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2
## Uncovering the environmental drivers of short-term temporal dynamics in an epibenthic community from the Western English Channel

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8  ## Abstract

9  Benthic communities, critical to the health and function of marine ecosystems, are under

10  increasing pressure from anthropogenic impacts such as pollution, eutrophication and

11  climate change. In order to refine predictions of likely future changes in benthic

12  communities resulting from these impacts, we must first better constrain their responses to

13  natural seasonality in environmental conditions. Epibenthic time series data (July 2008 –

14  May 2014) have been collected from Station L4, situated 7.25 nautical miles south of

15  Plymouth in the Western English Channel. These data were analysed to establish patterns in

16  community abundance, wet biomass and composition, and to link any observed patterns to

17  environmental variables. A clear response to the input of organic material from

18  phytoplankton blooms was detected, with sediment surface living deposit feeders showing

19  an immediate increase in abundance, while predators and scavengers responded later, with

20  an increase in biomass.  We suggest that this response is a result of two factors. The low

21  organic content of the L4 sediment results in food limitation of the community, and the mild

22  winter/early spring bottom water temperatures allow the benthos to take immediate

23  advantage of bloom sedimentation. An inter-annual change in community composition was

24  also detected, as the community shifted from one dominated by the anomuran Anapagurus

25  laevis to one dominated by the gastropod Turitella communis. This appeared to be related

26    to a period of high larval recruitment for T. communis in 2013/2014, suggesting that

27    changes in the recruitment success of one species can affect the structure of an entire

28    community.

29    **Keywords:** Benthic epifauna, benthic community, natural variability, Western English

30    Channel, time series, phytodetrital input, bottom-water temperature, supply side ecology.

31    INTRODUCTION

32    Benthic epifaunal communities are under growing pressure from anthropogenic activities in

33    coastal seas, the strength and range of which have increased significantly over the last

34    century with the growth in global industrialisation and urbanisation (Daan et al., 1996,

35    Halpern et al., 2008).  As a result, impacts such as pollution, eutrophication and the effects

36    of climate change are of major concern to conservationists and resource managers alike

37    (Capasso et al., 2010). In order to assess long-term changes in epibenthic communities as a

38    result of these impacts, it is critical that we gain an improved understanding of the short-

39    term temporal variability in the responses of community abundance, biomass and

40    composition to environmental parameters (Chikina et al., 2014, Reiss & Kröncke, 2004,

41    Włodarska-Kowalczuk et al., 2016).

42    While descriptions of the large scale spatial distribution and structure of temperate, shelf-

43    sea epibenthic communities in connection with environmental factors are relatively

44    common, only a few studies have investigated the temporal variability of these

45    communities. Many of those focussed on the North Sea, and concluded that sea surface

46    temperature (SST) is a dominant factor influencing the temporal variability of epibenthic

47    communities, particularly in the shallow, well-mixed areas of the south-eastern North Sea

48    (Neumann et al., 2008, Neumann et al., 2009b, Reiss & Kröncke, 2004), which are

49    characterised by strong seasonal fluctuations in temperature (Neumann et al., 2008). The

50    influence of SST appears to be less dominant in the deeper, stratified areas of the northern

51    North Sea however. Neumann et al. (2009a) found no correlation between overall

52    epibenthic community structure and changing SST, although relationships were found

53    between SST and the abundance and biomass of some individual species, in some cases with

54    a one year lag.

55    Shallow-water communities are generally thought to have access to high quality, if

56    temporally variable, food (Pearson & Rosenberg, 1986), and as a result, the influence of

57    organic input on structuring the benthos may be secondary to other physical and biological

58    factors (Quijón et al., 2008). Again, there are comparatively few studies which focus on the

59    responses of benthic epifauna to bloom sedimentation, but a number have investigated

60    macro-infaunal community structures and responses to phytodetrital inputs. The trophic

61    structure of North Sea macrofauna communities was found to reflect differences in the

62    relative quality of organic matter received (Dauwe et al., 1998, Wieking & Kröncke, 2005),

63    and between 55% and 84% of year to year variability in benthic infaunal abundance off the

64    coast of Northumberland was explained by changes in primary production (Buchanan,

65    1993). A marked increase in macrofaunal abundance in the same area in the 1980s was

66    attributed to increases in phytodetrital input (Frid et al., 1996), as were decadal-scale

67    variations in taxonomic composition (Clare et al., 2017, Frid et al., 2009a, Frid et al., 2009b).

