

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

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Published

2015

Journal Title

Marine Environmental Research

Version

Accepted Manuscript (AM)

DOI

[10.1016/j.marenvres.2015.03.012](https://doi.org/10.1016/j.marenvres.2015.03.012)

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

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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.
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48 **1. Introduction**

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

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

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

78 In the central-western North Sea, two benthic stations (M1 & P) have been sampled
79 annually for over 40 years. The composition of macroinfauna has changed over time
80 at both stations in relation to multiple environmental factors. Quasi-decadal shifts in
81 community structure have been reported at M1 (Frid et al., 2009a); with fluctuations
82 in detrital input and winter temperature apparently destabilising the assemblage
83 (Buchanan & Moore, 1986, Buchanan, 1993). At P, temporal variability appears to
84 have been influenced by heavy trawling activity during the 1980s; evidenced by
85 patterns in taxa abundances (Frid et al., 1999; Frid et al., 2009b) and traits that
86 determine species sensitivity to disturbance (i.e. ‘*response* traits’; *sensu* Lavorel &
87 Garnier, 2002) (Bremner et al., 2003a; Bremner et al., 2005). A recent trait-based
88 analysis, which focussed on the most temporally variable taxa, also suggests that
89 functional delivery at the sites has varied over time; mainly due to changing aggregate
90 density as characteristically dissimilar taxa fluctuated in synchrony (Frid, 2011).

91 Here, temporal variability in the benthos at stations M1 and P was assessed using
92 traditional analysis of taxonomic composition in tandem with biological traits analysis
93 (BTA; Townsend & Hildrew, 1994; Bremner et al., 2003b). For BTA, we focused on
94 the composition of *effect* traits that link macroinfauna to the delivery of key ecological
95 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.

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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

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149 **Table 2.** Six ecological functions performed by macroinfaunal species and the trait
 150 modalities that drive them. References that demonstrate the links between traits and
 151 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
Carbon sequestration	Lifespan	< 1 yrs
	Feeding mode	Suspension feeder ¹
	Sediment reworking mode	Downward conveyor ¹
	Protective structure	Shelled ¹⁰
	Maximum body length	>100 mm ⁹
Food for fish	Lifespan	> 10 yrs
	Maximum body length	10-29 mm, 30-100 mm, 100 mm
	Life zone	Surface, Shallow
Reef-formation	Protective structure	None
	Epibenthic habitat modification	Emergent structure
Sediment heterogeneity	Epibenthic habitat modification	Cast or mound, Burrow ditch/hollow

References: ¹Welsh (2003), ²Norling et al. (2007), ³Braeckman et al. (2010),
⁴Mermillod-Blondin et al. (2004), ⁵Thrush et al. (2006), ⁶Norkko et al. (2013), ⁷Day et al. (1989), ⁸Solan et al. (2004), ⁹Brown et al. (2004), ¹⁰Lee et al. (2010)

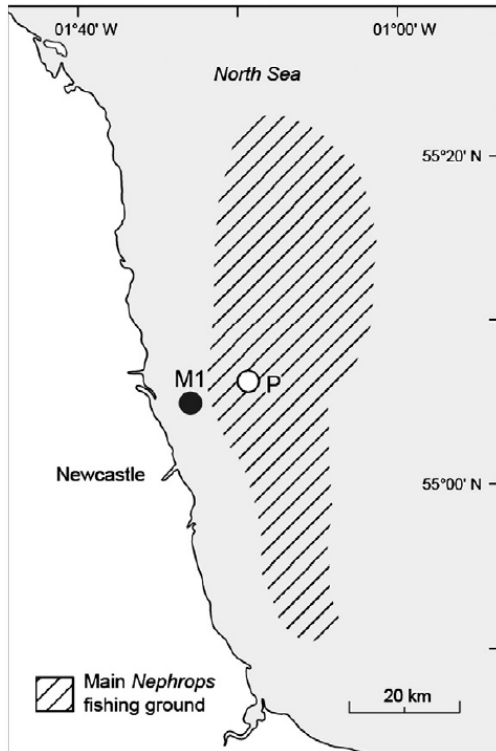
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154 **2. Materials and methods**

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.



