1 **Marine Environmental Research**
2 **Community variability and ecological functioning: 40 years**
3 **of change in the North Sea benthos**

4
5 D.S. Clare^{1,*}, L.A. Robinson¹ and C.L.J. Frid^{1,2}
6

7
8 ¹*School of Environmental Sciences, University of Liverpool, Brownlow Street,*
9 *Liverpool, L69 3GP, UK*

10
11 ²*Present address: Griffith School of Environment, Griffith University, Gold Coast*
12 *Campus, G24 Parklands Drive, Southport, QLD 4222, Australia*

13
14 *Correspondence author. Email: David.Clare@liverpool.ac.uk
15
16
17
18

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

37
38 **KEY WORDS:** Biological traits analysis, ecosystem function, *effect* traits, functional
39 compensation, marine biodiversity, regime shift, temporal change, time series.
40
41
42
43
44
45
46
47

1. Introduction

The composition of species assemblages varies temporally in response to natural and anthropogenic drivers (Gonzalez & 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 & 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 & 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 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 & 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; Frid et al., 2009b) and traits that determine species sensitivity to disturbance (i.e. ‘*response* traits’; *sensu* Lavorel & Garnier, 2002) (Bremner et al., 2003a; Bremner et al., 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 & 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 & 2). Our analyses aimed to: 1) identify years in which abrupt

96 changes to taxonomic composition occurred, 2) compare changes in taxonomic and
97 trait compositions in these years, and 3) assess patterns in taxonomic and trait
98 compositions across periods divided by these years. We took concurrent changes in
99 taxonomic and trait compositions to be indicative of either substitutions of
100 characteristically dissimilar taxa or uncompensated population fluctuations. Changes
101 to taxonomic composition alone were taken to imply functional compensation. If trait
102 composition changed significantly across periods, we inferred the potential
103 consequences for ecological functioning. An increase or decrease in the number of
104 individuals exhibiting a modality was taken as evidence for potentially enhanced or
105 reduced levels of associated functions, respectively.

106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140

141 **Table 1.** Life history, morphological and behavioural traits (and codes) used to
142 describe the functional composition of macroinfauna at Dove stations M1 and P.
143 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)	Tubicolous 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

144
145
146
147
148

Table 2. Six ecological functions performed by macroinfaunal species and the trait modalities that drive them. References that demonstrate the links between traits and functions are numbered in superscript.

Ecological function	Trait	Modalities
Nutrient regeneration	Feeding mode	Deposit feeder ¹ , Suspension feeder ¹
	Sediment reworking mode	Upward conveyor ¹ , Regenerator ²
	Burrow ventilation mode	Blind-ended ^{1, 3} , Open-ended ^{1, 3, 4}
	Maximum body length	10-29 mm ⁵ , 30-100 mm ^{5, 6} , >100 mm
	Life zone	Intermediate ⁴ , Deep ²
Carbon turnover	Mobility within sediment	Free movement ^{7, 8}
	Maximum body length	< 10 mm ⁹
	Lifespan	< 1 yrs
Carbon sequestration	Feeding mode	Suspension feeder ¹
	Sediment reworking mode	Downward conveyor ¹
	Protective structure	Shelled ¹⁰
	Maximum body length	>100 mm ⁹
	Lifespan	> 10 yrs
Food for fish	Maximum body length	10-29 mm, 30-100 mm, 100 mm
	Life zone	Surface, Shallow
	Protective structure	None
Reef-formation	Epibenthic habitat modification	Emergent structure
Sediment heterogeneity	Epibenthic habitat modification	Cast or mound, Burrow ditch/hollow
References: ¹ Welsh (2003), ² Norling et al. (2007), ³ Braeckman et al. (2010), ⁴ Mermillod-Blondin et al. (2004), ⁵ Thrush et al. (2006), ⁶ Norkko et al. (2013), ⁷ Day et al. (1989), ⁸ Solan et al. (2004), ⁹ Brown et al. (2004), ¹⁰ Lee et al. (2010)		

152

153

154 **2. Materials and methods**

155 *2.1. Study sites*

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

Fig. 1. Location of Dove stations M1 and P in relation to the grounds of a *Nephrops* fishery in the central-western North Sea.

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 m²). 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 & 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;

191 Bremner et al., 2005) or taxa that contributed most to temporal variation in
192 community structure (Frid, 2011). Here, taxa that made up $\geq 0.1\%$ of total abundance
193 (N) over the entire time series, or occurred at a density of at least 10 individuals m^{-2} in
194 a single year, were retained in the taxonomic dataset. Taxa that were consistently rare
195 were removed (see Appendix 1). Using this approach at least 98% of total N was
196 represented each year at both stations.

197

198 2.3.2. Trait composition

199 Nine biological traits were chosen for analysis; reflecting the life history, morphology
200 and behaviour of taxa (Table 1). Traits were selected to cover a suite of characteristics
201 that are empirically demonstrated or logically deduced to drive six key ecological
202 functions (Table 2). As such, changes in the prevalence of these characteristics within
203 communities imply changes to the potential levels of associated functions.

204 To represent species characteristics each trait was divided into modalities (categories;
205 Table 1). For example, 'feeding mode' was divided into: deposit feeder, suspension
206 feeder, predator, scavenger and parasite. Information on the modalities taxa exhibit
207 was derived from the MarLIN open-access trait database
208 (<http://www.marlin.ac.uk/biotic/biotic.php>) and a trait database compiled by staff
209 from the Norsk Institutt for Vannforskning (NIVA). Literature searches and expert
210 consultation were used to corroborate and fill in gaps in information. Where species-
211 specific trait information was unavailable, modalities were inferred using well-
212 studied, closely-related taxa.