68    Josefson et al. (1993) showed that the abundance, biomass and growth of macro-infaunal

69    species were closely related to bloom sedimentation in the Skagerrak-Kattegat region, while

70    macrofaunal deposit feeders were found to increase in abundance immediately following

71     bloom sedimentation in the Western English Channel, while other trophic groups responded

72     more slowly, primarily with an increase in biomass (Zhang et al., 2015). However, not all

73     studies found a clear response to organic input. Quijon et al. (2008) found that the effects of

74     phytodetrital input were short term, and were minor in comparison to the seasonal

75     differences observed in the macrofaunal community, and studies of the infauna of the

76     western Baltic (Graf et al., 1982) and of the epifauna in the German Bight area of the North

77     Sea (Reiss & Kröncke, 2004) failed to find any response to bloom sedimentation at all.

78     In this study, the seasonal and interannual variability of the epibenthic community at Station

79     L4 in the Western English Channel was investigated from July 2008 until May 2014. Since

80     little is known about the ecology and biology of the epibenthos in the Western English

81     Channel, these data provide valuable information on the short-term variation of several

82     epibenthic groups. The purpose of this study was to (I) describe the seasonal and

83     interannual variability in diversity, abundance, and biomass of the epibenthos at Station L4

84     and (II) to identify and discuss environmental drivers in accordance with faunal patterns.

85     ## MATERIALS AND METHODS

86     **The L4 sampling station**

87     Station L4 is part of the Western Channel Observatory (WCO, www.westernchannel

88     observatory.org.uk), and represents a long term oceanographic and marine biodiversity

89     time series, having been routinely sampled since 1988. In 2008, a benthic series was added

90     – an element often missing from other observatories (Smyth et al., 2015). Situated in the

91     Western English Channel, 7.25 nautical miles south of Plymouth, UK (50°15.00'N,

92     4°13.02'W), it can be considered representative of a temperate coastal environment (Tait et

93     al., 2015). Water column depth is approximately 53m, and the station is well mixed during

94    the winter and stratified over the summer (Figure 1A). Bottom water temperature varies

95    from approximately 8°C - 16°C (Figure 1A). Chlorophyll-*a* concentration is at its lowest

96    during winter, and higher during the characteristic spring and autumn phytoplankton

97    blooms (Figure 1B, note that these are fluorescence measurements, a proxy for chlorophyll-

98    *a*). Phytoplankton cells can sink very quickly at L4, with high chlorophyll-*a* and

99    phytoplankton carbon values measured at the seabed within two weeks of the start of a