163
 164 **Fig. 1.** Location of Dove stations M1 and P in relation to the grounds of a *Nephrops* fishery in
 165 the central-western North Sea.

166

167 *2.2. Benthic time series*

168 Sampling of benthic macroinfauna began in January 1971 at P and September 1972 at
 169 M1. Subsequently data have been collected once a year in January/February at P and
 170 twice a year in March/April (spring) and September/October (autumn) at M1. In this
 171 study we consider two time series: one consisting of samples collected at M1 in spring
 172 and the other consisting of all samples collected at P. Data are missing for 1977 and
 173 1998 at P and for 1998 and 2004 at M1, as weather conditions and/or operational
 174 constraints prevented sampling.

175 Samples were extracted using Van Veen grabs (0.1 m²). Each sample was sieved over
 176 0.5 mm mesh and the residue fixed with 4% buffered formalin. Organisms were
 177 identified to the lowest taxonomic level possible and enumerated. Sampling methods
 178 are described in detail in Buchanan & Warwick (1974). Information on sampling
 179 effort over time is provided in the online supplementary material (Appendix 1).

180

181 *2.3. Assembling community datasets*

182 *2.3.1. Taxonomic composition*

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

189 Previous trait analyses of the Dove benthic time series have used subsets of the
 190 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.

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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.

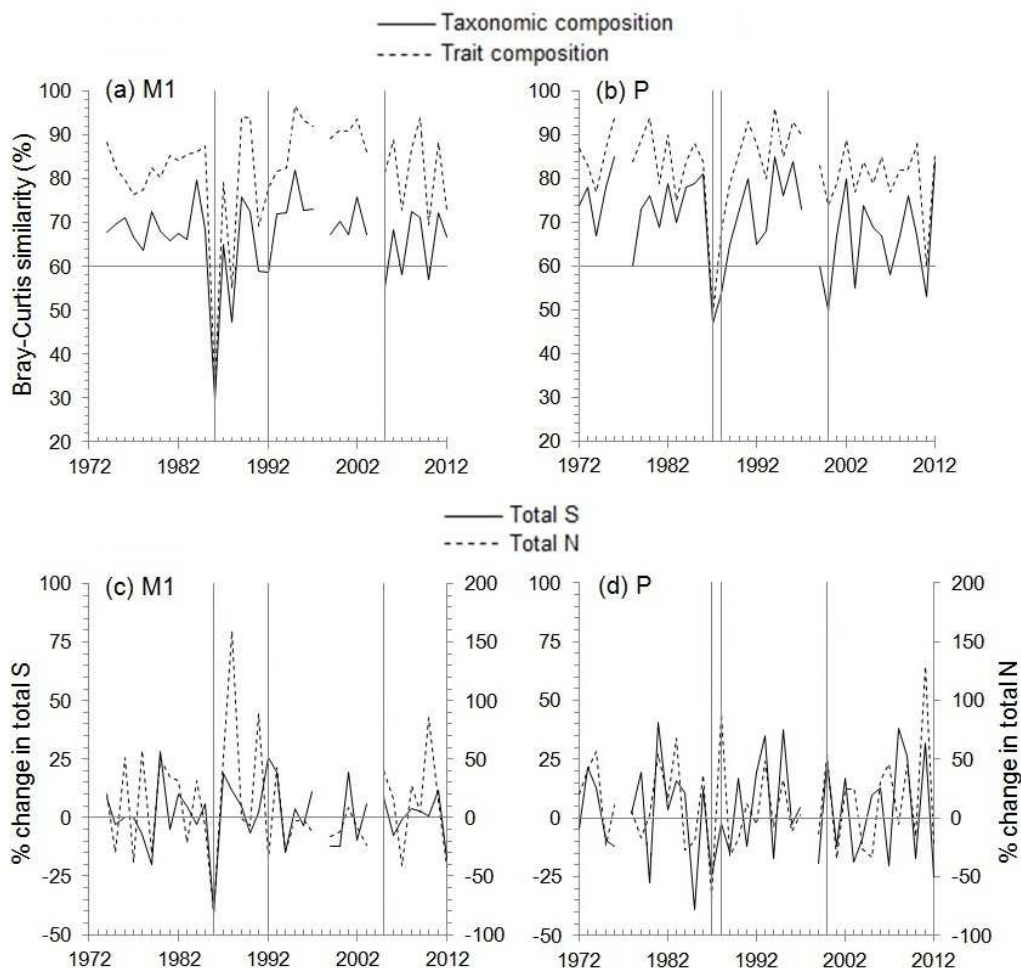
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274 **3. Results**

