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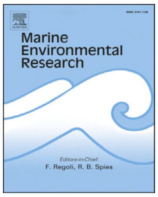

Community variability and ecological functioning: 40 years of change in the North Sea benthos

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ABSTRACT

Using established associations between species traits (life history, morphological and behavioural characteristics) and key ecological functions, we applied biological traits analysis (BTA) to investigate the consequences of 40 years of change in two North Sea benthic communities. Ecological functioning (trait composition) was found to be statistically indistinguishable across periods that differed significantly in taxonomic composition. A temporary alteration to functioning was, however, inferred at both sampling stations; coinciding with the North Sea regime shift of the 1980s. Trait composition recovered after 1 year at the station located inside the grounds of a trawl fishery, whereas the station located outside the main area of fishing activity underwent a six-year period of significantly altered, and temporally unstable, trait composition. A further alteration to functioning was inferred at the fished station, when the population of a newly established species rapidly increased in numbers. The results suggest that density compensation by characteristically similar (redundant) taxa acts to buffer changes to ecological functioning over time, but that functional stability is subject to aperiodic disruption due to substitutions of dissimilar taxa or uncompensated population fluctuations. The rate at which ecological functioning stabilises and recovers appears to be dependent on environmental context; e.g. disturbance regime.

1. Introduction

The composition of species assemblages varies temporally in response to natural and anthropogenic drivers (Gonzalez and Loreau, 2009). Experimental evidence suggests that such changes to biodiversity can alter the functioning of ecosystems and the provision of ecosystem services to society (Hooper et al., 2005). However, long-term empirical studies on ecological functioning are rare, and the available data are derived mainly from assemblages that have had aspects of their biodiversity manipulated and maintained over time (Hector et al., 2010). Therefore, the impacts of long-term community variability on the functioning of natural ecosystems are yet to be discerned.

In lieu of empirical data, indirect methods can be used to assess how changes to biodiversity affect ecological functioning. Biotic control over ecosystem processes is largely determined by the abundance and functional characteristics (i.e. ‘*effect* traits’; *sensu* Lavorel and Garnier, 2002) of the constituent species (Chapin et al., 1997). Therefore, when taxonomic composition is altered, the associated change in *effect* trait composition can be used to predict changes in ecological functioning (Bremner, 2008; Mouillot et al., 2011) and ecosystem service provision (Diaz et al., 2007).

It is recognised that where multiple species with shared *effect* traits coexist — i.e. there is functional redundancy (Walker, 1992) — the impact of population loss on ecological functioning may be buffered by compensatory population growth of characteristically similar taxa (Naeem, 1998). If such ‘species substitutions’ occur, then *effect* trait composition would experience little change over time despite alterations to taxonomic composition. However, the capacity for functional compensation depends on the extent to which characteristically similar taxa differ in their responses to environmental variability (Gonzalez and Loreau, 2009). If similar taxa show similar responses, then *effect* trait composition will vary temporally due to uncompensated population fluctuations or substitutions of dissimilar taxa. It is currently unclear what effect long-term changes in taxonomic composition have on *effect* trait composition, or whether the degree of association between these two ecological properties varies over time.

In the central-western North Sea, two benthic stations (M1 & P) have been sampled annually for over 40 years. The composition of

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macroinfauna has changed over time at both stations in relation to multiple environmental factors. Quasi-decadal shifts in community structure have been reported at M1 (Frid et al., 2009a); with fluctuations in detrital input and winter temperature apparently destabilising the assemblage (Buchanan and Moore, 1986; Buchanan, 1993). At P, temporal variability appears to have been influenced by heavy trawling activity during the 1980s; evidenced by patterns in taxa abundances (Frid et al., 1999, 2009b) and traits that determine species sensitivity to disturbance (i.e. '*response* traits'; *sensu* Lavorel and Garnier, 2002) (Bremner et al., 2003a, 2005). A recent trait-based analysis, which focussed on the most temporally variable taxa, also suggests that functional delivery at the sites has varied over time; mainly due to changing aggregate density as characteristically dissimilar taxa fluctuated in synchrony (Frid, 2011).