100   bloom (Tait et al., 2015, Zhang et al., 2015).
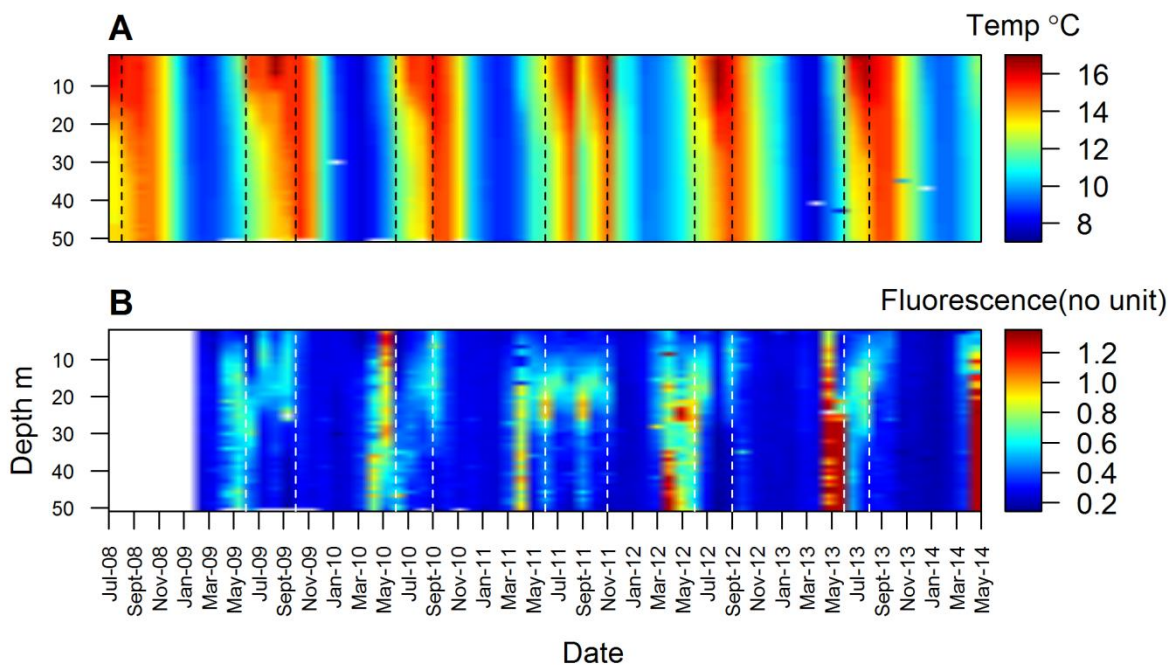


101
102   **Fig. 1.** Monthly mean water temperature (A), between July 2008 and May 2014 and fluorescence (B) between
103   Jan 2009 and May 2014 at station L4. Data were collected weekly (weather permitting) using a SeaBird SBE 19+
104   CTD deployed from the *RV Plymouth Quest*. Dotted vertical lines denote periods of thermal stratification.

105   **Animal collection and processing**

106   Using a 60cm wide Naturalist dredge with a 22mm mesh, three replicate samples were

107   taken every other month during the period July 2008 - May 2014 from Station L4. For each

108   replicate the dredge was lowered to the seabed and then towed for approximately 2 mins at

109   a speed of approximately 0.3 knots. Total towed distance was calculated for each replicate

110   using the formula:

$$\cos^{-1}(\cos lat_S * \cos lat_E + \sin lat_S * \sin lat_E * \cos(lon_S - lon_E)) * 6371$$

111    Where: $lat_S$ is start latitude (in radians), $lat_E$ is end latitude (in radians), $lon_S$ is start

112    longitude (in radians), $lon_E$ is end longitude (in radians) and 6371 is the approximate radius

113    of the Earth (in Km).

114    All organisms collected in the dredge were fixed in 10% formalin solution. Prior to analysis,

115    samples were rinsed at 4mm and epifaunal individuals carefully picked out. All individuals

116    were identified to species level, wherever possible, using a stereo microscope (Leica M32

117    Kombistereo). Individuals within each of the identified taxonomic groups were counted,

118    carefully blotted dry and weighed on a Sartorius R220D microbalance (± 0.01 mg, European

119    Instruments). Standardised values for abundance and biomass for each time point were

120    calculated by dividing the total abundance (or biomass) in three replicate samples by the

121    total area covered by the dredge. Those species which were only ever represented by a

122    single individual across the course of the time series (N = 23) were excluded from further

123    analysis.

124    **Ancillary data**

125    During the study period (July 2008 – May 2014), a suite of environmental and biological data

126    were collected from L4 every week (weather permitting) from the *RV Plymouth Quest*.

127    Vertical profiles of temperature and fluorescence were measured using a SeaBird SBE 19+

128    CTD. Water samples for phytoplankton analysis were collected from a depth of 10m using

129    10L Niskin bottles attached to the CTD rosette, and zooplankton were collected in two

130    vertical WP2 net hauls (mesh size = 200µm, mouth aperture = 57cm diameter) taken from

131    the seabed to the surface (UNESCO, 1968).