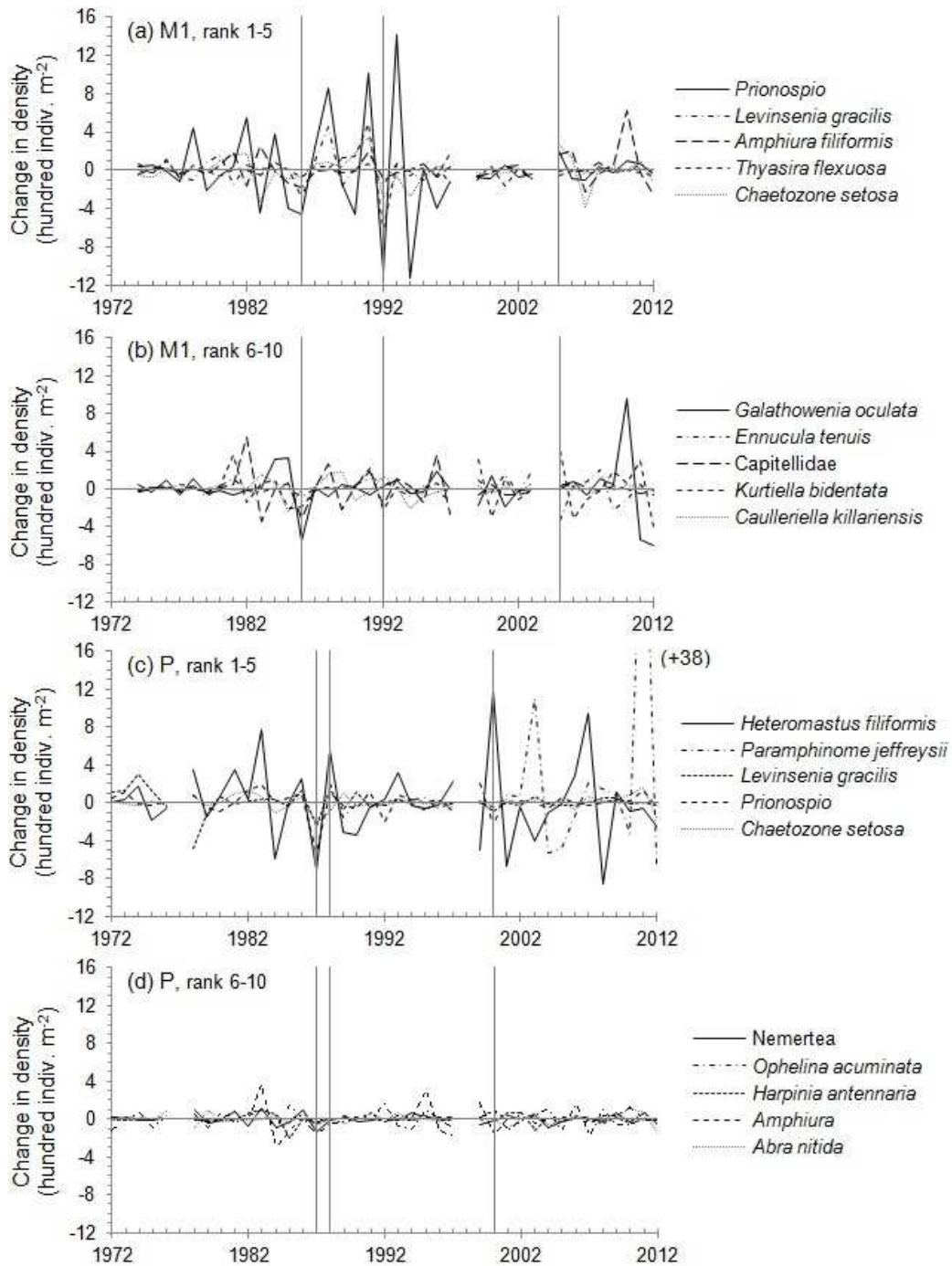
275 *3.1. Station M1*

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



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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.

