

1 IS LONG-TERM ECOLOGICAL FUNCTIONING STABLE: 2 THE CASE OF THE MARINE BENTHOS?

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7 C.L.J. Frid* and B.A. Caswell

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10 School of Environmental Sciences, University of Liverpool, Liverpool, L69
11 3GP, UK.

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13 *Email: cljfrid@liverpool.ac.uk, Tel: +441517954382.
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16 17 18 **ABSTRACT**

19
20 It is widely acknowledged that human activities are contributing to substantial
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22 biodiversity loss and that this threatens ecological processes underpinning
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24 human exploitation of 'ecosystem services' (defined by the Millennium
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26 Ecosystem Assessment as 'the benefits people obtain from ecosystems'). In
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28 the present study we consider three 'intermediate ecosystem services' in both
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30 contemporary and ancient marine systems and although 'ecosystem services'
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32 per se did not exist in the Jurassic our study seeks to consider the future
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34 provision of these services and so the term is retained. We consider the
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36 temporal patterns in benthic marine ecosystems: (1) spanning four decades at
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38 two offshore stations in the North Sea, UK; and (2) over millennial scales in
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40 Late Jurassic UK palaeocommunities. Biological traits analysis is used to link
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42 changes in taxonomic composition to variations in ecological functioning and
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44 the potential supply of three 'intermediate' ecosystem services: the ability to
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46 provide food to fish and other predators, benthic nutrient regeneration and
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48 carbon cycling. We examine whether changes in taxonomic composition drive
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50 temporal variation in functioning, whether this variation increases over time
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52 and the extent to which species turnover is comparable in contemporary and
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29 ancient systems. Taxonomic variability was of a similar magnitude in all three
30 systems and there was evidence for changes in functioning linked to changes
31 in several (key or rivet) taxa. During other periods resilience maintained
32 functioning in the face of taxonomic change. These results suggest that in
33 these benthic systems the Biodiversity–Ecosystem Functioning relationship is
34 idiosyncratic, but a degree of temporal stability in functioning is maintained
35 such that the ecosystem services they underpin would also be stable during
36 decadal and longer-term changes.

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

41 **INTRODUCTION**

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

50 Biodiversity loss is predicted to continue to increase (Cheung et al., 2009,
51 Perreira et al., 2010) for example, the bioclimate envelope models of Cheung
52 et al. (2009) predict a 60% turnover of marine biodiversity from present levels
53 by 2050. Biodiversity loss has severe impacts on the way that ecosystems

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function (e.g. Cardinale et al., 2012) and thus is often cited as a significant threat to the delivery of the ecosystem services that underly human well-being and livelihoods (United Nations, 2005). Marine ecosystems provide many important ecosystem services such as providing ~15% of our dietary animal protein, natural sea defences, waste treatment and recreational services and high diversity systems consistently provide more ecosystem services with less variability in delivery (Worm et al., 2006, Beaumont et al., 2007).

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

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78 simple relationship between the time since restoration and the recovery of
79 functioning and therefore ecosystem service provision by the oyster reefs.
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81 The biological processes associated with sea floor ecosystems contribute to a
82 number of important ecological functions and in turn key ecosystem services,
83 including food production (fish and shellfish), genetic resources (including
84 pharmaceutically active compounds), climate regulation, natural hazard
85 protection, and maintenance of water and sediment quality (Beaumont et al.,
86 2007). It is becoming increasingly clear that biodiversity underpins a range of
87 critical ecosystem services and that changes in the composition and
88 abundance of species, genes and habitats can have effects ranging from
89 small scale (local) to major, cascading, impacts on global processes, such as
90 the biogeochemical cycles of nutrients and carbon (Naeem et al., 2012).
91 Understanding the effects of these biodiversity changes requires both the
92 classic reductionist experimental approaches to understanding the biodiversity
93 – ecosystem function relationships and large scale (temporal and spatial)
94 investigation of patterns of ecological and functional change (Raffaelli and
95 White, 2013).
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97 While populations show spatial and temporal variability in their abundance
98 such that communities appear to undergo changes over time, if the net result
99 of these changes is that individuals of one taxa are substituted (in the simplest
100 terms) by those of another species with similar biological attributes the impact
101 of this species turnover on the functioning of the system may be small. This
102 extension of the ‘redundancy model’ of Biodiversity-Ecosystem Functioning

103 (BEF; Walker, 1992) leads us to propose the following hypotheses; (i)
104 ecosystem functioning will show less temporal variation than species
105 composition, and (ii) that longer time series will show greater variation in
106 functional composition than short time series. Furthermore, we can ask
107 whether the degree of species level change that does cause a change in
108 functioning is similar in contemporary communities to those in the deep past.
109 We examine these three assertions by drawing on two recent studies
110 (Caswell and Frid, 2013; Frid, 2011) that have considered the temporal
111 variations in ecosystem functioning to understand the potential of benthic
112 systems to deliver ecosystem services in the face of long-term variations in
113 the environment. We consider data for a contemporary shelf sea system in
114 which species composition is known to vary on decadal and inter-annual time
115 scales in response to varying food input, and a palaeocommunity from a shelf
116 sea ecosystem subject to fluctuating periods of deoxygenation. Gogina et al.
117 (2014) have shown that contemporary benthic systems subject to hypoxia
118 have reduced diversity and they hypothesised, but were unable to confirm that
119 this led to a decreased ability of the system to maintain functioning through
120 compensatory mechanisms. Here we consider derived measures of ecological
121 functioning and proxies for 'intermediate ecosystem services', where
122 intermediate services are benefits derived from the ecosystem but which are
123 not directly traded in a market (sensu Norris, 2012), so 'food for fish'
124 underpins the 'final' service of food (fish) production.

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125 METHODS

126 ***Decadal Scale Change: The Dove Benthic time series***

127 Three multi-decadal time-series are collected off the northeast coast of
128 England in the central-west North Sea (Clark and Frid, 2001; Fig. 1a-b).
129 Originally established by staff from the University of Newcastle's Dove Marine
130 Laboratory, data collection continues using the same methods as when the
131 time series commenced (Clark and Frid, 2001). One series considers
132 mesozooplankton and is not considered further. The other series are of
133 benthic macrofauna at two offshore stations located in areas away from local
134 river discharges.

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

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147 The second station M1 (55° 07' N, 01° 20' W) lies some 10.5 km off of the
148 Northumberland coast (Fig. 1b). The station has a predominantly sandy
149 sediment, with a 20% silt-clay content and lies in 55 m of water (Frid et al.,
150 1996, Frid et al., 1999). Benthic sampling commenced in September 1972

151 and the dataset analysed here covers samples taken in March of each year
152 between September 1973 and 2005. No samples were collected, due to
153 weather or operational constraints, in March 1998.

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

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

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170 For multivariate analyses of community composition the dataset was reduced
171 to make computation manageable and reduce any influence of very rare or
172 under-sampled taxa. For the more diverse M1 station, only those genera
173 representing more than 0.1% of the individuals recorded (i.e. more than 15
174 individuals found during the entire survey period) were included in these
175 analyses, leaving 89 genera in the ordination at M1. At station P the original

176 dataset included 262 taxa, which was reduced to 173 genera (or higher taxa)
177 all of which were included. For multivariate analyses of the community
178 composition the dataset was transformed (Log (x+1)) to reduce the influence
179 of common taxa.

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

181 The palaeocommunity data comprise the benthic species composition and
182 abundance data (number, expressed as percentage, per 0.2 m³ of rock
183 sampled) collected by Wignall (1989, 1990) from coastal exposures of the
184 Kimmeridge Clay Formation (KCF), Kimmeridge, UK (Fig. 1a and c). Wignall
185 (1990) classified these data into 21 unique associations, hereafter refer to as
186 palaeocommunities. The 21 palaeocommunities spanned between 0.05 m–
187 24.4 m of vertical rock and had an average thickness of 0.90 m equivalent to
188 an average temporal duration of ~7000 years based on the cyclostratigraphic
189 timescale of Weedon et al. (2004).