132 **Phytoplankton analysis**

133 Paired water-bottle samples were preserved with 2% Lugol's iodine solution (Throndsen,

134 1978) and 4% buffered formaldehyde. Between 10 and 100 ml of sample (depending on cell

135 density) were settled for at least 48 h (Widdicombe et al., 2010). Cell volumes were

136 calculated according to the equations of Kovala and Larrance (1966) and converted to

137 carbon (pgC cell$^{-1}$) (Menden-Deuer & Lessard, 2000) and then expressed per unit volume of

138 seawater (mgC m$^{-3}$).

139 **Meroplankton analysis**

140 Haul samples were preserved and stored in 5% formalin. Two subsamples were extracted

141 using a Folsom splitter and a Stempel pipette, to identify large and small organisms

142 separately, then counted and identified under a microscope. Abundances in the two hauls

143 were averaged to reduce the variability related to the sampling, and counts were converted

144 to individuals per m$^3$ (John et al., 2001). Due to the difficulties in larval identification and

145 because different analysts have worked on the data set over the years, meroplankton are

146 only identified to major taxonomic groups. These groups are: Decapoda, Brachyura,

147 Cirripedia, Bivalvia, Gastropoda, Echinodermata and Polychaeta. These groups provide an

148 overall picture of the seasonal changes in the meroplankton assemblage at L4. For this

149 study, all groups except Cirripedia were considered, because although Cirripede larvae can

150 dominate the meroplankton at L4 (Highfield et al., 2010) mature animals are rarely present

151 in the epibenthic faunal samples.

152 **Statistical analysis**

153 All statistical analyses were conducted in R statistical software. Time series of epibenthic

154 abundance and wet biomass per square metre between July 2008 and May 2014 were

155    compiled. Missing data were interpolated using the "zoo" package in R (Zeileis et al., 2018).

156    Data for each sampling month (January, March, May, July, September and November) were

157    pooled across the whole time series and overall means of community, major phyla and

158    dominant species abundance and wet biomass were calculated to establish the structure of

159    the community. Average individual body mass of the whole community and each phylum

160    was calculated by dividing the overall mean wet biomass by the overall mean abundance for

161    each sampling month. To establish whether responses to environmental drivers were more

162    easily identifiable when considering functional groups rather than taxa, species were

163    grouped into one of five feeding guilds (predator/scavenger, omnivore, surface-deposit

164    feeder, subsurface-deposit feeder, suspension feeder). Information on polychaete feeding

165    mode was retrieved from Jumars et al. (2015). Information on feeding mode for all other

166    phyla was retrieved from the Marine Life Information Network's biological traits catalogue

167    (MarLIN, 2006). Where a species exhibited more than one feeding method, it was classified

168    by the preferred or most frequently documented method. While we appreciate that the

169    "fuzzy coding" method (Chevene et al., 1994, Neumann & Kröncke, 2011), which uses

170    positive scores to describe the affinity of species to trait categories, would reflect a wider

171    range of ecological function than the method adopted here, the aim of the present study

172    was to provide a broad overview of the structure of the community and its responses to

173    environmental variables, rather than an in-depth analysis of biological traits. Data on

174    meroplanktonic larval abundance, water temperature and phytoplankton carbon for the

175    duration of the time series were also collected and monthly means calculated.

176    The "vegan" package in R (Oksanen et al., 2017) was used to construct a species

177    accumulation curve to determine whether the full diversity of Station L4 had been captured,

178    and to calculate rarefied species richness as an indicator of changes in diversity over the

179    course of the time series. Rarefied species richness was chosen as the measure of diversity

180    as the total area covered by the dredge varied between sampling dates. As a consequence,

181    it is likely that the number of species (and individuals) collected in each sample was a

182    function of the area sampled. Rarefaction techniques can correct for this difference in

183    sampling effort by generating the expected number of species in a small collection of $n$

184    individuals drawn at random from a larger pool of $N$ individuals (Gotelli & Colwell, 2001).