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317 While acknowledging that, had it been available, the inclusion of 2004 data might
 318 affect the designation of 2005 as a break point, the time series was divided into four
 319 periods with respect to the three apparently abrupt changes in taxonomic composition:
 320 1973-1985, 1986-1991, 1992-2003 and 2005-12. During 1986-91 there were short-
 321 term fluctuations in taxonomic composition (1986, 1988 and 1991 were all < 60%
 322 similar to preceding years; Fig. 2a), while trait composition fluctuated from 1986-88
 323 (1986 and 1988 were < 60% similar to preceding years) but remained relatively stable
 324 between the years 1989-91 (all were \geq 60% similar to preceding years; Fig. 2a). The
 325 periods 1973-85 and 1992-2003 were characterised by taxonomic and functional
 326 stability (all years were \geq 60% and $>$ 75% similar to the preceding year for taxonomic
 327 and trait compositions, respectively; Fig. 2a). Temporal variability increased again
 328 during 2005-12, with multiple years showing < 60% similarity to the preceding year
 329 in taxonomic composition, while year-to-year similarity in trait composition dropped
 330 to below 75% in 2007 (for the first time since 1992) and again in 2009 and 2012 (Fig.
 331 2a).

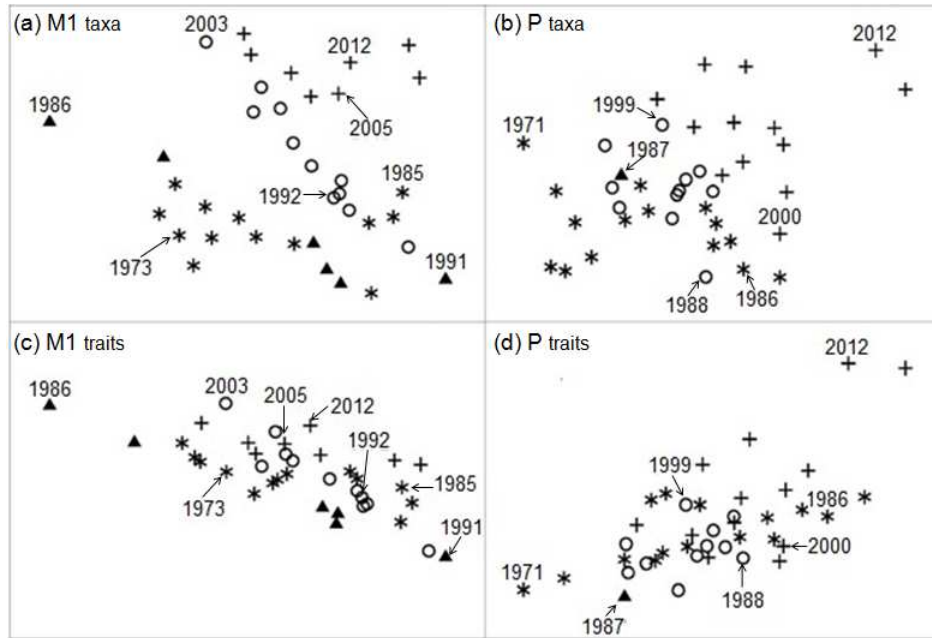
332 Taxonomic composition was significantly different across all periods (Table 3; Fig.
 333 4a), while only 1986-91 differed significantly from other periods in terms of trait
 334 composition (Table 3; Fig. 4c). Total S was significantly lower during 1986-91
 335 compared to other periods (Table 3; Fig. 5a); however, there were no significant
 336 differences in total N (Table 3; Fig. 5c). Compositional changes were therefore driven
 337 by shifts in relative taxa abundances, with substitutions of characteristically dissimilar
 338 taxa occurring during 1986-91 – when the community was relatively species-poor –
 339 and substitutions of similar taxa (functional compensation) occurring across other
 340 periods.

