Walker, 1992, Cardinale et al., 2006, Cardinale et al., 2012).

Although fisheries during the 1980s were shown to have impacted the benthos at station P both of the Dove benthic stations show, approximately, decadal shifts in species composition (Fig. 3). However, these changes involve species turnover in the sub-dominant taxa (Frid et al., 2009a, Frid et al., 2009b) such that the distribution of biological traits in the assemblage does not change markedly (Frid, 2011; Fig. 2b and d). At station M1 the increase in total infaunal abundance and inter-annual variability (Frid et al., 2009b) in the late 1980s and 1990s drove an increase in the delivery of all three intermediate services (Fig. 4a). In contrast, changes in the total infaunal abundance at station P were much less marked (Frid et al., 2009a) and only resulted in changes in the delivery of one of the intermediate services (Fig.
This lack of separation in the ordination of traits and the overriding effect of macro-infaunal abundance on the delivery of ecosystem services suggests that over decadal scales the functioning of these communities and the types of ecosystem service they could deliver is conserved although the quantity of available service varied with inter-annual variations in infaunal abundance. This inter-annual variation is driven to a large extent by the input of food (Pearson and Rosenberg, 1986, Buchanan, 1993). So does this quasi-stability extend beyond multi-decadal timeframes?

A recent study, of plant communities, also concluded that ecosystem functioning did not vary greatly over multi-decadal time scales (Vellend et al., 2013). Using a systematic review and meta-analysis of 168 published studies with data from over 16,000 sites and Vellend et al. (2013) showed that plant diversity change did not differ significantly from zero over periods of 5-260 years. Sites were as likely to experience an increase in plant diversity (mainly through post-disturbance succession) as they were to undergo a decrease in diversity (mainly driven by species invasions). Although the authors did not directly assess functioning they asserted, on the basis of the diversity changes, that functioning probably did not significantly vary either.

The processes of preservation in the KCF mean that the data for the KCF includes a degree of ‘time averaging’ such that decadal scale changes in species (relative) abundances are not discernible at this sampling resolution. However, the dominant driver of change in these benthic assemblages is the degree of oxygenation. The changes in environmental conditions, associated...
with regional scale changes in oxygenation, caused a shift in the taxonomic
composition (Fig. 3e) of the benthos whereby only the most severe
deoxygenation (as indicated by high sedimentary TOC (>~3.8%)) resulted in
changes in the composition of the biological traits (Fig. 3f). These changes in
biological traits only produced changes in the delivery of the intermediate
service nutrient regeneration, presumably this is a reflection of the greater
abundance of infaunal/bioturbating taxa during oxic conditions in the surface

The analyses presented in this study depend on two assumptions, (1) that the
biological traits of a taxon can be used to infer its ecological role (functioning),
and (2) that these can be mapped on to ‘intermediate ecosystem services’
sensu Norris, 2012). In addition, for the KCF data we must assume that none
of the taxa responsible for a major (in terms of quantity or uniqueness)
contribution to ecosystem functioning have been so poorly preserved that they
do not feature in the fossil record (as either body or trace fossils). This does
not seem unreasonable considering that although some trace fossils are
reported sporadically in a few oxygenated intervals of the KCF (Wignall 1991)
they are rare (Oschmann, 1988, Wignall, 1990, Wignall, 1991) (Morgans-Bell
et al., 2001) and none are reported from the hypoxic strata (Oschmann 1988).

Biological traits analysis, and similar approaches, focus on functional groups
or specific sets of morphological or life history traits are routinely being used
to index ecological functioning in a range of ecosystems (Werner and Peacor,
2003, Usseglio-Polatera et al., 2000b, Kleyer et al., 2008, Bremner, 2008,
Paganelli et al., 2012). Although these approaches are limited by the available information on the biology of the taxa involved, and is more challenging for offshore taxa than terrestrial (Webb, 2012), the traits approach allows us to make a number of predictions about changes in relative functioning (and hence intermediate ecosystem service delivery) even if we are not certain that our current level of biological knowledge covers all of the ecological functions.