190
191 The links between changes in the palaeoenvironment and benthic community
192 functioning were investigated using geochemical proxy data, measured from
193 bulk rock samples, collected from the KCF exposed on the coast (i.e. the
194 same facies as those from which the palaeontological data were collected)
195 and two nearby boreholes sections (Fig. 1a and c). The KCF represents the
196 longest period (~8 million years; Weedon et al., 2004) of organic carbon
197 accumulation during the Mesozoic (Jenkyns et al., 2002) although not the
198 most severe (cf. Caswell and Coe, 2013), and was deposited under
199 fluctuating levels of oxygenation (Pearce et al., 2010) that ranged from

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200 hypoxic (low dissolved oxygen, 1-30% of saturation) to anoxic (the absence of
201 oxygen) to euxinic (oxygen absent and toxic H₂S present).

202 ***Biological traits and ecosystem functioning***

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

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215 For the Dove Benthic Series five trait categories (size, trophic role, burrow
216 depth, bioturbation capacity, and longevity) (Table 1) were used. For each
217 taxa identified, by SIMPER, as being a major contributor to the between
218 period shifts in assemblage composition the biological traits profile was
219 determined (Frid, 2011). Trait information was derived from the University of
220 Liverpool's trait database (Frid et al. unpub.), the BIOTIC database
221 maintained by the Marine Biological Association UK
222 (<http://www.marlin.ac.uk/biotic/>) and by targeted literature searches to fill
223 any gaps.

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225 For the Kimmeridge Clay Formation eight biological traits were selected to
226 represent aspects of the organisms morphology, life habit, feeding patterns
227 and life histories (Table 2). Each trait comprised five modalities, except for
228 *sociability* that comprised only three (Table 2). This assignment was based on
229 published accounts of the palaeobiology of each species and information from
230 The Treatise of Invertebrate Palaeontology (Geological Society of America
231 Inc., 1953-2009), The Palaeobiology Database (<http://palaeodb.org>), and for
232 extant taxa the BIOTIC database (<http://www.marlin.ac.uk/biotic/>). When
233 information was not available at the species level data used were based on
234 accounts of other members of the genera or, more rarely, the family. When no
235 information on a particular trait was available for a taxon, zero values were
236 entered for each category and, therefore, the taxon did not contribute to the
237 trait weightings.

238
239 The frequency of each trait modality in the two datasets was calculated by
240 weighting the category scores by the abundance of each taxon exhibiting that
241 modality (Charvet et al., 1998). This resulted in a sample by trait table
242 showing the abundance of biological traits for each palaeocommunity/
243 assemblage over the interval studied.

244
245 The composition of the assemblage in terms of the abundance of each of the
246 trait modalities (Table 1, Table 2) present was analyzed for all the scored
247 traits by non-metric MDS and then for combinations of traits that mapped on
248 to the principle intermediate ecosystem services carbon cycling, provision of
249 food for fish and nutrient cycling/regeneration. The traits were deemed to be

1 250 associated with ecological functions (Frid et al., 2008), and the ecological
2 251 functions in turn were deemed to support intermediate ecosystem service
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4 252 provision (Hussain et al., 2010). For example, ecological processes that
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6 253 contribute to sediment turnover are assumed to underpin organic matter
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8 254 breakdown and nutrient regeneration. The intermediate ecosystem service,
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10 255 nutrient regeneration, in the modern ocean underpins our use of the seas as a
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12 256 repository and treatment option for organic waste. High carbon cycling was
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14 257 associated with small body size and thus short longevity, high value as a food
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16 258 source for fish with a large body size, and a surface or shallow burrowing
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18 259 habit whilst nutrient cycling/regeneration was indexed by high or moderate
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20 260 bioturbation, deep burrowing and a deposit feeding habit.
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30 262 Similarity between each pair of palaeocommunities was calculated using the
31 263 Bray-Curtis index (after a log (x+1) transformation of the abundance data to
32 264 reduce the influence of dominant species) and a dendrogram of similarity of
33 265 species composition of the palaeocommunities was produced. All multivariate
34 266 analyses were carried out using the statistical software PRIMER v. 6
35 267 (PRIMER-e, Plymouth, UK; Clarke and Warwick 1994) and univariate
36 268 comparisons were made using SPSS v. 20 (IBM, Ltd).
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47 269 **RESULTS**

48 270 The species composition and ecology of the three systems has been
49 271 described extensively elsewhere (see Frid, 2011, Frid et al., 2009b, Frid et al.,
50 272 2009a and references therein) but the following summary is offered to provide
51 273 context for the subsequent analyses and their interpretation. A total of 516
52 274 taxa, from 327 genera, have been recorded at the Dove benthic station
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275 M1(Frid et al., 2009b). The macro-infaunal assemblage may be considered a
276 variant of the classical Petersen *Amphiura filiformis* benthic community
277 (Petersen, 1913), except that it is often dominated by small-bodied
278 polychaetes with *Prionospio fallax* (Söderström) being the top-ranked species
279 in most years (Table 3; Frid et al., 1996). During the period 1973–2005, the
280 total abundance of infauna at M1 in March, the seasonal low, averaged 380
281 individuals per 0.1m⁻² (Table 3; range 104–720 per 0.1m⁻²) whilst genera
282 richness ranged from 63–124 genera (with a mean of 94). Throughout the
283 time-series the top ten genera, comprised four taxa of polychaete worms, one
284 phoronid worm, four bivalve molluscs and one brittlestar and together
285 accounted for approximately 43% of all the individuals observed (Table 3).

286
287 At the Dove benthic station P, the ten most abundant genera accounted for
288 ~70% of the individuals present, and in total 173 genera (or higher taxa) were
289 recorded (Table 3). The polychaete *Heteromastus* accounted for nearly 30%
290 of all the individuals recorded in the time series, and over the 36 year period
291 *Heteromastus* was the dominant taxon every year except between 1973 and
292 1977 when the polychaete *Levinsenia* was dominant. Although polychaetes
293 dominated the benthos, the top ten taxa also included nemerteans, an
294 amphipod, a bivalve mollusc and an ophiuroid (Table 3).

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296 The KCF assemblage included a total of 99 taxa, mostly true species, with
297 taxa richness of individual assemblages varying between seven and 42. The
298 dominant taxa were bivalve molluscs, followed by gastropods, and
299 brachiopods (Table 4). The bivalves *Protocardia morinica*, *Isocyprina*

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300 *minuscula* and *Corbulomima suprajuresnis* accounted for ~70% of all
301 specimens found (Table 4) and together dominated 16 of the 21
302 palaeocommunities. The species composition of two assemblages (E6 and
303 E9) were highly distinct (Bray-Curtis similarity <5%) from each other and all
304 the other samples and so were omitted from the cluster analysis and
305 ordinations of the taxonomic composition because they were sufficiently
306 distinct as to cause the remaining samples to ordinate in one tight cluster
307 making it impossible to distinguish patterns.

308 ***Ecosystem functioning will show less temporal variation than species***
309 ***composition***

310 The species composition at station M1 showed a high degree of consistency
311 between years with successive years (i.e. 1972 to 1973) having a Bray-Curtis
312 similarity of >80% (Fig. 2a). The exceptions to this pattern have been used to
313 define periods of change in species composition and generally resulted in a
314 shift to a 'new configuration' of species in the assemblage that persisted for a
315 number of years before undergoing a further shift. These patterns were
316 observable from both the pairwise similarities (Fig. 2a) and the non-Metric
317 Multidimensional Scaling ordinations (nMDS; Fig. 3a). For the station M1
318 samples collected in March there were four main taxonomic groups (with a
319 Bray-Curtis similarity >77%; Figs 2a and 3a) these were 1973-1985, 1986-87,
320 1988-1991, and 1992-2005. There were more minor shifts between 1997-
321 1999 (1998 missing) and between 2002-2003 (Fig. 2a).