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 342

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

		1973-85	1973-85	1973-85	1986-91	1986-91	1992-2003
	<i>P</i>	vs.	vs.	vs.	vs.	vs.	vs.
		1986-91	1992-2003	2005-12	1992-2003	2005-12	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	-	-	-	-	-	-

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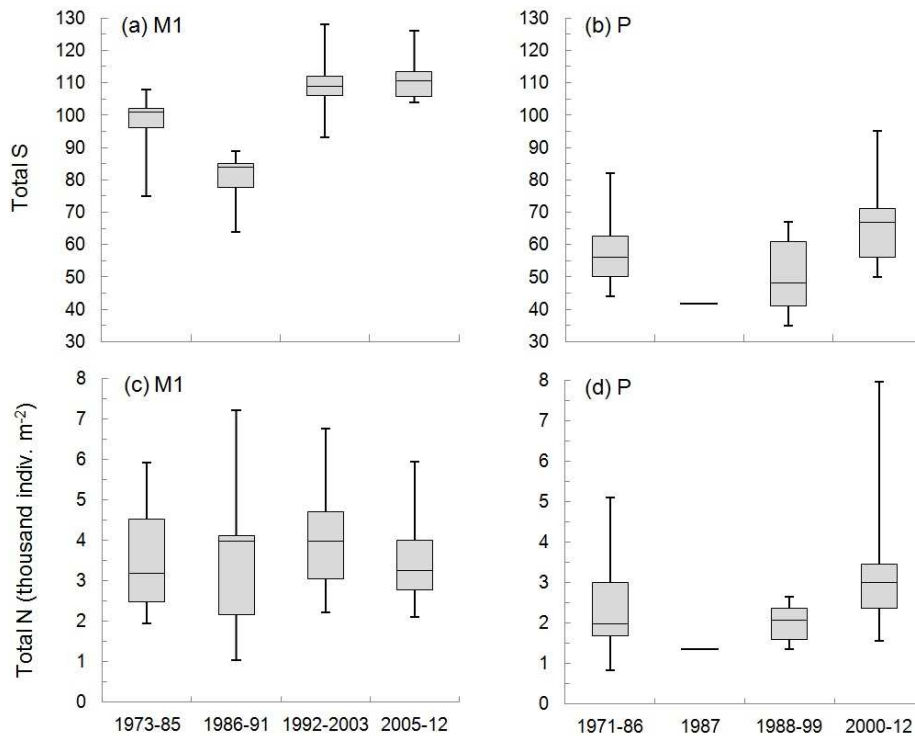


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350 **Fig. 4:** nMDS ordinations of temporal variation in taxonomic composition (a, b) and trait
 351 composition (c, d) of macroinfauna at Dove stations M1 (a, c) and P (b, d). Periods are
 352 divided by abrupt changes in taxonomic composition (see Fig. 2): 1973-85*, 1986-91▲,
 353 1992-2003○ and 2005-12+ for M1; 1971-86*, 1987▲, 1988-99○ and 2000-12+ for P.
 354 First and last years of periods are labelled. 2D stress = 0.16 (a), 0.13 (b), 0.04 (c) & 0.04 (d).

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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).

361 No individual modalities identified by SIMPER (using untransformed data) emerged
 362 as clear drivers of changes to trait composition during 1986-91 ($p > 0.05$; Table 4).
 363 This was due to high within-period variation in these modalities, which were each
 364 among the most commonly exhibited by the taxa (Appendix 2). Using transformed
 365 modality data, two of the six modalities identified (sediment regenerator and < 1 yrs
 366 lifespan) occurred at significantly different densities in 1986-91 compared to other
 367 periods (Table 4). Declines in these modalities during 1986-91 predict reduced rates
 368 of nutrient regeneration and carbon turnover, respectively (Table 2).
 369

370 **Table 4.** Differences in the number of individuals exhibiting twelve trait modalities in 1986-
 371 91 compared to other periods at Dove station M1. The analysed modalities were identified as
 372 top contributors to compositional dissimilarity using untransformed data (above double-
 373 border) and $\ln(x+1)$ transformed data (below double-border). Significant differences ($p <$
 374 0.05) are in bold. Changes to mean density are presented for modalities that differed
 375 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	-	-	-