185    In order to identify any correlation between the biological (community, feeding guild and

186    phyla abundance and biomass) and the environmental (water temperature, phytoplankton

187    carbon) data series, cross correlation analysis was performed (Olden & Neff, 2001, Probst et

188    al., 2012) in R using the "astsa" package (Stoffer, 2016). Where relationships between data

189    series were found, linear regressions were used to quantify the relationship for a particular

190    time lag.  Cross correlation analysis was also performed on the phyla abundance and larval

191    abundance data series. Prior to this analysis, all data series were checked for

192    homoscedasticity by fitting a simple ordinary least squares regression model and checking

193    the residuals against the fitted values. The community abundance and biomass series, and

194    the larval abundance data series were found to be heteroscedastic and were log-n

195    transformed to achieve homoscedasticity. All data series were differenced to remove any

196    trends or seasonal effects (Probst et al., 2012), and then checked for stationarity using an

197    Augmented Dickey-Fuller test in the "tseries" package for R (Trapletti et al., 2017). Finally, to

198    ensure that estimates of cross correlations were not inflated by any temporal

199    autocorrelation, series were checked for any autocorrelation by generating ACF and PACF

200    plots (Olden & Neff, 2001).

201 RESULTS

202 **Variations in the epibenthic community 2008-2014**

203 The total area covered by the dredge across the three replicate samples varied from

204 326.1m$^2$ in March 2009 to 1170.3m$^2$ in September 2012. A total of 169 species were

205 recorded over the course of the series, 143 of which were used for analysis. The number of

206 species represented by only a single individual in each sample ranged from 4 (17% of total

207 species recorded in the sample) in January 2012 to 23 (38% of total species recorded in the

208 sample) in July 2009. The species accumulation curve for Station L4 started to level off after

209 approximately 20 samples (corresponding to a sampling period of 2.5 years) had been

210 collected (Figure 2A).  Rarefied species richness varied across the course of the series (Figure

211 2B) with values ranging from 7 – 24 species. Spring/summer values were generally higher

212 than values in the preceding winter. Rarefied richness reached a maximum in

213 spring/summer 2011, and declined steadily to the end of the series.
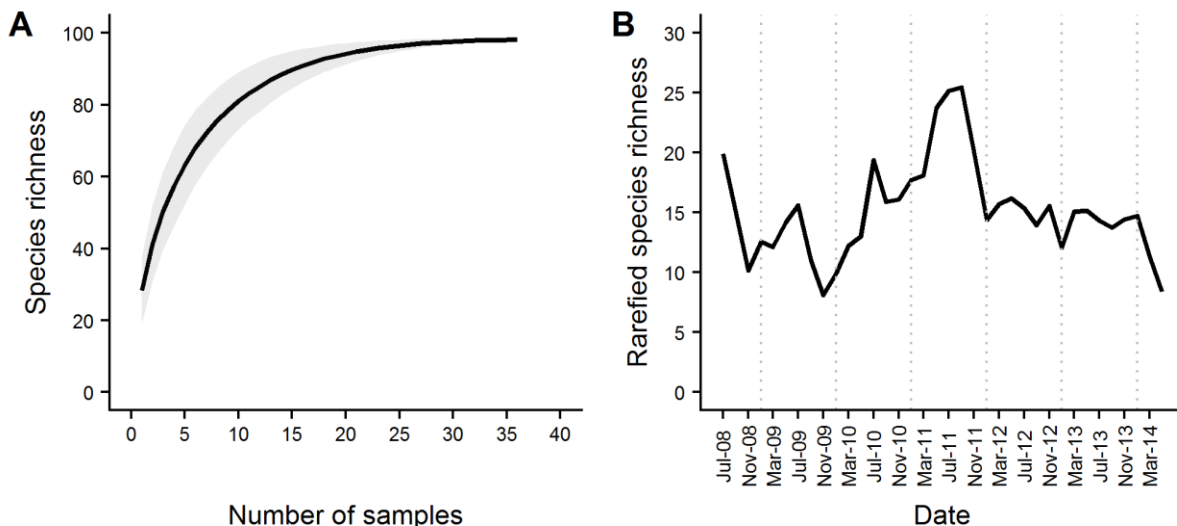


214
215 **Fig. 2.** Species accumulation curve (A) and rarefied species richness (B) over the course of the L4 epibenthic
216 time series, July 2008 – May 2014. The species accumulation curve started to level off after approximately 20
217 samples (representing a sampling period of 2.5 years) were collected. Grey shading denotes standard deviation
218 from the mean curve, generated from 1000 random permutations of the data. In terms of diversity, the series
219 is characterised by a period of high species richness in late 2010/2011, with periods of lower richness at the
220 beginning and end of the series. Dotted vertical lines denote January of each year.