The biological assemblages present within the sea floor deliver a range of key ecosystem services (Beaumont et al., 2007) and undergo temporal variations on a range of scales that are driven by biotic (food supply) and abiotic (climate, hypoxia) factors. Our analyses suggest that changes in macro-infaunal abundance (which can vary by a factor of 7 or more over a decade; Frid et al., 2009a) drives changes in the quantity of some intermediate services. Furthermore, there is considerable stability in ecosystem functioning and hence the types of service potentially being delivered and the quantity delivered over time. These findings are preliminary and are of necessity constrained by the available data and the assumptions required to link taxonomic composition to ecosystem service delivery. However, if further analyses of these and other data sets confirm the pattern established in the present study, it will suggest that benthic ecosystem functioning conforms to some broad patterns, such as ‘evolving’ into a configuration that maximises the recycling of nutrients and ‘efficient’ food web structures, concepts that would be recognised in the writings of the first generation of ecosystem scientists back in the 1960s (Odum, 1969).
In this study we examined three hypotheses concerning the temporal stability of ecosystem functioning (i) ecosystem functioning will show less temporal variation than species composition; (ii) longer time series will show greater variation in functional composition than shorter time (i.e. decadal) series; and (iii) the degree of species level change that causes a functional change will be similar in contemporary and ancient marine communities. As ecosystem functions deliver the ecological goods and services that human societies derive from the natural world, understanding these three hypotheses may offer insights into the scale of the challenges that widespread environmental changes may pose. It is generally believed that biodiversity confers stability and provides a level of insurance against losses in ecological function (Worm et al., 2006). Our results show that in both contemporary and ancient marine ecosystems the natural assemblages do contain ecological redundancy that can protect functioning in the face of species turnover. However, in all of the communities investigated there were also instances of small changes in taxonomic composition resulting in more significant changes in functioning (and hence the potential delivery of ecosystem services). This implies that in these benthic systems ‘idiosyncratic’ models (Pueyo et al., 2007) best describe the Biodiversity-Ecosystem Functioning relationship, representing a considerable challenge for managers attempting to predict and mitigate the impacts of anthropogenic environmental change.

ACKNOWLEDGEMENTS

The CLJF is greatly indebted to the late Jack Buchanan for starting the Dove benthic series and trusting him with its continuation. We acknowledge the financial support at various times of DEFRA, DETR, DOE, NERC,
Northumbria Water Plc and the Universities of Newcastle and Liverpool. We would also like to thank the master and crew of the RV *Bernicia* and RV *Princess Royal*, Angela Coe, Leonie Robinson, Peter Garwood, Matt Spencer, Robin Clark, Kirsty Nicholas, Kirsty Harwood, Julie Bremner and colleagues at the Dove Marine Laboratory. The manuscript was greatly improved as a result of advice from the editor and two referees, and we thank them for their assistance.

**REFERENCES**


Caswell, B., and Coe, A. 2013. Primary productivity controls on opportunistic bivalves during Early Jurassic oceanic deoxygenation. Geology, 41: 1163-1166.


Figure 1. (a) Map of the UK showing location of the Dove stations offshore of the Tyne estuary, Newcastle and the village of Kimmeridge, Dorset, UK. (b) The location of the Dove benthic stations M1 and P in the central western North Sea. The dark shaped area is the extent of the main Nephrops fishing ground. (c) Location of the coastal exposure of the Kimmeridge Clay Formation type section; the positions of the Swanworth Quarry and Metherhills borehole (from which samples for the geochemical analyses were collected by Morgans-Bell et al. 2001).

Figure 2. Dendrograms showing Bray Curtis similarity of taxonomic composition (a, c and e) and biological trait composition (b, d and f) for Dove benthic station M1 (a and b; transformed data Log (X+1) for both), Dove benthic station P (c and d) and the Kimmeridge Clay Formation palaeocommunities (e and f; species composition data transformed Log (X+1)).