213 All individuals retained in the taxonomic datasets were used to create trait datasets.
214 Taxa were coded to represent their affinities to modalities within each trait, ranging
215 from 0 to 1. For example, an obligate predator was coded 1 for predator and 0 for all
216 other modalities within 'feeding mode', whereas a species that either deposit feeds or
217 suspension feeds with equal probability was coded 0.5 for both of these modalities
218 and 0 for all others. This 'fuzzy coding' procedure (Chevenet et al., 1994) accounts
219 for phenotypic plasticity within species as well as phenotypic variability across
220 species when using higher taxonomic levels. The annual abundance of each taxon was
221 then multiplied by its affinity to the suite of trait modalities (across all nine traits), and
222 the number of individuals exhibiting each modality was totalled across taxa. The
223 resulting trait-by-year time series is analogous to the taxa-by-year time series, with
224 densities of trait modalities replacing taxa abundances.

225

226 2.4. Data analysis

227 Taxa abundances were not transformed prior to analysis as we were interested in like-
228 for-like changes in taxonomic and trait compositions, with all individuals accounted
229 for. This approach assumes that contribution to function increases with population
230 density and, therefore, that dominant taxa dominate function (see Grime, 1998).

231 Line graphs of Bray-Curtis similarity to the preceding year were used to show year-to-
232 year variability in taxonomic and trait compositions, which were compared to assess
233 the degree of functional compensation. Additional line graphs of year-to-year
234 percentage change in the total number of species (S), total N, and the densities of the
235 ten dominant taxa were used to distinguish between substitutions of dissimilar taxa
236 and uncompensated population fluctuations when trait composition showed a high
237 degree of change. If data were missing for a year, then values the following year were
238 calculated with respect to two years prior; e.g. 1999 against 1997.

239 The time series were divided into periods of stability and instability. 'Break points',
240 that mark the start of a new period, were assigned to years in which there was an
241 abrupt change to taxonomic composition ($< 60\%$ similarity to the preceding year) that
242 was preceded or followed by ≥ 5 consecutive years of relatively-low temporal
243 variability (each year showing $\geq 60\%$ similarity to the preceding year). Non-metric
244 multidimensional scaling (nMDS) ordinations were used to assess temporal variation
245 in taxonomic and trait compositions. Statistical analyses of changes to taxonomic
246 composition across periods were performed using ANOSIM in PRIMER v6 (Primer-E
247 Ltd, Plymouth, UK). The same approach was applied to trait composition for BTA
248 (Bremner et al., 2005; Neumann & Kröncke; 2011). A significant difference was
249 taken as $p < 0.05$.

250 Variation in the total S and total N across periods were analysed using the Kruskal-
251 Wallis (KW) test in SPSS 20, with the Mann-Whitney (MW) U-test used for pairwise
252 comparisons. Data were transformed to meet the assumption of homogenous variance
253 when required. Changes to total S and total N were used to interpret patterns in
254 taxonomic and trait compositions, rather than constituting distinct hypotheses.
255 Therefore, we did not apply statistical corrections for multiple testing. We present
256 results for total S and total N with all individuals accounted for. Excluding from these
257 univariate analyses rare taxa that were removed for the multivariate analyses had a
258 minor effect on p and no effect on statistical significance.

259 SIMPER in PRIMER v6 was used to identify modalities that contributed most to
260 dissimilarity across periods that were significantly different in trait composition. The
261 densities of the top six contributing modalities were then analysed statistically across
262 periods using the KW and MW tests. No statistical correction was applied as these
263 analyses were aimed at identifying changes implied by BTA. To skew the weighting
264 toward less common modalities, which may be relatively variable and thus contribute
265 to observed changes in trait composition across periods, SIMPER was performed after
266 transforming modality densities by $\ln(x+1)$; followed again by analysis of top six
267 contributors to dissimilarity using KW and MW tests. Differences in the densities of
268 trait modalities across periods were analysed without transformations (unless required
269 to meet test assumptions). When top contributors to dissimilarity differed depending
270 on the period of comparison, modalities that were most frequently among the top six
271 in the pairwise comparisons were selected for analysis.

272
273

274 **3. Results**

275 *3.1. Station M1*

276 On average 100 taxa and 3700 individuals m^{-2} were recorded each year at M1. Total S
277 and total N reached series lows of 64 and 1044 (both in 1986) and peaked at 128 (in
278 1993) and 7212 (in 1991), respectively. The ten dominant taxa over the duration of
279 the time series accounted for over half of N, and consisted of six polychaetes, three
280 bivalves, and an ophiuroid (Appendix 2). The most common trait modalities included
281 deposit feeding, shallow life zone, limited mobility and slow movement within the
282 sediment (Appendix 2). Short body length (10 - 29 mm) and short lifespan (1 - 2 yrs)
283 were also prevalent. No sediment reworking mode was particularly common, but
284 blind-ended burrow ventilation was often exhibited. Individuals that did not ventilate
285 burrows were also common, and the majority of individuals present lacked a
286 protective structure and did not add structural heterogeneity to the seabed.

287 Abrupt changes to taxonomic composition ($< 60\%$ similarity to the previous year;
 288 preceded or followed by $\geq$ five consecutive years of $\geq 60\%$ similarity) were identified
 289 for the years 1986, 1992 and 2005 (Fig. 2a). Among these 'break points', change to
 290 taxonomic composition was most pronounced in 1986 (30% similarity to 1985); the
 291 only year of the three in which trait composition showed a similar degree of change
 292 (also 30% similarity to 1985; Fig. 2a). Large declines in total S (40% loss) and total N
 293 (80% loss) (Fig. 2c), and reduced densities of dominant taxa (nine taxa declined and
 294 one remained stable; i.e. N changed by < 50 individuals m^{-2} ; Fig. 3a,b), indicate an
 295 uncompensated collapse of populations and associated functions in 1986. In 1992 and
 296 2005 there was evidence for functional compensation; trait composition showed little
 297 change from the previous year ($\sim 80\%$ similarity; Fig. 2a) and dominant taxa exhibited
 298 mixed responses (seven declined, two increased and one remained stable in 1992; two
 299 declined, four increased and four remained stable in 2005; Fig. 3a,b). Total S
 300 increased by 25% from 1991 to 1992 as total N declined by 35% (Fig. 2c). In 2005
 301 total S increased by 10% and total N increased by 40% (Fig. 2c); however, as no data
 302 are available for 2004 these results represent net changes over two years (2003-05).