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378 3.2. Station P

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

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

394 in 1987 (by 25% and 70%, respectively; Fig. 2d), as did the densities of dominant taxa
395 (nine declined and one remained stable; Fig. 3c,d); indicating an uncompensated
396 collapse of populations and associated functions. Total N recovered somewhat in
397 1988 (90% increase; Fig. 2d), as four of the five dominant taxa increased in numbers
398 (including the first recording of *Paramphinome jeffreysii* (McIntosh); *Chaetozone*
399 *setosa* (Malmgren) decreased in numbers) and the remainder of the top ten remained
400 stable (Fig. 3c,d). Total S, on the other hand, declined by just 2% (Fig. 2d) and trait
401 composition in 1988 was 68% similar to 1987 (Fig. 2b). In 2000 there was evidence
402 for functional compensation, as trait composition remained 75% similar to 1999 (Fig.
403 2b) and dominant taxa showed mixed responses (three decreased, two increased and
404 five remained stable; Fig. 3c,d). From 1999 to 2000 total S and total N increased by
405 25% and 55%, respectively (Fig. 2d).

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

416 Trait composition did not differ significantly between 1971-86 and 1988-99, but both
417 were significantly different to 2000-12 (Table 5; Fig. 4d). Taxonomic composition, on
418 the other hand, differed significantly across all periods (Table 5; Fig. 4b). The
419 collapse of populations and associated functions in 1987 was therefore quickly
420 reversed as a new species assemblage emerged during 1988-99. During 2000-12, there
421 was a significant increase in total S and total N compared to 1987-99 (Table 5; Fig.
422 5b,d); indicating that changes to trait composition across these periods resulted at least
423 partly from increased aggregate density, as the assemblage became relatively species-
424 rich.

425 Multiple modalities explained changes to trait composition during 2000-12. Of the top
426 six contributors to compositional dissimilarity, five increased significantly during
427 2000-12 compared to 1988-99 and three increased significantly compared to 1971-86
428 (Table 6). Only deposit feeding showed no significant variation across periods. Using
429 transformed data, six different modalities emerged as the top contributors to
430 compositional dissimilarity. Five of these increased significantly during 2000-12
431 compared to both other periods (Table 6). No significant differences were observed
432 only for animals with > 10 yrs lifespan. Increases in the densities of these modalities
433 predict enhanced rates of nutrient regeneration, carbon sequestration and turnover,
434 and increased availability of food for fish, during 2000-12 (Table 2).

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

	<i>P</i>	1971-86	1971-86	1971-86	1987	1987	1988-99
		vs. 1987	vs. 1988-99	vs. 2000-12	vs. 1988-99	vs. 2000-12	vs. 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

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449 **Table 6.** Differences in the number of individuals exhibiting twelve trait modalities in 2000-
 450 12 compared to other periods at Dove station P. The analysed modalities were identified as
 451 top contributors to compositional dissimilarity using untransformed data (above double-
 452 border) and $\ln(x+1)$ transformed data (below double-border). Significant differences ($p <$
 453 0.05) are in bold. Changes to mean density are presented for modalities that differed
 454 significantly across periods. The modalities '10-29 mm' and '< 1 yrs' were \ln transformed
 455 prior to analysis to meet the assumption of homogenous variance. See Table 1 for list of traits
 456 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

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467 **4. Discussion**

468 Previous analyses of the Dove benthic time-series show long-term variation in
469 taxonomic composition (Frid et al., 2009a, b); with natural and anthropogenic factors
470 apparently influencing community dynamics (Buchanan & Moore, 1986; Buchanan,
471 1993; Frid et al., 1999; Bremner et al., 2003a; Bremner et al., 2005; Frid et al., 2009a,
472 b). Using established associations between species traits and key ecological functions;
473 we applied biological traits analysis (BTA; Bremner et al., 2003b) and found *effect*
474 trait composition (*sensu* Lavorel & Garnier, 2002) to be statistically indistinguishable
475 across periods that experienced significant changes to taxonomic composition at
476 stations M1 and P (Fig. 4; Tables 3 & 5). Periods of significantly altered trait
477 composition did, however, occur at both stations (Fig. 4; Tables 3 & 5). We infer that
478 density compensation by characteristically similar (redundant) taxa acted to buffer
479 changes to ecological functioning over time (*sensu* Naeem, 1998), but that
480 substitutions of dissimilar taxa and uncompensated population fluctuations caused
481 temporary disruptions to functioning.