Figure 3. Non-metric multi-dimensional scaling ordinations of the Bray Curtis similarity of taxonomic composition (a, c and e) and biological trait composition (b, d and f) for Dove benthic station M1 (a and b; both transformed Log (X+1)), Dove benthic station P (c and d) and Kimmeridge Clay Formation palaeocommunities (e and f; species composition data transformed Log (X+1)). Kimmeridge Clay Formation palaeocommunities are grouped by the mean total organic carbon content of the sedimentary deposits. Note: E6 and E9 omitted from the taxonomic ordination for the Kimmeridge Clay Formation as the palaeocommunities were so dissimilar to the remaining stations that it obscured the detail for the remaining stations (see text for details of data sets).
Figure 4. Differences in the delivery (arbitrary units scaled with abundance; mean ± SE) of three ‘intermediate’ ecosystem services provided by benthic communities from (a) Dove Benthic station M1, (b) Dove Benthic station P and (c) palaeocommunities from the Kimmeridge Clay Formation (KCF; Late Jurassic). For the Dove series the data are presented by decade and for the KCF by degree of deoxygenation, as indexed by the total organic carbon (TOC) content where high TOC suggests deoxygenated and low TOC oxygenated conditions (see text for details).

Table 1. Traits and trait modalities used to classify the Dove benthic time series from stations M1 and P, North Sea, UK.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Modality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body size</td>
<td>(1) Small (&lt;10 mm), (2) Large (&gt;10 mm)</td>
</tr>
<tr>
<td>Longevity</td>
<td>(1) 1–3 years, (2) &gt;3 years</td>
</tr>
<tr>
<td>Bioturbation</td>
<td>(1) Low, (2) Moderate, (3) High</td>
</tr>
<tr>
<td>Life Zone</td>
<td>(1) Surface (Epibenthic), (2) Shallow infauna (&lt;5 cm), (3) Deep infauna</td>
</tr>
<tr>
<td>Feeding Mode</td>
<td>(1) Deposit, (2) Filter, (3) Omnivore, (4) Carnivore</td>
</tr>
</tbody>
</table>

Table 2. Traits and trait modalities used to classify the 21 Kimmeridgian benthic palaeocommunities.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Modality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Organism body size</td>
<td>(1) &lt;10 mm, (2) 10-50 mm, (3) 50-100 mm, (4) 100-200 mm, (5) &gt;200 mm</td>
</tr>
<tr>
<td>Skeletal composition</td>
<td>(1) Chitin, (2) Aragonite, (3) Calcite (low Mg), (4) Calcite (high Mg), (5) Phosphate</td>
</tr>
<tr>
<td>Skeletal thickness</td>
<td>(1) &lt;0.1 mm, (2) 0.1-0.5 mm, (3) 0.5-1 mm (4) 1-5 mm, (5) &gt;5 mm</td>
</tr>
<tr>
<td>Adult movement</td>
<td>(1) Sessile, (2) Burrowing, (3) Crawling, (4) Swimming, (5) Gliding</td>
</tr>
<tr>
<td>Living habit</td>
<td>(1) Semi-shallow infaunal, (2) Mid-deep infaunal, (3) Epifaunal attached, (4) Epifaunal free living, (5) Borer</td>
</tr>
<tr>
<td>Feeding habit</td>
<td>(1) Deposit feeder, (2) Grazer, (3) Suspension/filter feeder, (4) Scavenger/carnivore, (5) Chemosymbiont</td>
</tr>
<tr>
<td>Sociability</td>
<td>(1) Solitary, (2) Gregarious, (3) Colonial</td>
</tr>
<tr>
<td>Reproductive method</td>
<td>(1) Asexual budding, (2) Planktrophic larvae, (3) Lecithotrophic larvae, (4) Brood to larvae, (5) Brood to juvenile</td>
</tr>
</tbody>
</table>
Table 3. The mean abundance (per m\(^2\)) and percent contribution of the top ten ranked taxa to the total abundance of macro-infauna encountered during 33 years of sampling at benthic station M1, and 35 years at Dove station P, off the Northumberland coast, North Sea, UK.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Mean no. individuals (m(^2))</th>
<th>Contribution to total abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dove station M1</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polychaete Prionospio</td>
<td>495.11</td>
<td>10.09%</td>
</tr>
<tr>
<td>Polychaete Levinsenia</td>
<td>257.79</td>
<td>5.26%</td>
</tr>
<tr>
<td>Polychaete Chaetozone</td>
<td>198.19</td>
<td>4.04%</td>
</tr>
<tr>
<td>Ophiuroid Amphiura</td>
<td>193.54</td>
<td>3.95%</td>
</tr>
<tr>
<td>Bivalve Thyasira</td>
<td>191.03</td>
<td>3.89%</td>
</tr>
<tr>
<td>Bivalve Abra</td>
<td>186.98</td>
<td>3.81%</td>
</tr>
<tr>
<td>Isopod Mysella</td>
<td>158.62</td>
<td>3.23%</td>
</tr>
<tr>
<td>Polychaete Phoronis</td>
<td>153.67</td>
<td>3.13%</td>
</tr>
<tr>
<td>Polychaete Pholoe</td>
<td>150.86</td>
<td>3.08%</td>
</tr>
<tr>
<td>Bivalve Nuculoma</td>
<td>140.81</td>
<td>2.87%</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>4906.64</td>
<td>43.35%</td>
</tr>
<tr>
<td><strong>Dove station P</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polychaete Heteromastus</td>
<td>659.44</td>
<td>29.01%</td>
</tr>
<tr>
<td>Polychaete Levinsenia</td>
<td>208.09</td>
<td>9.15%</td>
</tr>
<tr>
<td>Polychaete Prionospio</td>
<td>151.11</td>
<td>6.65%</td>
</tr>
<tr>
<td>Polychaete Chaetozone</td>
<td>101.60</td>
<td>4.47%</td>
</tr>
<tr>
<td>Polychaete Paramphinome</td>
<td>97.77</td>
<td>4.30%</td>
</tr>
<tr>
<td>Polychaete Ophelina</td>
<td>90.21</td>
<td>3.97%</td>
</tr>
<tr>
<td>Nemertean Nemertea spp.</td>
<td>73.99</td>
<td>3.25%</td>
</tr>
<tr>
<td>Amphipod Harpinia</td>
<td>73.40</td>
<td>3.23%</td>
</tr>
<tr>
<td>Bivalve Abra</td>
<td>70.24</td>
<td>3.09%</td>
</tr>
<tr>
<td>Ophiuroid Amphiura</td>
<td>61.46</td>
<td>2.70%</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1587.31</td>
<td>69.83%</td>
</tr>
</tbody>
</table>