303 **Fig. 2.** Bray-Curtis similarity to the previous year in taxonomic and trait compositions (a, b)
 304 and total S and total N (c, d) of macroinfauna at Dove stations M1 (a, c) and P (b, d). Abrupt
 305 changes in taxonomic composition ($< 60\%$ similarity to previous year, preceded or followed
 306 by $\geq$ five years of year-to-year stability) are marked by vertical grey lines.
 307

Fig. 3. Change in abundance from the previous year of the ten dominant macroinfaunal taxa at Dove stations M1 (rank 1-5 (a), rank 6-10 (b)) and P (rank 1-5 (c), rank 6-10 (d)). Abrupt changes in taxonomic composition (see Fig. 2) are marked by vertical grey lines.

While acknowledging that, had it been available, the inclusion of 2004 data might affect the designation of 2005 as a break point, the time series was divided into four periods with respect to the three apparently abrupt changes in taxonomic composition: 1973-1985, 1986-1991, 1992-2003 and 2005-12. During 1986-91 there were short-term fluctuations in taxonomic composition (1986, 1988 and 1991 were all < 60% similar to preceding years; Fig. 2a), while trait composition fluctuated from 1986-88 (1986 and 1988 were < 60% similar to preceding years) but remained relatively stable between the years 1989-91 (all were $\geq 60\%$ similar to preceding years; Fig. 2a). The periods 1973-85 and 1992-2003 were characterised by taxonomic and functional stability (all years were $\geq 60\%$ and $> 75\%$ similar to the preceding year for taxonomic and trait compositions, respectively; Fig. 2a). Temporal variability increased again during 2005-12, with multiple years showing < 60% similarity to the preceding year in taxonomic composition, while year-to-year similarity in trait composition dropped to below 75% in 2007 (for the first time since 1992) and again in 2009 and 2012 (Fig. 2a).

Taxonomic composition was significantly different across all periods (Table 3; Fig. 4a), while only 1986-91 differed significantly from other periods in terms of trait composition (Table 3; Fig. 4c). Total S was significantly lower during 1986-91 compared to other periods (Table 3; Fig. 5a); however, there were no significant differences in total N (Table 3; Fig. 5c). Compositional changes were therefore driven by shifts in relative taxa abundances, with substitutions of characteristically dissimilar taxa occurring during 1986-91 – when the community was relatively species-poor – and substitutions of similar taxa (functional compensation) occurring across other periods.

Table 3. Differences in taxonomic composition (ANOSIM: Global R = 0.554), trait composition (ANOSIM: Global R = 0.112), total S (Kruskal-Wallis: H = 24.000; 3 d.f.) and total N (Kruskal-Wallis: H = 0.846; 3 d.f.) of macroinfauna at Dove station M1 across periods divided by abrupt changes in taxonomic composition. A significant difference (in bold) was taken as $p < 0.05$.

	<i>P</i>	1973-85	1973-85	1973-85	1986-91	1986-91	1992-2003
		vs. 1986-91	vs. 1992-2003	vs. 2005-12	vs. 1992-2003	vs. 2005-12	vs. 2005-12
Taxa comp.	< 0.001	0.004	< 0.001	< 0.001	< 0.001	0.002	< 0.001
Trait comp.	0.030	0.040	0.150	0.323	0.042	0.043	0.178
Total S	< 0.001	0.003	0.004	< 0.001	0.001	0.002	0.709
Total N	0.838	-	-	-	-	-	-

Fig. 4: nMDS ordinations of temporal variation in taxonomic composition (a, b) and trait composition (c, d) of macroinfauna at Dove stations M1 (a, c) and P (b, d). Periods are divided by abrupt changes in taxonomic composition (see Fig. 2): 1973-85 *, 1986-91 ▲, 1992-2003 ○ and 2005-12 + for M1; 1971-86 *, 1987 ▲, 1988-99 ○ and 2000-12 + for P. First and last years of periods are labelled. 2D stress = 0.16 (a), 0.13 (b), 0.04 (c) & 0.04 (d).

Fig. 5. Median, interquartile range and minimum and maximum values for Total S (a, b) and Total N (c, d) of macroinfauna across periods divided by abrupt changes in taxonomic composition (see Fig. 2) at Dove stations M1 (a, c) and P (b, d).

No individual modalities identified by SIMPER (using untransformed data) emerged as clear drivers of changes to trait composition during 1986-91 ($p > 0.05$; Table 4). This was due to high within-period variation in these modalities, which were each among the most commonly exhibited by the taxa (Appendix 2). Using transformed modality data, two of the six modalities identified (sediment regenerator and < 1 yrs lifespan) occurred at significantly different densities in 1986-91 compared to other periods (Table 4). Declines in these modalities during 1986-91 predict reduced rates of nutrient regeneration and carbon turnover, respectively (Table 2).

Table 4. Differences in the number of individuals exhibiting twelve trait modalities in 1986-91 compared to other periods at Dove station M1. The analysed modalities were identified as top contributors to compositional dissimilarity using untransformed data (above double-border) and $\ln(x+1)$ transformed data (below double-border). Significant differences ($p < 0.05$) are in bold. Changes to mean density are presented for modalities that differed significantly across periods. See Table 1 for list of traits matched to trait codes.