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323 At station P Bray-Curtis similarity between successive years was generally
324 >70% (Fig. 2c) except, as at M1, when the system under went a 'shift'
325 suggesting that the composition of species in the assemblage was quasi-

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326 stable for a number of years before undergoing a change to a new
327 configuration of species. This pattern is visible from both the pairwise
328 similarities (Fig. 2c) and the nMDS ordinations (Fig. 3c). At station P the
329 'stable' periods with Bray-Curtis similarity > 69% (Fig. 2c and 3c were 1971-
330 81 (plus 1987), 1982-1986, 1989-1991, 1992-1999 and 2000-2006 (1988 was
331 an outlier).

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333 At both station M1 and P the species composition of the macro-infaunal
334 community exhibited periods of relatively high stability (Bray-Curtis similarity
335 >~70%) in species composition that persisted for 4-14 years and then shifted
336 to a different species composition. At station M1 the trait composition is more
337 variable than the species composition with four groups being defined by a
338 Bray-Curtis similarity of 70% (cf. 77% for taxonomy, Figs 2b and 3b) and with
339 less congruency with the temporal separation of samples. At station P five
340 groups of years (~65% similar, Fig. 2c) and a singleton with distinct taxonomic
341 composition occur and for trait composition four groups and a singleton were
342 identified (~75% similar, Fig. 2d). However, the temporal structure evident in
343 the taxonomic clustering is not repeated in the trait composition based
344 analysis (cf. Figs 2d and 3d). For example, the species composition at Station
345 P was similar during 1982-86 (Figs 2a and 3a) whereas the trait composition
346 for the same period differs (Figs 2b and 3b). The trait composition shows
347 1982, 1984 and 1986 clustered together but 1983 and 1985 occurred in
348 different clusters to each other and the other three years (cf. Figs 2c and 2d).
349 Such patterns suggest that while changes in species composition were often
350 minor, in terms of species abundance patterns, species changes often

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351 resulted in certain trait modalities disappearing from or appearing in the
352 assemblage.
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354 The Bray-Curtis similarity in species composition between the 21 KCF
355 palaeocommunities was lower than the similarity between the contemporary
356 communities at stations M1 and P, from the successive years, and Bray-
357 Curtis similarity was generally >60% between the KCF samples compared to
358 ~70% in the two contemporary series. With the most extreme outliers (E6 and
359 E9) excluded the palaeocommunities formed three distinct groups that were
360 60% similar (A/E1, B1-B3; E2a and E5; B4, E2e, E4, and E7; and A1, E1a,
361 E1b, E2b, E2c, E3 with E8 being an outlier; Fig. 2d), these groupings were
362 less apparent in the nMDS ordination (Fig. 3d). The trait composition of the
363 21 palaeocommunities (NB all palaeocommunities included) had a Bray-Curtis
364 similarity of 45% and delimited three groups and two singletons (Fig. 2f). As
365 was found for the contemporary communities the grouping of
366 palaeocommunities by trait composition showed little similarity to that for the
367 taxonomic composition. For example, the two extreme outliers in the
368 taxonomic analysis (E6 and E9) ordinated in the largest cluster of trait
369 composition (Fig. 3e-f) while palaeocommunities A1 and B5, which had been
370 nested within groups in the taxonomic analysis, formed the singletons in the
371 traits based analysis (Fig. 2e-f).
372
373 The main influence on the taxonomic composition of the two Dove time series
374 appears to be temporal with shifts in community composition occurring at,
375 approximately, decadal intervals with a major shift occurring in the late 1980's

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376 at both sites (Figs 3a and c). In the KCF data the main effect on taxonomic
377 composition is the separation of sites with high total organic carbon (TOC;
378 E1a, E2d, E2e, E4, E5, E6 and E9), indicative of deoxygenation, from the
379 remainder (Figs 3e–f). Ordinations of the biological traits composition for the
380 Dove time series (Figs 3b, d and f) showed samples were spread in a band
381 across the centre of the ordination space (suggesting a trend rather than step
382 wise changes). In comparison the KCF trait composition of the
383 palaeocommunities from the deoxygenated periods (as indexed by TOC)
384 differed significantly from the others (Pair wise ANOSIM, $R = 0.449$, $p =$
385 0.001).

386
387 In all three data sets the degree of variation in taxonomic composition and
388 trait composition was similar (Fig. 2). However, it is also apparent that the
389 variation in trait composition was not simply a reflection of the changing
390 taxonomic composition, as in each case the patterns observed from cluster
391 analysis were distinct from each other (Figs 2 and 3).

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

394 In both of the Dove series the decadal scale shifts in taxonomic composition
395 suggest that longer time series show greater total variation in taxonomic
396 composition than shorter time series. However, the intermingling of samples
397 from across the time periods in the ordinations of trait composition (Figs 3 b
398 and d) points to the existence of a stabilising mechanism maintaining trait
399 composition in the face of taxonomic change. For the KCF the relative
400 distribution of palaeocommunities in taxonomic ordination space and trait

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401 ordination space are distinct from each other, and both show a clear influence
402 of deoxygenation (Figs 3 e and f; Caswell and Frid, 2013).

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

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

418 **DISCUSSION**

419 The result of this study show that in two contemporary benthic time series and
420 one ecologically comparable palaeoecological data set 'background'
421 taxonomic turnover resulted in samples with a taxonomic composition that is
422 ~70% similar. It is also clear that environmental drivers periodically caused
423 larger scale changes in species composition (Caswell and Frid, 2013, Frid et
424 al., 2009a, Frid et al., 2009b). Biological traits can be used to index the
425 ecological functioning of assemblages and one might expect large-scale

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426 changes in taxonomic composition to result in changes in trait composition
427 and hence ecological functioning. Our data show that trait composition in the
428 three data sets had comparable variability but critically the pattern of changes
429 in trait composition did not match the changes in taxonomic composition. At
430 times the trait composition, and hence ecological functioning, was maintained
431 in the face of taxonomic changes, implying a degree of redundancy in the
432 system. In other instances trait composition changed to a greater extent than
433 taxonomic composition suggesting that 'key' taxa, i.e. those that were critical
434 in supplying certain traits, changed. Thus, in both the long-term
435 palaeoecological systems and the shorter (still multi-decadal) contemporary
436 systems there is evidence of both ecological redundancy and the existence of
437 key or rivet species (Walker, 1992, Cardinale et al., 2006, Cardinale et al.,
438 2012).

439
440 Although fisheries during the 1980s were shown to have impacted the
441 benthos at station P both of the Dove benthic stations show, approximately,
442 decadal shifts in species composition (Fig. 3). However, these changes
443 involve species turnover in the sub-dominant taxa (Frid et al., 2009a, Frid et
444 al., 2009b) such that the distribution of biological traits in the assemblage
445 does not change markedly (Frid, 2011; Fig. 2b and d). At station M1 the
446 increase in total infaunal abundance and inter-annual variability (Frid et al.,
447 2009b) in the late 1980s and 1990s drove an increase in the delivery of all
448 three intermediate services (Fig. 4a). In contrast, changes in the total infaunal
449 abundance at station P were much less marked (Frid et al., 2009a) and only
450 resulted in changes in the delivery of one of the intermediate services (Fig.