221    Community abundance over the course of the series varied from 0.13 individuals m$^{-2}$ in May

222    2010, to 3.93 individuals m$^{-2}$ in May 2014 (Figure 3A). Community wet biomass ranged from

223    0.21 g m$^{-2}$ in September 2008 – 5.99 g m$^{-2}$ in May 2014 (Figure 3B). The peak in community

224    abundance seen in summer 2009 was largely attributable to a peak in crustacean

225    abundance (Figure 3E). The increase in abundance in autumn 2013 was driven by increases

226    in crustaceans (Figure 3E), molluscs (Figure 3E) and to a lesser extent, echinoderms (Figure

227    3C). The abundance maximum in spring 2014 was due predominantly to an increase in

228    mollusc numbers (Figure 3E). All but one of the observed peaks in wet biomass were driven

229    by increases in echinoderm biomass (Figure 3F). The very high wet biomass maximum in

230    spring 2014 can be attributed to increases in biomass of molluscs and crustaceans (Figure

231    3F). The increase in polychaete biomass in spring 2014 (Figure 3D) was due to the presence

232    of a single large *Aphrodita aculeata* (Linnaeus 1758) in the sample. The species which

233    contribute to these peaks in community abundance and biomass can be found in Table 1.

234    **Table 1:** Species which contributed to the observed peaks in abundance and/or biomass at station L4 between
235    July 2008-May 2014.