Trait code	Modality	H	P	1986-91 vs		
				1973-85	1992-2003	2005-12
(I)	No modification	1.133	0.769	-	-	-
(G)	Deposit	2.550	0.466	-	-	-
(H)	Shallow (< 5 cm)	0.375	0.945	-	-	-
(D)	Limited	2.309	0.511	-	-	-
(A)	1-2 yrs	1.419	0.701	-	-	-
(E)	Blind-ended burrow	0.651	0.885	-	-	-
(F)	Regenerator	13.039	0.004	-4.8	-11.7	-6.1
(I)	Cast or mound	5.272	0.153	-	-	-
(F)	Upward conveyor	4.369	0.224	-	-	-
(A)	< 1 yrs	8.720	0.033	-166.6	-204.0	-245.3
(F)	Downward conveyor	0.735	0.735	-	-	-
(B)	> 100 mm	7.441	0.059	-	-	-

3.2. Station P

An average of 60 taxa and 2500 individuals m^{-2} were recorded each year at P. The lowest total S recorded in any year was 35, in 1989, and the highest was 95, in 2011. Total N was at a series low of 825 in 1971 and peaked at 7960 in 2011. As at M1, polychaetes dominated the community at P; making up all of the five dominant taxa and six of the top ten (Appendix 3). Other dominant taxa included an amphipod, a bivalve, an ophiuroid, and members of the phylum Nemertea. Together these taxa made up 70% of total N. Nine of the ten most common trait modalities exhibited by taxa at M1 were also among the top ten at P, the only difference being the replacement of blind-ended burrow ventilation by maximum body length of > 100 mm (Appendix 3). The high density of the latter at P was due to the dominance of the threadlike capitellid *Heteromastus filiformis* (Claparède).

Break points ($< 60\%$ similarity in taxonomic composition to the previous year; preceded or followed by ≥ 5 consecutive years of $\geq 60\%$ similarity) were assigned to 1987, 1988 & 2000. Only the first was associated with a similarly large change in trait composition ($\sim 50\%$ similarity to 1986; Fig. 2b). Total S and total N both declined

in 1987 (by 25% and 70%, respectively; Fig. 2d), as did the densities of dominant taxa (nine declined and one remained stable; Fig. 3c,d); indicating an uncompensated collapse of populations and associated functions. Total N recovered somewhat in 1988 (90% increase; Fig. 2d), as four of the five dominant taxa increased in numbers (including the first recording of *Paramphionome jeffreysii* (McIntosh); *Chaetozone setosa* (Malmgren) decreased in numbers) and the remainder of the top ten remained stable (Fig. 3c,d). Total S, on the other hand, declined by just 2% (Fig. 2d) and trait composition in 1988 was 68% similar to 1987 (Fig. 2b). In 2000 there was evidence for functional compensation, as trait composition remained 75% similar to 1999 (Fig. 2b) and dominant taxa showed mixed responses (three decreased, two increased and five remained stable; Fig. 3c,d). From 1999 to 2000 total S and total N increased by 25% and 55%, respectively (Fig. 2d).

The time series was divided into four periods for analysis: 1971-86, 1987, 1988-99 and 2000-12. Both taxonomic and trait compositions showed year-to-year stability during the periods 1971-86 and 1988-99 ($\geq 60\%$ and $> 75\%$ similarity, respectively), which were separated only by a brief fluctuation in both ecological properties in 1987 (Fig. 2b). Temporal variability in taxonomic composition increased during 2000-12 (often $< 60\%$ similarity between consecutive years), whereas trait composition generally remained stable ($> 75\%$ similarity; Fig. 2b). Stability in trait composition broke down, however, when there was a large increase in the abundance of *Paramphionome jeffreysii* in 2011 (Fig. 3c), which boosted total N (Fig. 2d) and ended a sustained period of compensatory population fluctuations (Fig. 2b).

Trait composition did not differ significantly between 1971-86 and 1988-99, but both were significantly different to 2000-12 (Table 5; Fig. 4d). Taxonomic composition, on the other hand, differed significantly across all periods (Table 5; Fig. 4b). The collapse of populations and associated functions in 1987 was therefore quickly reversed as a new species assemblage emerged during 1988-99. During 2000-12, there was a significant increase in total S and total N compared to 1987-99 (Table 5; Fig. 5b,d); indicating that changes to trait composition across these periods resulted at least partly from increased aggregate density, as the assemblage became relatively species-rich.

Multiple modalities explained changes to trait composition during 2000-12. Of the top six contributors to compositional dissimilarity, five increased significantly during 2000-12 compared to 1988-99 and three increased significantly compared to 1971-86 (Table 6). Only deposit feeding showed no significant variation across periods. Using transformed data, six different modalities emerged as the top contributors to compositional dissimilarity. Five of these increased significantly during 2000-12 compared to both other periods (Table 6). No significant differences were observed only for animals with > 10 yrs lifespan. Increases in the densities of these modalities predict enhanced rates of nutrient regeneration, carbon sequestration and turnover, and increased availability of food for fish, during 2000-12 (Table 2).

Table 5. Differences in taxonomic composition (ANOSIM: Global R = 0.339), trait composition (ANOSIM: Global R = 0.097), total S (Kruskal-Wallis: H = 10.334; 3 d.f.) and total N (Kruskal-Wallis: H = 9.525; 3 d.f.) of macroinfauna at Dove station P across periods divided by abrupt changes in taxonomic composition. A significant difference (in bold) was taken as $p < 0.05$. Pairwise analyses with 1987 were not possible as $n = 1$.

		1971-86	1971-86	1971-86	1987	1987	1988-99
		vs.	vs.	vs.	vs.	vs.	
	<i>P</i>	1987	1988-99	2000-12	1988-99	2000-12	2000-12
Taxa comp.	< 0.001	-	0.012	< 0.001	-	-	< 0.001
Trait comp.	0.023	-	0.372	0.038	-	-	0.012
Total S	0.016	-	0.180	0.058	-	-	0.005
Total N	0.023	-	0.646	0.065	-	-	0.004

447

448

Table 6. Differences in the number of individuals exhibiting twelve trait modalities in 2000-12 compared to other periods at Dove station P. The analysed modalities were identified as top contributors to compositional dissimilarity using untransformed data (above double-border) and $\ln(x+1)$ transformed data (below double-border). Significant differences ($p < 0.05$) are in bold. Changes to mean density are presented for modalities that differed significantly across periods. The modalities '10-29 mm' and '< 1 yrs' were $\ln$ transformed prior to analysis to meet the assumption of homogenous variance. See Table 1 for list of traits matched to trait codes.