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451 4b). This lack of separation in the ordination of traits and the overriding effect
452 of macro-infaunal abundance on the delivery of ecosystem services suggests
453 that over decadal scales the functioning of these communities and the types
454 of ecosystem service they could deliver is conserved although the quantity of
455 available service varied with inter-annual variations in infaunal abundance.

456 This inter-annual variation is driven to a large extent by the input of food
457 (Pearson and Rosenberg, 1986, Buchanan, 1993). So does this quasi-stability
458 extend beyond multi-decadal timeframes?

459
460 A recent study, of plant communities, also concluded that ecosystem
461 functioning did not vary greatly over multi-decadal time scales (Vellend et al.,
462 2013). Using a systematic review and meta-analysis of 168 published studies
463 with data from over 16,000 sites and Vellend et al. (2013) showed that plant
464 diversity change did not differ significantly from zero over periods of 5-260
465 years. Sites were as likely to experience an increase in plant diversity (mainly
466 through post-disturbance succession) as they were to undergo a decrease in
467 diversity (mainly driven by species invasions). Although the authors did not
468 directly assess functioning they asserted, on the basis of the diversity
469 changes, that functioning probably did not significantly vary either.

470
471 The processes of preservation in the KCF mean that the data for the KCF
472 includes a degree of 'time averaging' such that decadal scale changes in
473 species (relative) abundances are not discernible at this sampling resolution.
474 However, the dominant driver of change in these benthic assemblages is the
475 degree of oxygenation. The changes in environmental conditions, associated

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476 with regional scale changes in oxygenation, caused a shift in the taxonomic
477 composition (Fig. 3e) of the benthos whereby only the most severe
478 deoxygenation (as indicated by high sedimentary TOC (>~3.8%)) resulted in
479 changes in the composition of the biological traits (Fig. 3f). These changes in
480 biological traits only produced changes in the delivery of the intermediate
481 service nutrient regeneration, presumably this is a reflection of the greater
482 abundance of infaunal/bioturbating taxa during oxic conditions in the surface
483 sediments (Wignall, 1990).

484
485 The analyses presented in this study depend on two assumptions, (1) that the
486 biological traits of a taxon can be used to infer its ecological role (functioning),
487 and (2) that these can be mapped on to 'intermediate ecosystem services'
488 (sensu Norris, 2012). In addition, for the KCF data we must assume that none
489 of the taxa responsible for a major (in terms of quantity or uniqueness)
490 contribution to ecosystem functioning have been so poorly preserved that they
491 do not feature in the fossil record (as either body or trace fossils). This does
492 not seem unreasonable considering that although some trace fossils are
493 reported sporadically in a few oxygenated intervals of the KCF (Wignall 1991)
494 they are rare (Oschmann, 1988, Wignall, 1990, Wignall, 1991) (Morgans-Bell
495 et al., 2001) and none are reported from the hypoxic strata (Oschmann 1988).

496
497 Biological traits analysis, and similar approaches, focus on functional groups
498 or specific sets of morphological or life history traits are routinely being used
499 to index ecological functioning in a range of ecosystems (Werner and Peacor,
500 2003, Usseglio-Polatera et al., 2000b, Kleyer et al., 2008, Bremner, 2008,

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501 Paganelli et al., 2012). Although these approaches are limited by the available
502 information on the biology of the taxa involved, and is more challenging for
503 offshore taxa than terrestrial (Webb, 2012), the traits approach allows us to
504 make a number of predictions about changes in relative functioning (and
505 hence intermediate ecosystem service delivery) even if we are not certain that
506 our current level of biological knowledge covers all of the ecological functions.

507

508 The biological assemblages present within the sea floor deliver a range of key
509 ecosystem services (Beaumont et al., 2007) and undergo temporal variations
510 on a range of scales that are driven by biotic (food supply) and abiotic
511 (climate, hypoxia) factors. Our analyses suggest that changes in macro-
512 infaunal abundance (which can vary by a factor of 7 or more over a decade;
513 Frid et al., 2009a) drives changes in the quantity of some intermediate
514 services. Furthermore, there is considerable stability in ecosystem functioning
515 and hence the types of service potentially being delivered and the quantity
516 delivered over time. These findings are preliminary and are of necessity
517 constrained by the available data and the assumptions required to link
518 taxonomic composition to ecosystem service delivery. However, if further
519 analyses of these and other data sets confirm the pattern established in the
520 present study, it will suggest that benthic ecosystem functioning conforms to
521 some broad patterns, such as 'evolving' into a configuration that maximises
522 the recycling of nutrients and 'efficient' food web structures, concepts that
523 would be recognised in the writings of the first generation of ecosystem
524 scientists back in the 1960s (Odum, 1969).

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526 In this study we examined three hypotheses concerning the temporal stability
527 of ecosystem functioning (i) *ecosystem functioning will show less temporal*
528 *variation than species composition; (ii) longer time series will show greater*
529 *variation in functional composition than shorter time (i.e. decadal) series; and*
530 *(iii) the degree of species level change that causes a functional change will be*
531 *similar in contemporary and ancient marine communities. As ecosystem*
532 *functions deliver the ecological goods and services that human societies*
533 *derive from the natural world, understanding these three hypotheses may*
534 *offer insights into the scale of the challenges that wide spread environmental*
535 *changes may pose. It is generally believed that biodiversity confers stability*
536 *and provides a level of insurance against losses in ecological function (Worm*
537 *et al., 2006). Our results show that in both contemporary and ancient marine*
538 *ecosystems the natural assemblages do contain ecological redundancy that*
539 *can protect functioning in the face of species turnover. However, in all of the*
540 *communities investigated there were also instances of small changes in*
541 *taxonomic composition resulting in more significant changes in functioning*
542 *(and hence the potential delivery of ecosystem services). This implies that in*
543 *these benthic systems ‘idiosyncratic’ models (Pueyo et al., 2007) best*
544 *describe the Biodiversity-Ecosystem Functioning relationship, representing a*
545 *considerable challenge for managers attempting to predict and mitigate the*
546 *impacts of anthropogenic environmental change.*

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

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

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747 **Figure 3.** Non-metric multi-dimensional scaling ordinations of the Bray Curtis
748 similarity of taxonomic composition (a, c and e) and biological trait composition (b, d
749 and f) for Dove benthic station M1 (a and b; both transformed Log (X+1)), Dove
750 benthic station P (c and d) and Kimmeridge Clay Formation palaeocommunities (e
751 and f; species composition data transformed Log (X+1)). Kimmeridge Clay
752 Formation palaeocommunities are grouped by the mean total organic carbon
753 content of the sedimentary deposits. Note: E6 and E9 omitted from the taxonomic
754 ordination for the Kimmeridge Clay Formation as the palaeocommunities were so
755 dissimilar to the remaining stations that it obscured the detail for the remaining
756 stations (see text for details of data sets).

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758 **Figure 4.** Differences in the delivery (arbitrary units scaled with abundance; mean \pm
759 SE) of three ‘intermediate’ ecosystem services provided by benthic communities
760 from (a) Dove Benthic station M1, (b) Dove Benthic station P and (c)
761 palaeocommunities from the Kimmeridge Clay Formation (KCF; Late Jurassic). For
762 the Dove series the data are presented by decade and for the KCF by degree of
763 deoxygenation, as indexed by the total organic carbon (TOC) content where high
764 TOC suggests deoxygenated and low TOC oxygenated conditions (see text for
765 details).