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

498 Our results are largely consistent with other studies that have applied BTA to assess
499 temporal variability in the functioning of benthic communities. Veríssimo et al.,
500 (2012) analysed changes in the subtidal macroinfauna before and after the
501 environmental restoration of a Portuguese estuary. They found that, despite shifts in
502 taxonomic composition, trait composition either persisted or changed and recovered
503 during the five-year study period at each of 15 sites. Similar patterns of functional
504 change and recovery have been reported for epifauna responding to a cold winter in
505 the German Bight (Neumann & Kröncke, 2011) and macroinfauna responding to
506 hypoxia events over a 19-year period at a site in the south-western Baltic Sea (Gogina
507 et al., 2014). Benthic invertebrate communities have also been shown to exhibit a
508 level of seasonal stability in trait expression, despite taxonomic composition being
509 highly variable on this timescale (Beche et al., 2006; Munari, 2013); while recent
510 analyses suggest that similar patterns emerge across millennia (Caswell & Frid, 2013;
511 Frid & Caswell, in press). Substitutions of characteristically similar benthic species
512 may therefore occur widely and across multiple temporal scales; thus acting to
513 conserve ecological functioning.

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

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

528 We found that alterations to *effect* trait composition occurred when taxonomic
529 composition shifted at approximately the same time at both stations (1986 at M1 and
530 1987 at P; Fig. 2a,b). This event coincided with the North Sea climatic regime shift
531 (Beaugrand, 2004), and therefore the implied alteration to benthic functioning may
532 have been driven by broad-scale hydro-climatic forcing or the associated changes to
533 the North Sea ecosystem. For example, community composition of the plankton
534 changed around this time (Beaugrand, 2004) and detrital flux to the seabed
535 surrounding the stations was estimated to be particularly low in 1986 (see Buchanan,
536 1993; a one-year lag between community trends at M1 and P has been suggested by
537 Buchanan (pers. comm.) to result from differences in the depth and hydrodynamics at
538 the two sites). Given that deposit feeders dominate at both sites, it is plausible that
539 such changes to the quantity and, possibly, quality of detrital food supply caused the
540 large, uncompensated declines in species populations and the ecological functions
541 they deliver. This result suggests that climatic variability can cause temporary
542 changes to benthic functioning, even within systems exhibiting long-term functional
543 stability; a finding that echoes the results of Neumann & Kröncke (2011).

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

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

565 occur; thus impairing the delivery of ecological functions, as argued by Naeem
566 (1998). Substitutions of characteristically dissimilar taxa did, however, maintain the
567 same aggregate density during 1986-91 as the preceding period. The association
568 between species sensitivity and functional characteristics (a major determinant of the
569 ecological consequences of species extinction; Solan et al., 2004) therefore appears to
570 vary over time and, possibly, with respect to the drivers of ecological change.

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

587 In applying BTA, we assumed that the characteristics and density of a species
588 determine its functional potential. While these assumptions are empirically supported
589 (Chapin et al., 1997), it should be noted that species can show plasticity in trait
590 expression with respect to physical habitat (Ólafsson, 1986), levels of disturbance
591 (Cesar & Frid, 2012) and potentially many other environmental conditions. We used
592 fuzzy coding of traits to address this issue (Chevenet et al., 1994), but this reduces
593 specificity; making it possible that temporal changes to trait composition were
594 underestimated as a result. Our results therefore represent a conservative estimate of
595 functional change over time. Furthermore, the degree to which species drive
596 functioning may also vary with respect to environmental context (Hiddink et al.,
597 2009) or the nature of interspecific interactions; i.e. facilitative (Cardinale et al., 2002)
598 or antagonistic (Polley et al., 2003). This issue will need to be resolved if we are to
599 progress from inferring changes to functional potential and use species traits to
600 accurately predict levels of functional delivery across a range of biotic and abiotic
601 conditions.

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603 **5. Conclusions**

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

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612

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

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