Trait code	Modality	H	<i>P</i>	2000-12 vs.		
				1971-86	1987	1988-99
(E)	No ventilation	13.625	0.003	+1228.7	+1856.0	+1310.7
(C)	Unprotected	10.953	0.012	+952.9	+1689.7	+1194.5
(I)	No modification	9.679	0.022	+833.6	+1786.6	+1251.5
(G)	Deposit	6.514	0.089	-	-	-
(D)	Slow movement	11.790	0.008	+912.5	+1503.2	+1031.0
(B)	10-29 mm	10.927	0.012	+851.0	+1373.8	+1092.5
(A)	< 1 yrs	21.467	< 0.001	+980.7	+1156.2	+962.5
(A)	> 10 yrs	5.003	0.172	-	-	-
(G)	Predator	21.993	< 0.001	+528.3	+594.3	+516.5
(C)	Shelled	12.686	0.005	+138.7	+189.8	+129.8
(B)	< 10 mm	14.100	0.003	+150.1	+287.0	+154.2
(F)	Diffusive	13.349	0.004	+912.0	+1139.8	+967.8

457

458

459

460

461

462

463

464

465

466

4. Discussion

Previous analyses of the Dove benthic time-series show long-term variation in taxonomic composition (Frid et al., 2009a, b); with natural and anthropogenic factors apparently influencing community dynamics (Buchanan & Moore, 1986; Buchanan, 1993; Frid et al., 1999; Bremner et al., 2003a; Bremner et al., 2005; Frid et al., 2009a, b). Using established associations between species traits and key ecological functions; we applied biological traits analysis (BTA; Bremner et al., 2003b) and found *effect* trait composition (*sensu* Lavorel & Garnier, 2002) to be statistically indistinguishable across periods that experienced significant changes to taxonomic composition at stations M1 and P (Fig. 4; Tables 3 & 5). Periods of significantly altered trait composition did, however, occur at both stations (Fig. 4; Tables 3 & 5). We infer that density compensation by characteristically similar (redundant) taxa acted to buffer changes to ecological functioning over time (*sensu* Naeem, 1998), but that substitutions of dissimilar taxa and uncompensated population fluctuations caused temporary disruptions to functioning.

A previous trait analysis by Frid (2011) suggested that key ecological functions have varied temporally at stations M1 and P due to changing aggregate density of infauna. In contrast to the present study, which found no differences in aggregate density across periods at M1, a crash in function delivery was implied during the late 1990s and 2000s at this station (however, both studies reported increased availability of food for fish at P in the 2000s). Whereas Frid (2011) focused on taxa with the highest inter-period variability, over 98% of total N was used to derive trait composition here. Taken together, these results suggest that the functional impact of the most temporally variable taxa can be buffered by changes in the densities of taxa with relatively low temporal variability. These findings echo previous suggestions that deriving traits for a subset of a community dataset may provide an incomplete picture of ecological functioning (Bremner 2008). It should, however, be noted that the approach to assessing functioning differed between the two studies. For example, the former used traits to reconstruct temporal patterns in specific functions; whereas the present study assessed temporal changes to trait composition and then inferred the consequences for specific functions. The results of the two studies are therefore not strictly comparable.

Our results are largely consistent with other studies that have applied BTA to assess temporal variability in the functioning of benthic communities. Veríssimo et al., (2012) analysed changes in the subtidal macroinfauna before and after the environmental restoration of a Portuguese estuary. They found that, despite shifts in taxonomic composition, trait composition either persisted or changed and recovered during the five-year study period at each of 15 sites. Similar patterns of functional change and recovery have been reported for epifauna responding to a cold winter in the German Bight (Neumann & Kröncke, 2011) and macroinfauna responding to hypoxia events over a 19-year period at a site in the south-western Baltic Sea (Gogina et al., 2014). Benthic invertebrate communities have also been shown to exhibit a level of seasonal stability in trait expression, despite taxonomic composition being highly variable on this timescale (Beche et al., 2006; Munari, 2013); while recent analyses suggest that similar patterns emerge across millennia (Caswell & Frid, 2013; Frid & Caswell, in press). Substitutions of characteristically similar benthic species may therefore occur widely and across multiple temporal scales; thus acting to conserve ecological functioning.

The capacity for functional compensation has previously been demonstrated using direct measurements of biomass/abundance stocks or rates of production in simple,

low diversity assemblages; with examples found in microbes (Jiang, 2007), terrestrial plants (Hector et al., 2010), nematodes (Ruess et al., 2001) and marine fishes (Dulvy et al., 2002). Results of the present study, and those mentioned above, therefore suggest that such patterns of functional stability extend to natural, biodiverse systems experiencing long-term compositional change. Moreover, our finding that functional stability can occasionally break down is consistent with counter-examples in the literature; such as an experiment which found no evidence of density compensation among protist species subjected to environmental warming (Fox & Morin, 2001) and another that found compensation among stream insects to depend on which species was experimentally removed (Ruesink & Srivastava, 2001). Both direct and indirect analyses therefore suggest that, while ecological functioning can be sustained over time, aperiodic disruption can occur under some conditions.

We found that alterations to *effect* trait composition occurred when taxonomic composition shifted at approximately the same time at both stations (1986 at M1 and 1987 at P; Fig. 2a,b). This event coincided with the North Sea climatic regime shift (Beaugrand, 2004), and therefore the implied alteration to benthic functioning may have been driven by broad-scale hydro-climatic forcing or the associated changes to the North Sea ecosystem. For example, community composition of the plankton changed around this time (Beaugrand, 2004) and detrital flux to the seabed surrounding the stations was estimated to be particularly low in 1986 (see Buchanan, 1993; a one-year lag between community trends at M1 and P has been suggested by Buchanan (pers. comm.) to result from differences in the depth and hydrodynamics at the two sites). Given that deposit feeders dominate at both sites, it is plausible that such changes to the quantity and, possibly, quality of detrital food supply caused the large, uncompensated declines in species populations and the ecological functions they deliver. This result suggests that climatic variability can cause temporary changes to benthic functioning, even within systems exhibiting long-term functional stability; a finding that echoes the results of Neumann & Kröncke (2011).