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

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Trait	Modality
Body size	(1) Small (<10 mm), (2) Large (>10 mm)
Longevity	(1) 1–3 years, (2) >3 years
Bioturbation	(1) Low, (2) Moderate, (3) High
Life Zone	(1) Surface (Epibenthic), (2) Shallow infauna (<5 cm), (3) Deep infauna
Feeding Mode	(1) Deposit, (2) Filter, (3) Omnivore, (4) Carnivore

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

Trait	Modality
Organism body size	(1) <10 mm, (2) 10-50 mm, (3) 50-100 mm, (4) 100-200 mm, (5) >200 mm
Skeletal composition	(1) Chitin, (2) Aragonite, (3) Calcite (low Mg), (4) Calcite (high Mg), (5) Phosphate
Skeletal thickness	(1) <0.1 mm, (2) 0.1-0.5 mm, (3) 0.5-1 mm (4) 1-5 mm, (5) >5 mm
Adult movement	(1) Sessile, (2) Burrowing, (3) Crawling, (4) Swimming, (5) Gliding
Living habit	(1) Semi-shallow infaunal, (2) Mid-deep infaunal, (3) Epifaunal attached, (4) Epifaunal free living, (5) Borer
Feeding habit	(1) Deposit feeder, (2) Grazer, (3) Suspension/filter feeder, (4) Scavenger/carnivore, (5) Chemosymbiont
Sociability	(1) Solitary, (2) Gregarious, (3) Colonial
Reproductive method	(1) Asexual budding, (2) Planktotrophic larvae, (3) Lecithotrophic larvae, (4) Brood to larvae, (5) Brood to juvenile

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Table 3. The mean abundance (per m⁻²) and percent contribution of the top ten ranked taxa to the total abundance of macro-infauna encountered during 33 years of sampling at benthic station M1, and 35 years at Dove station P, off the Northumberland coast, North Sea, UK.

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

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

Taxa		Mean abundance per palaeocommunity	Contribution to total abundance (%)
Bivalve	<i>Protocardia morinica</i>	1134.87	30.57
Bivalve	<i>Isocyprina minuscula</i>	986.57	26.58
Bivalve	<i>Corbulomima suprajurensis</i>	580.46	15.64
Bivalve	<i>Liostrea multififormis</i>	176.14	4.75
Bivalve	<i>Nicaniella extensa</i>	89.36	2.41
Gastropod	<i>Pseudorhytidopilus latissima</i>	73.07	1.97
Bivalve	<i>Grammatodon longipunctata</i>	65.62	1.77
Bivalve	<i>Nanogyra virgula</i>	60.93	1.64
Gastropod	<i>Quadrinervus ornatus</i>	59.09	1.59
Brachiopod	<i>Lingula ovalis</i>	44.93	1.21
Total		3271.03	88.12

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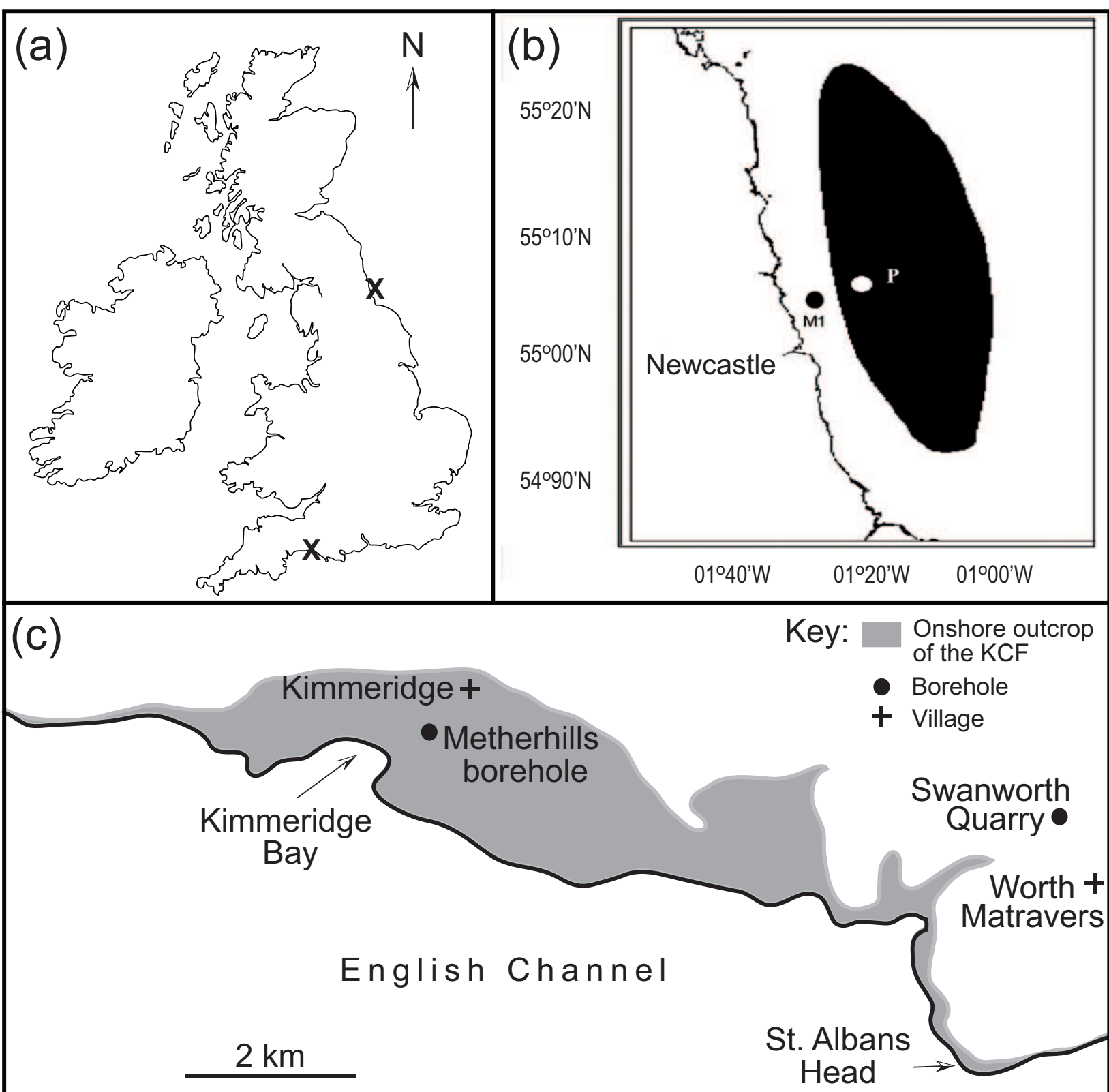


Fig. 1 Frid & Caswell

Figure(s)