Table 4. The mean abundance and percent contribution of the top ten ranked taxa to the total abundance of macrofossils found throughout the 21 palaeocommunities of the Kimmeridge Clay Formation, Dorset, UK.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Mean abundance per palaeocommunity</th>
<th>Contribution to total abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bivalve Protocardia morinica</td>
<td>1134.87</td>
<td>30.57%</td>
</tr>
<tr>
<td>Bivalve Isocyprina minuscula</td>
<td>986.57</td>
<td>26.58%</td>
</tr>
<tr>
<td>Bivalve Corbulomima suprajurensis</td>
<td>580.46</td>
<td>15.64%</td>
</tr>
<tr>
<td>Bivalve Liostrea multiformis</td>
<td>176.14</td>
<td>4.75%</td>
</tr>
<tr>
<td>Bivalve Nicaniella extensa</td>
<td>89.36</td>
<td>2.41%</td>
</tr>
<tr>
<td>Gastropod Pseudorhodytidipilus latissima</td>
<td>73.07</td>
<td>1.97%</td>
</tr>
<tr>
<td>Bivalve Grammatodon longipunctata</td>
<td>65.62</td>
<td>1.77%</td>
</tr>
<tr>
<td>Bivalve Nanogyra virgula</td>
<td>60.93</td>
<td>1.64%</td>
</tr>
<tr>
<td>Gastropod Quadrinervus ornatus</td>
<td>59.09</td>
<td>1.59%</td>
</tr>
<tr>
<td>Brachiopod Lingula ovalis</td>
<td>44.93</td>
<td>1.21%</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>3271.03</td>
<td>88.12%</td>
</tr>
</tbody>
</table>
Fig. 1 Frid & Caswell
Fig. 2. Frid and Caswell JSR
Figure(s)
Fig. 4. Frid and Caswell JSR