Following the abrupt functional change in 1986/87, trait composition at station P recovered after one year whereas M1 experienced a period of significantly altered, and temporally unstable, trait composition (1986-91). The rapid functional recovery at P possibly reflects the conditions at the site, which lies within the grounds of a *Nephrops* fishery. Given that the seabed at P is regularly subjected to trawling (Frid et al., 1999), it follows that the community should be comprised of species that are resilient to disturbances (see Jennings & Kaiser, 1998); thus facilitating recovery albeit with an altered taxonomic composition. This conjecture appears to be supported by a scarcity of disturbance-sensitive species and dominance by the opportunistic capitellid *Heteromastus fiiformis* at P (Appendix 3); whereas three disturbance-sensitive bivalves were among the top 10 most common taxa at M1 (Appendix 2). While previous studies reveal an impact of fishing disturbance on the trait composition of benthos (e.g. Bremner et al. 2005; Tillin et al., 2006; de Juan & Demestre, 2012), to our knowledge no study has yet assessed the effect of fishing disturbance history on the rate of functional recovery from other perturbations, such as climatic fluctuations.

The significant change to trait composition at M1 during 1986-91 (Table 3; Fig. 4c) suggests that characteristically similar taxa lacked the necessary range of population responses to sustain ecological functioning through this period. Given the decline in species richness and increased community variability, it is possible that the 1986 event eliminated redundant taxa that were necessary for functional compensation to

occur; thus impairing the delivery of ecological functions, as argued by Naeem (1998). Substitutions of characteristically dissimilar taxa did, however, maintain the same aggregate density during 1986-91 as the preceding period. The association between species sensitivity and functional characteristics (a major determinant of the ecological consequences of species extinction; Solan et al., 2004) therefore appears to vary over time and, possibly, with respect to the drivers of ecological change.

Changes to trait composition at P during 2000-12 (Table 4; Fig. 4d) involved an increase in total N (Fig. 5d) as the polychaete *Paramphinome jeffreysii* experienced rapid population rise (Fig. 3c); a trend that has occurred throughout much of the central and northern North Sea since its colonisation during the last 30 years (Kröncke et al., 2011). An increase in species richness and in the density of trait modalities not exhibited by *Paramphinome*, such as 'shelled' and '< 10 mm maximum body length', indicate that taxa other than *Paramphinome* also contributed to the enhanced rates of ecological functions predicted for this period (Table 6). These results can therefore be considered as complementary to those at M1; with species gains (in a relatively species-poor community; P) and losses (in a relatively species-rich community; M1) both associated with changes to the functional structure of communities (a topic addressed for marine systems in Byrnes et al. (2007)). It is currently unclear whether the *Paramphinome* will decline in numbers in the coming years, or if/how the community and functioning will respond to the proliferation of this species in the long term. Continued tracking of this species will answer these questions and provide insights into the ecological consequences of species invasions.

In applying BTA, we assumed that the characteristics and density of a species determine its functional potential. While these assumptions are empirically supported (Chapin et al., 1997), it should be noted that species can show plasticity in trait expression with respect to physical habitat (Ólafsson, 1986), levels of disturbance (Cesar & Frid, 2012) and potentially many other environmental conditions. We used fuzzy coding of traits to address this issue (Chevenet et al., 1994), but this reduces specificity; making it possible that temporal changes to trait composition were underestimated as a result. Our results therefore represent a conservative estimate of functional change over time. Furthermore, the degree to which species drive functioning may also vary with respect to environmental context (Hiddink et al., 2009) or the nature of interspecific interactions; i.e. facilitative (Cardinale et al., 2002) or antagonistic (Polley et al., 2003). This issue will need to be resolved if we are to progress from inferring changes to functional potential and use species traits to accurately predict levels of functional delivery across a range of biotic and abiotic conditions.

5. Conclusions

Our analyses suggest that ecological functioning can be sustained in communities undergoing long-term compositional change; as characteristically similar (redundant) taxa exhibit compensatory changes in population densities. Aperiodic disruption of *effect* trait composition can, however, occur due to substitutions of characteristically dissimilar taxa or uncompensated population fluctuations. The rate of stabilisation and recovery of ecological functioning appears to depend on environmental context, but can be of the order of 5-10 years in marine benthos.

613 **Acknowledgements**

614 The authors are indebted to the late Jack Buchanan for starting the time series used in
615 this study. We thank the masters and crew of the *RV Bernicia* and *RV Princess Royal*,
616 Peter Garwood and colleagues at the Dove Marine Laboratory for their efforts in data
617 collection. Our thanks also go to Eivind Oug and staff at NIVA for kindly providing
618 species traits information collected by their team. We acknowledge the financial
619 support at various times of DEFRA, DETR, DOE, NERC, Northumbria Water plc and
620 the universities of Newcastle and Liverpool. Production of this paper was funded by
621 the University of Liverpool.

622

623 **References**

624 Beaugrand G., 2004. The North Sea regime shift: evidence, causes, mechanisms and
625 consequences. *Progress in Oceanography* 60, 245–262.

626 Bêche L.A., McElravy E.P., Resh V.H., 2006. Long-term seasonal variation in the
627 biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams
628 in California, U.S.A. *Freshwater Biology* 51, 56–75.

629 Braeckman U., Provoost P., Gribsholt B., van Gansbeke D., Middelburg J.J., Soetaert
630 K., Vincx M., Vanaverbeke J., 2010. Role of macrofauna functional traits and density
631 in biogeochemical fluxes and bioturbation. *Marine Ecology Progress Series* 399, 173–
632 186.

633 Bremner, J., 2008. Species' traits and ecological functioning in marine conservation
634 and management. *Journal of Experimental Marine Biology and Ecology* 366, 37–47.