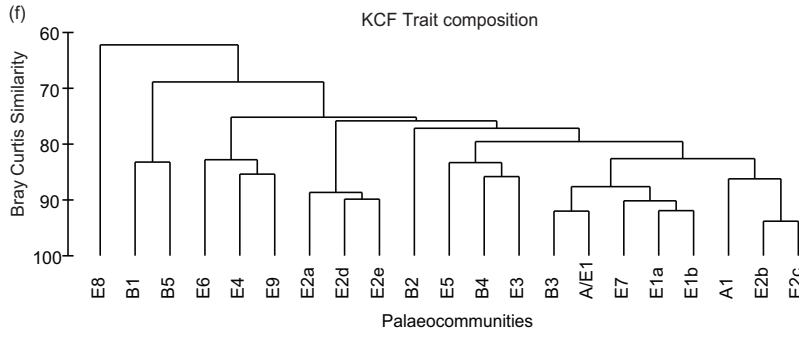
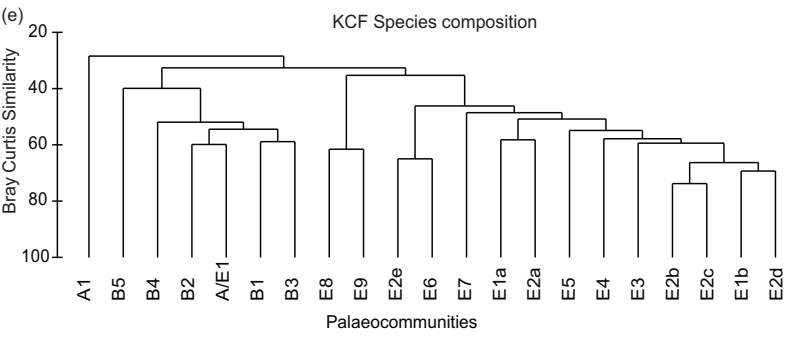
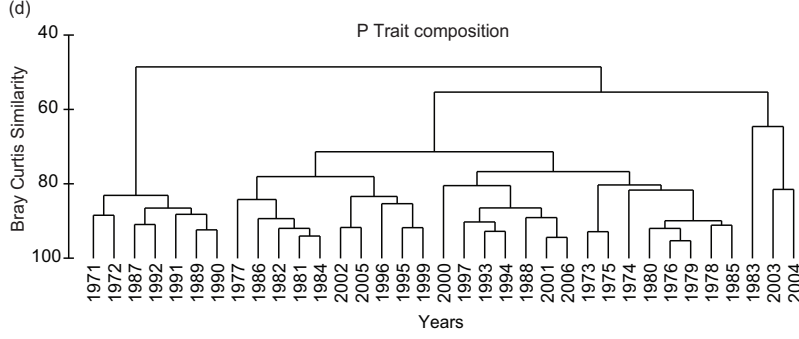
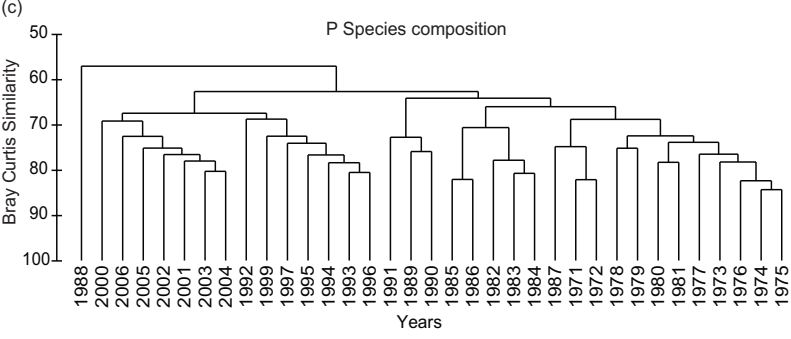
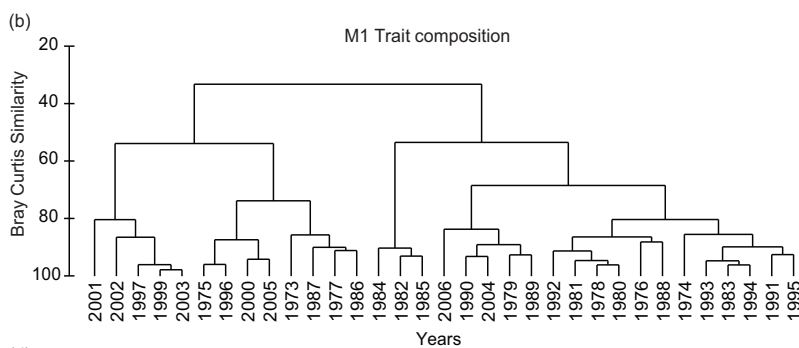
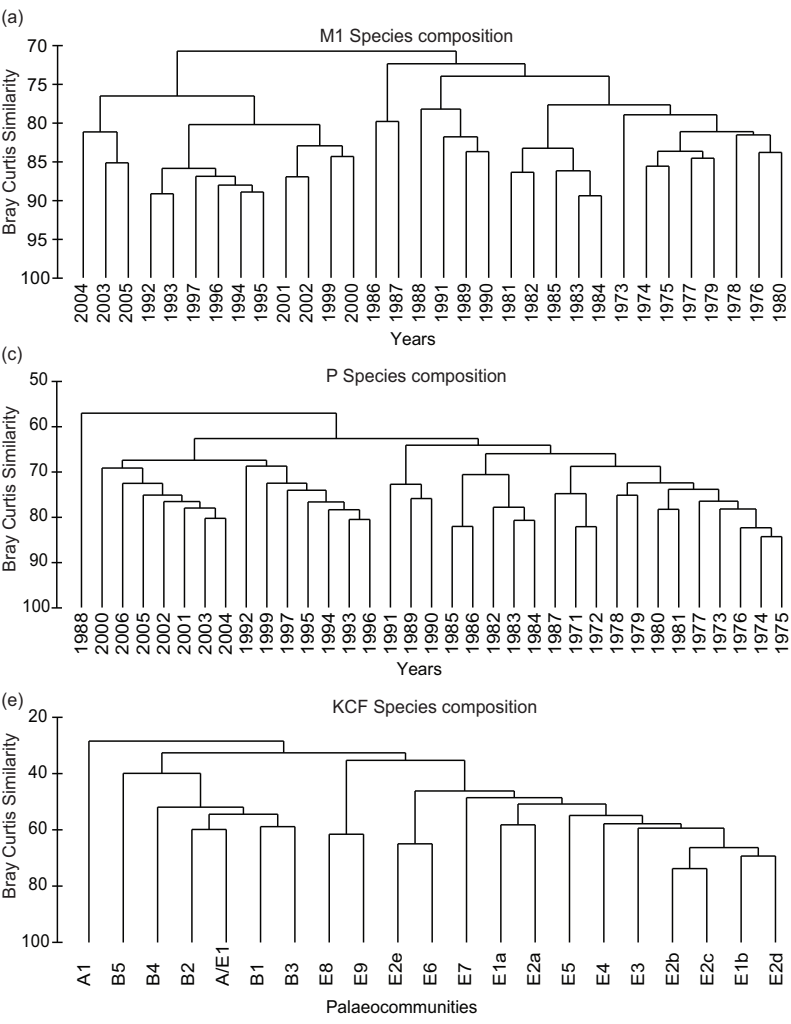