| Date | Peak in abundance/wet biomass? | Contributing species | Taxonomic authority |
|---|---|---|---|
| Summer 2009 | abundance | *Anapagurus laevis* | Bell, 1845 |
| Autumn 2013 | abundance | *A. laevis*<br>*Galathea nexa*<br>*Macropodia spp.*<br>*Turitella communis*<br>*Astropecten irregularis*<br>*Ophiothrix fragilis* | -<br>Embleton, 1834<br>-<br>Risso, 1826<br>Pennant, 1777<br>Abildgaard, 1789 |
| Spring 2014 | abundance & biomass | *T. communis* (abundance & biomass)<br>*Liocarcinus depurator* (biomass)<br>*Atelecyclus rotundatus* (biomass) | -<br><br>Linnaeus, 1758<br>Olivi, 1792 |
| March 2010 | biomass | *Marthasterias glacialis* | Linnaeus, 1758 |
| March 2011 | biomass | *Luidia ciliaris* | Philippi, 1837 |
| September 2012 | biomass | *Marthasterias glacialis* | - |
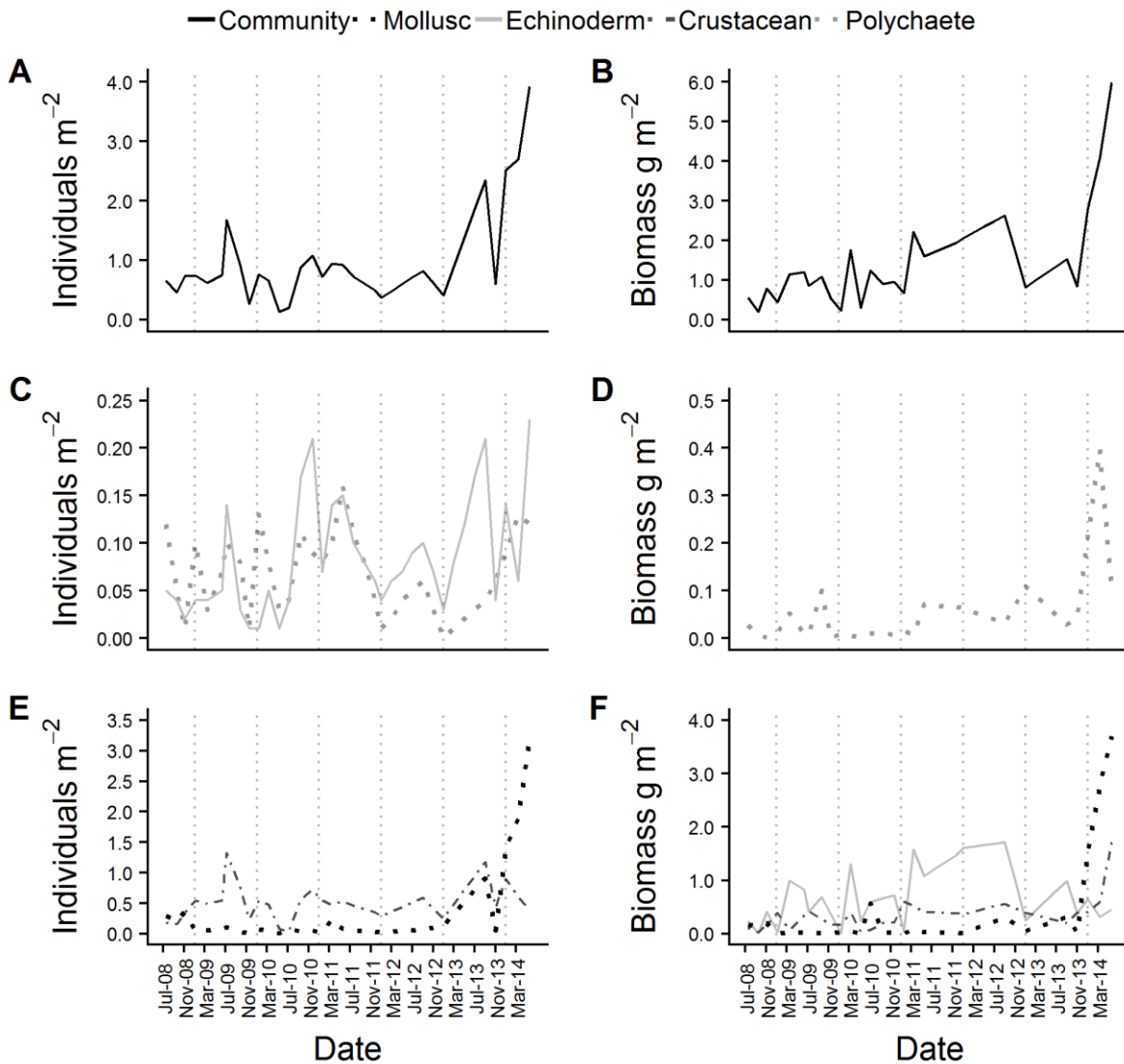
**Fig.3.** Abundance of the whole L4 epibenthic community (A), polychaetes and echinoderms (C) and molluscs and crustaceans (E) over the study period July 2008 – May 2014. Biomass of the whole community (B), polychaetes (D) and echinoderms, molluscs and crustaceans (F) over the same period. Dotted vertical lines denote January of each year.

Benthic larvae were always present in the water column over the course of the time series. Abundances ranged from 12 (± 8) individuals m$^{-3}$ in December 2009 to 2080 (± 3656) individuals m$^{-3}$ in July 2010. In 2009, 2010 and 2011, summer abundances of benthic larvae were very high, reaching more than 1000 individuals m$^{-3}$ (Figure 4A). In 2009, the majority of the benthic larvae recorded were gastropod molluscs (Figure 4C), while in 2010 and 2011,

247    echinoderm larvae were the primary contributors to the observed peaks in abundance