635 Bremner J., Frid C.L.J., Rogers S.I., 2003a. Assessing marine ecosystem health: the
636 long-term effects of fishing on functional biodiversity in North Sea benthos. *Aquatic*
637 *Ecosystem Health and Management* 6, 131–137.

638 Bremner J., Rogers S.I., Frid C.L.J., 2003b. Assessing functional diversity in marine
639 benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series*
640 254, 11–25.

641 Bremner J., Rogers S.I., Frid C.L.J., 2005. Biological traits of the North Sea benthos:
642 does fishing affect benthic ecosystem function? In: Barnes P, Thomas J (eds) *Benthic*
643 *habitats and the effects of fishing*. American Fisheries Society Symposium 41, p 477–
644 489.

645 Brown J.H., Gillooly J.F., Allen A.P., Savage V.M., West G.B., 2004. Toward a
646 metabolic theory of ecology. *Ecology* 85, 1771–1789.

647 Buchanan J.B., Moore J.J., 1986. A broad review of variability and persistence in the
648 Northumberland benthic fauna – 1971-85. *Journal of the Marine Biological*
649 *Association of the UK* 66, 641–657.

650 Buchanan J.B., Warwick R., 1974. An estimate of benthic macrofaunal production in
651 the offshore mud of the Northumberland coast. *Journal of the Marine Biological*
652 *Association of the UK* 54, 197–222.

653 Buchanan J.B., 1993. Evidence of Benthic pelagic coupling at a station off the
654 Northumberland Coast. *Journal of Experimental Marine Biology and Ecology* 172, 1–
655 10.

656 Byrnes J.E., Reynolds P.L., Stachowicz J.J., 2007. Invasions and extinctions reshape
657 coastal marine food webs. *PLoS ONE* 8, e295.

658 Cardinale B.J., Palmer M.A., Collins S.L., 2002. Species diversity enhances
659 ecosystem functioning through interspecific facilitation. *Nature* 415, 426–429.

660 Caswell, B.A., Frid, C.L.J., 2013. Learning from the past: functional ecology of
661 marine benthos during eight million years of aperiodic hypoxia, lessons from the Late
662 Jurassic. *Oikos* 122, 1687–1699.

663 Cesar C.P., Frid, C.L.J., 2012. Benthic disturbance affects intertidal food web
664 dynamics: implications for investigations of ecosystem functioning. *Marine Ecology*
665 *Progress Series* 466, 35–41.

666 Chapin F.S., Walker B.H., Hobbs R.J., Hooper D.U., Lawton J.H., Sala O.E., Tilman
667 D., 1997. Biotic control over the functioning of ecosystems. *Science* 277, 500–504.

668 Chevenet F., Dolédec S., Chessel D., 1994. A ‘fuzzy coding’ approach for the
669 analysis of long-term ecological data. *Freshwater Biology* 31, 295–309.

670 Day J.W., Crump B.C., Kemp W.M., Yanez-Arancibia A., 1989. *Estuarine Ecology*.
671 John Wiley & Sons, New York.

672 De Juan S., Demestre M., 2012. A Trawl Disturbance Indicator to quantify large scale
673 fishing impact on benthic ecosystems. *Ecological Indicators* 18, 183–190.

674 Diaz S., Lavorel S., de Bello F., Quétier F., Grigulis K., Robson T.M., 2007.
675 Incorporating plant functional diversity effects in ecosystem service assessments.
676 *Proceedings of the National Academy of Sciences* 104, 20684–20689.

677 Dulvy N.K., Metcalfe J.D., Glanville J., Pawson M.G., Reynolds J.D., 2002. Fishery
678 stability, local extinctions, and shifts in community structure in skates. *Conservation*
679 *Biology* 14, 283–293.

680 Fox J.W., Morin P.J., 2001. Effects of intra- and interspecific interactions on species
681 responses to environmental change. *Journal of Animal Ecology* 70, 80–90.

682 Frid C.L.J., 2011. Temporal variability in the benthos: Does the sea floor function
683 differently over time? *Journal of Experimental Marine Biology and Ecology* 400, 99–
684 107.

685 Frid, C.L.J., Caswell, B.A., in press. Does ecological redundancy maintain
686 functioning of marine benthos on centennial to millennial time scales? *Marine*
687 *Ecology*.

688 Frid C.L.J., Clark R.A., Hall J.A., 1999. Long-term changes in the benthos on a
689 heavily fished ground off the NE coast of England. *Marine Ecology Progress Series*
690 188, 13–20.

691 Frid C.L.J., Garwood P.R., Robinson L.A., 2009a. Observing change in a North Sea
692 benthic system: a 33 year time series. *Journal of Marine Systems* 77, 227–236.

693 Frid C.L.J., Garwood P.R., Robinson L.A., 2009b. The North Sea benthic system: a
694 36 year time-series. *Journal of the Marine Biological Association of the UK* 89, 1–10.

695 Gogina M., Darr A., Zettler M.L. (2014) Approach to assess consequences of hypoxia
696 disturbance events for benthic ecosystem functioning. *Journal of Marine Systems* 129,
697 203–213.

698 Gonzalez A., Loreau M., 2009. The causes and consequences of compensatory
699 dynamics in ecological communities. *Annual Review of Ecology, Evolution and*
700 *Systematics* 40, 393–414.

701 Grime J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and
702 founder effects. *Journal of Ecology* 86, 902–910.

703 Hector A., Hautier Y., Saner P., Wacker L., Bagchi R., Joshi J., Scherer-Lorezen M.,
704 Spehn E.M., Bazeley-White E., Weilenmann M., Caldeira M.C., Dimitrakopoulos
705 P.G., Finn J.A., Huss-Danell K., Jumpponen A., Mulder C.P.H., Palmborg C., Pereira
706 J.S., Siamantziouras A.S.D., Terry A.C., Troumbis A.Y., Schmid B., Loreau M.,
707 2010. General stabilizing effects of plant diversity on grassland productivity through
708 population asynchrony and overyielding. *Ecology* 91, 2213–2220.