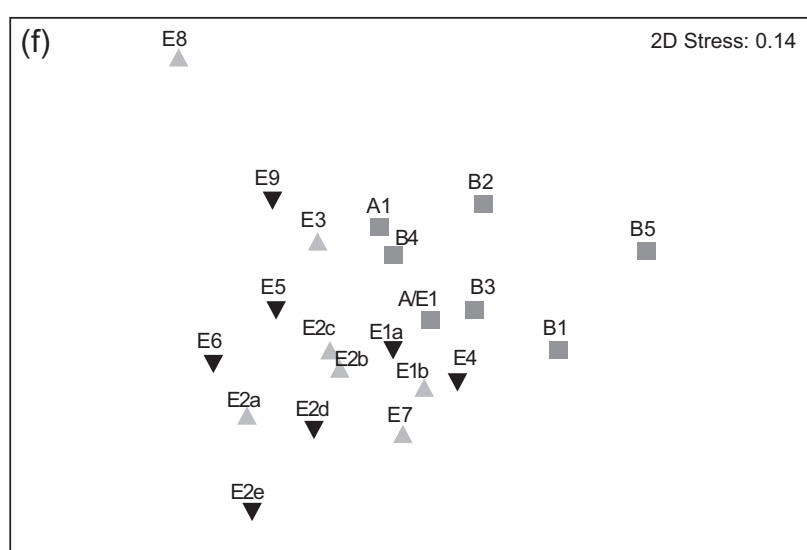
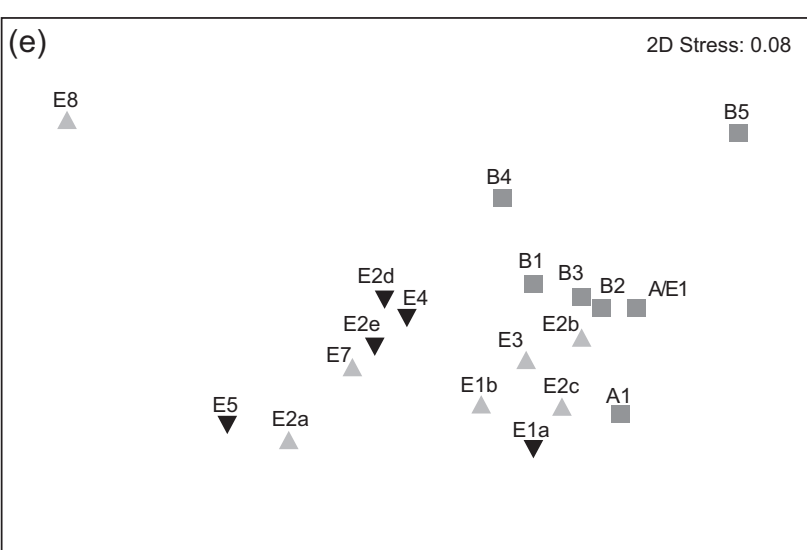
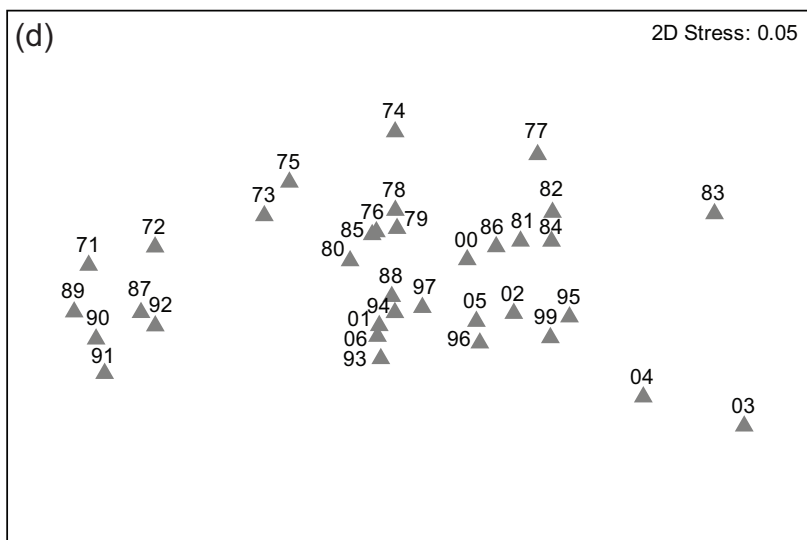
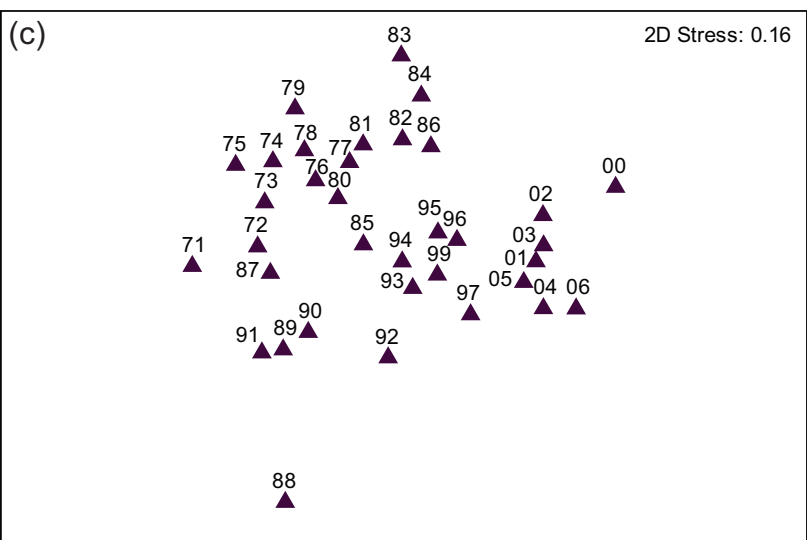
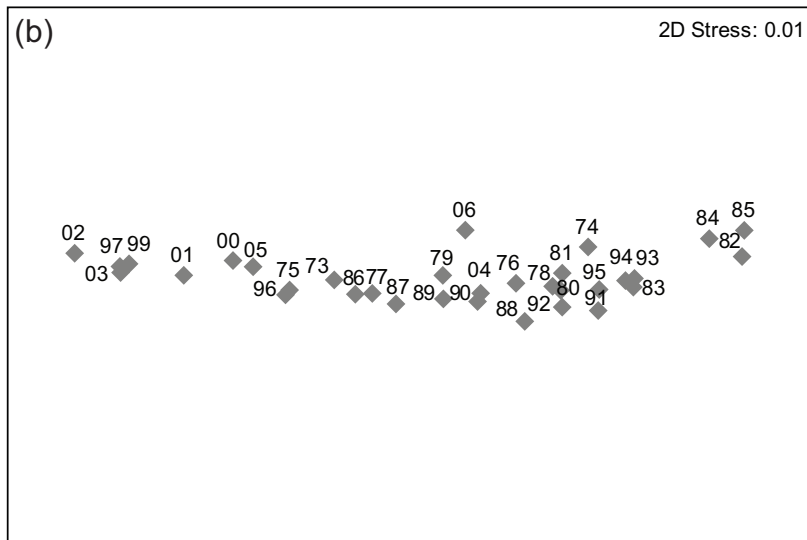
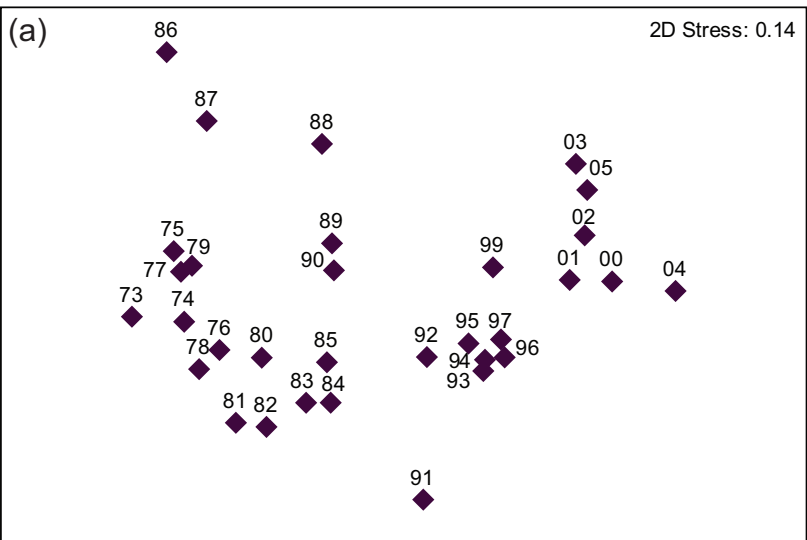