Here, temporal variability in the benthos at stations M1 and P was assessed using traditional analysis of taxonomic composition in tandem with biological traits analysis (BTA; Townsend and Hildrew, 1994; Bremner et al., 2003b). For BTA, we focused on the composition of *effect* traits that link macroinfauna to the delivery of key ecological functions (see Tables 1 and 2). Our analyses aimed to: 1) identify years in which abrupt changes to taxonomic composition occurred, 2) compare changes in taxonomic and trait compositions in these years, and 3) assess patterns in taxonomic and trait compositions across periods divided by these years. We took concurrent changes in taxonomic and trait compositions to be indicative of either substitutions of characteristically dissimilar taxa or uncompensated population fluctuations. Changes to taxonomic composition alone were taken to imply functional compensation. If trait composition changed significantly across periods, we inferred the potential consequences for ecological functioning. An increase or decrease in the number of individuals exhibiting a modality was taken as evidence for potentially enhanced or reduced levels of associated functions, respectively.

Table 1
Life history, morphological and behavioural traits (and codes) used to describe the functional composition of macroinfauna at Dove stations M1 and P. Modalities represent the different categories that taxa can exhibit for each trait.

Trait (code)	Modalities
Lifespan (A)	<1 yrs
	1–2 yrs
	3–10 yrs
	>10 yrs
Maximum body length (B)	<10 mm
	10–29 mm
	30–100 mm
	>100 mm
Protective structure (C)	Tubiculous
	Shelled
	Unprotected
Mobility within sediment (D)	Sessile
	Limited
	Slow movement
	Free movement
Burrow ventilation mode (E)	Blind-ended burrow
	Open-ended burrow
	No ventilation
Sediment reworking mode (F)	Diffusive
	Upward conveyor
	Downward conveyor
	Regenerator
	Surficial modifier
Feeding mode (G)	Deposit
	Suspension
	Scavenger
	Predator
	Parasite
Life zone (H)	Surface
	Shallow (<5 cm)
	Intermediate (5–10 cm)
	Deep (>10 cm)
Epibenthic habitat modification (I)	Cast or mound
	Burrow ditch/hollow
	Emergent structure
	No modification

2. Materials and methods

2.1. Study sites

Station M1 is located 10.5 km off the Northumberland coast (55°04′ N, 01°20′ W) and sits under 55 m of water in predominantly sandy sediment with 20% silt–clay content. Station P is located 18.5 km offshore (55°07′ N, 01° 15′ W) and is 80 m deep in sediment with >50% silt–clay content, around 20% of which is faecal pellets. Station P lies inside a *Nephrops* fishing ground while station M1 lies outside the main area of fishing activity (Fig. 1). Both stations are located away from local river discharges.

2.2. Benthic time series

Sampling of benthic macroinfauna began in January 1971 at P and September 1972 at M1. Subsequently data have been collected once a year in January/February at P and twice a year in March/April (spring) and September/October (autumn) at M1. In this study we consider two time series: one consisting of samples collected at M1 in spring and the other consisting of all samples collected at P. Data are missing for 1977 and 1998 at P and for 1998 and 2004 at M1, as weather conditions and/or operational constraints prevented sampling.

Samples were extracted using Van Veen grabs (0.1 m^2). Each sample was sieved over 0.5 mm mesh and the residue fixed with 4% buffered formalin. Organisms were identified to the lowest taxonomic level possible and enumerated. Sampling methods are described in detail in Buchanan and Warwick (1974). Information on sampling effort over time is provided in the online Supplementary material (Appendix 1).

2.3. Assembling community datasets

2.3.1. Taxonomic composition

Prior to collation of taxa abundance data, nomenclature was checked and updated, and synonymous taxa were merged under currently accepted names. Data were assembled at the lowest taxonomic level possible to minimise loss of information (over 70% of taxa in each time series were recorded at species level). Each year, population densities across all replicate samples were standardised to the number of individuals per square metre.

Previous trait analyses of the Dove benthic time series have used subsets of the community datasets; focussing either on dominant taxa (Bremner et al., 2003a, 2005) or taxa that contributed most to temporal variation in community structure (Frid, 2011). Here, taxa that made up $\geq$ 0.1% of total abundance (N) over the entire time series, or occurred at a density of at least 10 individuals m^{-2} in a single year, were retained in the taxonomic dataset. Taxa that were consistently rare were removed (see Appendix 1). Using this approach at least 98% of total N was represented each year at both stations.

2.3.2. Trait composition

Nine biological traits were chosen for analysis; reflecting the life history, morphology and behaviour of taxa (Table 1). Traits were selected to cover a suite of characteristics that are empirically demonstrated or logically deduced to drive six key ecological