709 Hiddink J.G., Davies T.W., Perkins M., Machairopoulou M., Neill S.P., 2009. Context
710 dependency of relationships between biodiversity and ecosystem functioning is
711 different for multiple ecosystem functions. *Oikos* 118, 1892–1900.

712 Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H.,
713 Lodge D.M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A.J., Vandermeer
714 J., Wardle D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus
715 of current knowledge. *Ecological Monographs* 75, 3–35.

716 Jennings S., Kaiser M.J., 1998. The effects of fishing on marine ecosystems. In:
717 Blaxter J.H.S., Southward A.J., Tyler P.A., (eds) *Advances in Marine Biology*.
718 Academic Press, London, p 201–352.

719 Jiang L., 2007. Density compensation can cause no effect of biodiversity on
720 ecosystem functioning. *Oikos* 116, 324–334.

721 Kröncke I., Reiss H., Eggleton J.D., Aldridge J., Bergman M.J.N., Cochrane S.,
722 Craeymeersch J.A., Degraer S., Desroy N., Dewarumez J-M., Duineveld G.C.A.,
723 Essink K., Hillewaert H., Lavaleye M.S.S., Moll A., Newring S., Newell R., Oug E.,
724 Pohlmann T., Rachor E., Robertson M., Rumohr H., Schratzberger M., Smith R.,
725 Vanden Berghe E., van Dalfsen J., van Hoey G., Vincx M., Williems W., Rees H.
726 2011. Changes in North Sea macrofauna communities and species distribution
727 between 1986 and 2000. *Estuarine, Coastal and Shelf Science* 94, 1–15.

728 Lavorel S., Garnier E., 2002. Predicting changes in community composition and
729 ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*
730 16, 545–556.

731 Lee S-W., Park S-B., Jeong S-K., Lim K-S., Lee S-H., Trachtenberg M.C., 2010. On
732 carbon dioxide storage based on biomineralization strategies. *Micron* 41, 273–282.

733 Mermillod-Blondin F., Rosenberg R., François-Carcaillet F., Norling K., Mauclair
734 L., 2004. Influence of bioturbation by three benthic infaunal species on microbial
735 communities and biogeochemical processes in marine sediment. *Aquatic Microbial*
736 *Ecology* 36, 271–284.

737 Mouillot D., Villéger S., Scherer-Lorezen M., Mason N.W.H., 2011. Functional
738 structure of biological communities predicts ecosystem multifunctionality. *PloS ONE*
739 6, e17476.

740 Munari, C. 2013. Benthic community and biological trait composition in respect to
741 artificial coastal defence structures: a study case in the northern Adriatic Sea. *Marine*
742 *Environmental Research* 90, 47–54.

743 Naeem S., 1998. Species redundancy and ecosystem reliability. *Conservation Biology*
744 12, 39–45.

- 745 Neumann H., Kröncke I., 2011. The effect of temperature variability on ecological
746 functioning of epifauna in the German Bight. *Marine Ecology* 32, 49–57.
- 747 Norkko A., Villnäs A., Norkko J., Valanko S., Pilditch C., 2013. Size matters:
748 implications of the loss of large individuals for ecosystem function. *Scientific Reports*
749 3, 2646.
- 750 Norling K., Rosenberg R., Hulth S., Grémare A., Bonsdorff E., 2007. Importance of
751 functional biodiversity and species-specific traits of benthic fauna for ecosystem
752 functions in marine sediment. *Marine Ecology Progress Series* 332, 11–23.
- 753 Ólafsson E.B. (1986) Density dependence in suspension-feeding and deposit-feeding
754 populations of the bivalve *Macoma balthica*: a field experiment. *Journal of Animal*
755 *Ecology* 55, 517–526.
- 756 Polley H.W., Wilsey B.J., Derner, J.D., 2003. Do species evenness and plant density
757 influence the magnitude of selection and complementarity effects in annual plant
758 species mixtures? *Ecology Letters* 6, 248–256.
- 759 Ruesink J.L., Srivastava D.S., 2001. Numerical and per capita responses to species
760 loss: mechanisms maintaining ecosystem function in a community of stream insect
761 detritivores. *Oikos* 93, 221–234.
- 762 Ruess L., Schmidt I.K., Michelsen A., Jonasson S., 2001. Manipulations of a
763 microbial based soil food web at two arctic sites — evidence of species redundancy
764 among the nematode fauna? *Applied Soil Ecology* 17, 19–30.
- 765 Solan M., Cardinale B.J., Downing A.L., Engelhardt K.A.M., Ruesink J.L., Srivastava
766 D.S., 2004. Extinction and ecosystem function in the marine benthos. *Science* 306,
767 1177–1180.
- 768 Thrush S.F., Hewitt J.E., Gibbs M., Lundquist C., Norkko A., 2006. Functional role of
769 large organisms in intertidal communities: community effects and ecosystem function.
770 *Ecosystems* 9, 1029–1040.
- 771 Tillin H.M., Hiddink J.G., Jennings S., Kaiser M.J., 2006. Chronic bottom trawling
772 alters the functional composition of benthic invertebrate communities on a sea-basin
773 scale. *Marine Ecology Progress Series* 318, 31–45.
- 774 Townsend C.R., Hildrew A.G., 1994. Species traits in relation to a habitat templet for
775 river systems. *Freshwater Biology* 31, 265–275.
- 776 Veríssimo H., Bremner J., Garcia C., Patrício J., van der Linden P., Marques J.C.,
777 2012. Assessment of the subtidal macrobenthic community functioning of a temperate
778 estuary following environmental restoration. *Ecological Indicators* 23, 312–322.
- 779 Walker BH (1992) Biodiversity and Ecological redundancy. *Conservation Biology* 6,
780 18–23.
- 781 Welsh D.T., 2003. It's a dirty job but someone has to do it: the role of marine benthic
782 macrofauna in organic matter turnover and nutrient recycling to the water column.
783 *Chemistry and Ecology* 19, 321–342.