Fig. 2. Frid and Caswell JSR

Figure(s)



■ 1.18-3.72 wt% ▲ 3.72-5.73 wt% ▼ >5.73 wt%

■ 1.18-3.72 wt% ▲ 3.72-5.73 wt% ▼ >5.73 wt%

Fig. 3 Frid and Caswell JSR

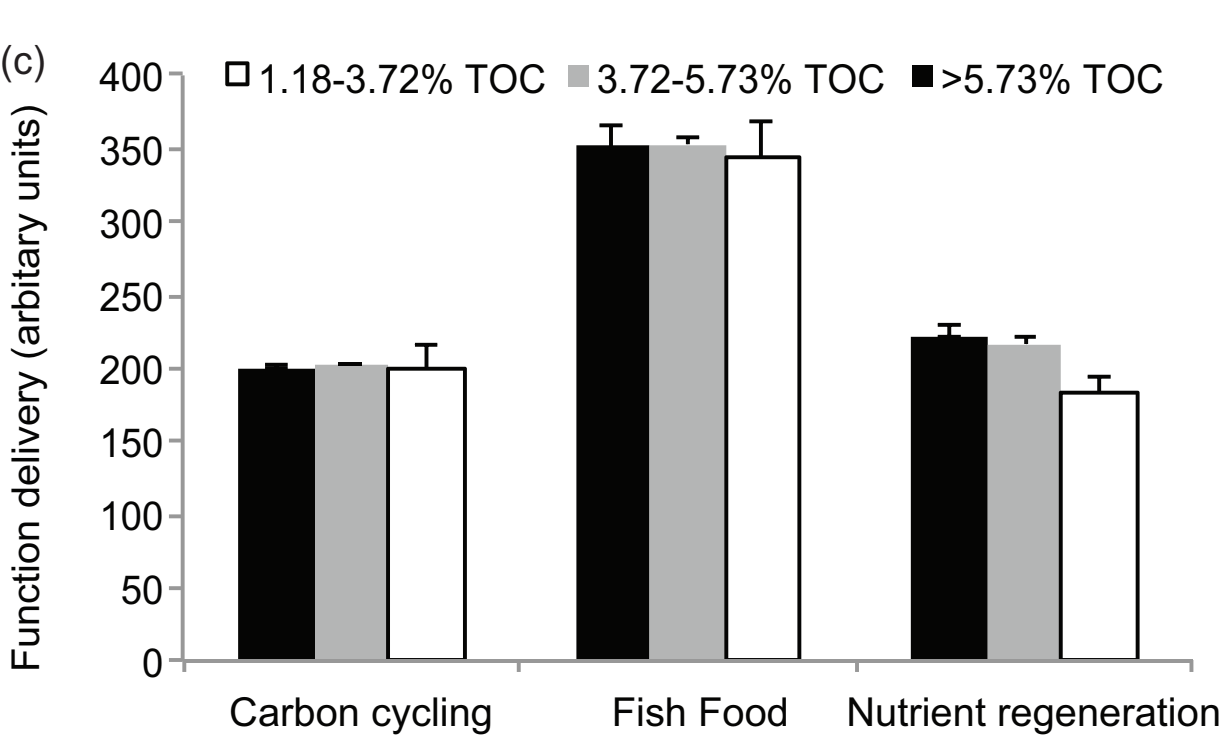
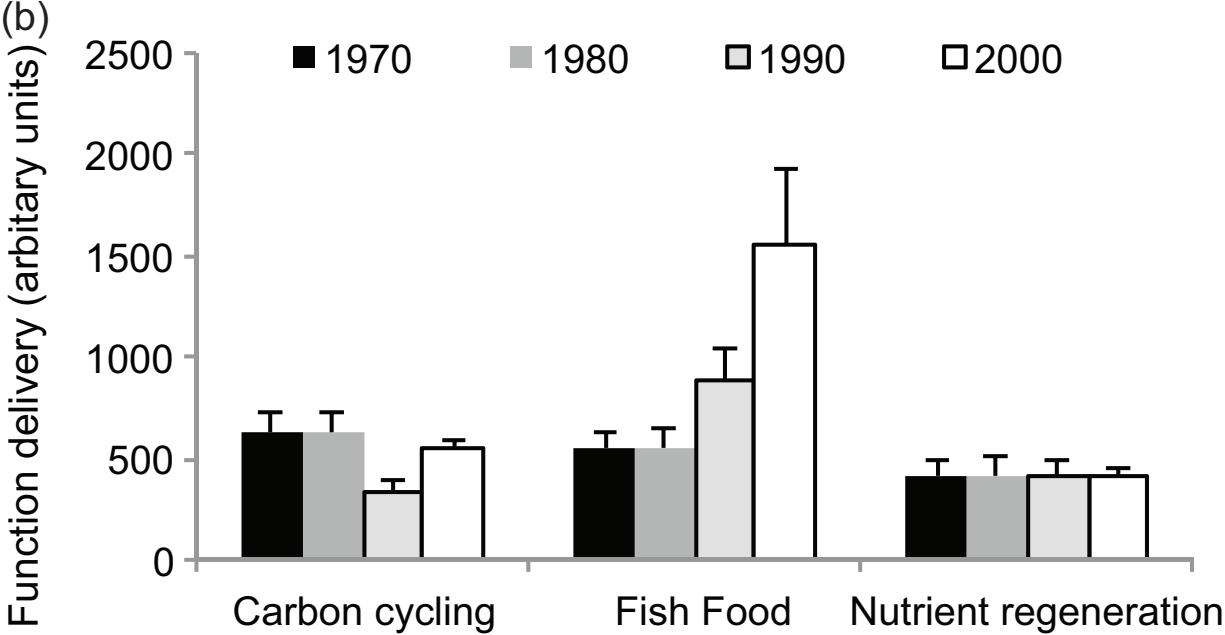
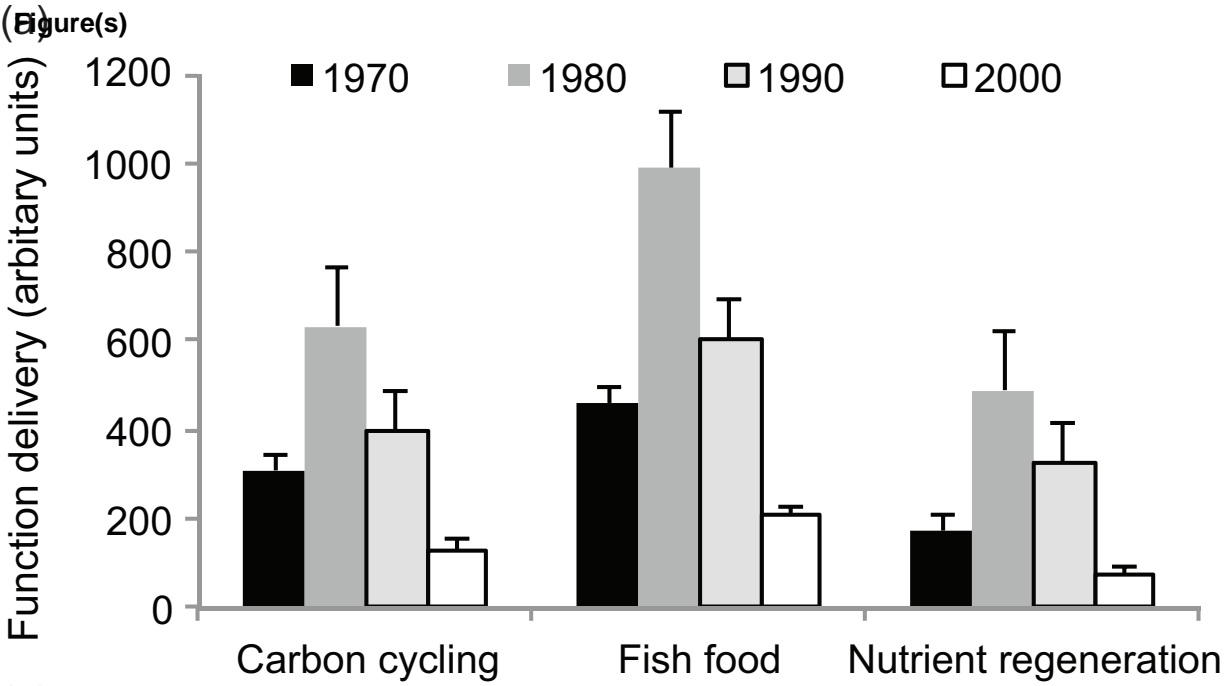


Fig. 4. Frid and Caswell JSR