248    (Figure 4D).
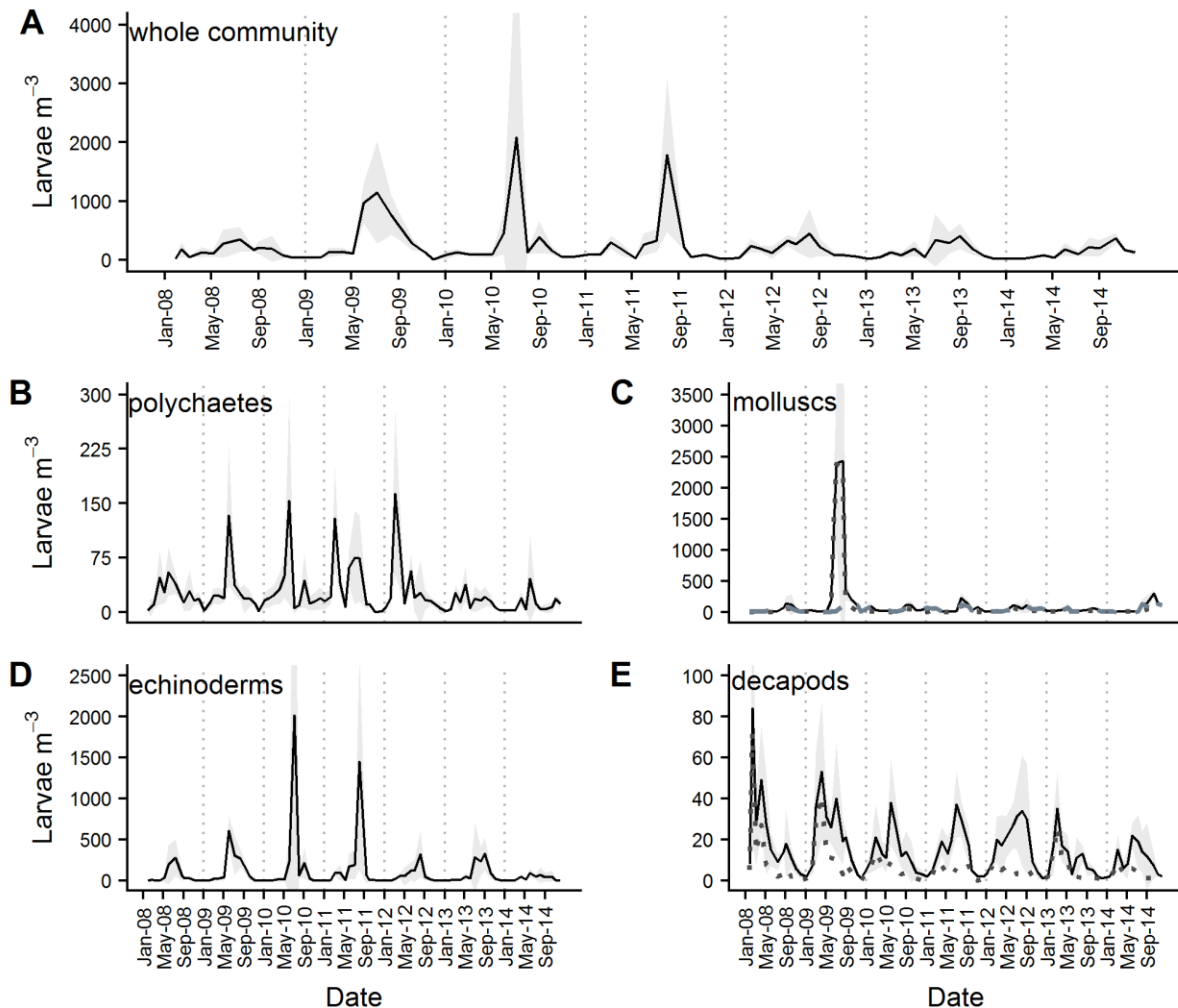


249
250    **Fig. 4.** Abundance of benthic larvae in the water column for (A) the four major benthic phyla, (B) polychaetes,
251    (C) molluscs, (D) echinoderms and (E) decapod crustaceans during the study period July 2008 – May 2014. The
252    grey dotted line in panel (C) is the abundance of gastropod larvae present, while the grey dashed line is the
253    abundance of bivalve larvae. The grey dotted line in panel (E) is the abundance of brachyuran larvae present.
254    Grey shading represents standard deviation from the mean calculated for the phyla.

255

256    Both the abundance and wet biomass of suspension and deposit feeders was relatively

257    stable over the course of the time series, although suspension feeder abundance increased

258    sharply in summer 2013 and spring 2014 (Figure 5A). Likewise, the wet biomass of

259    suspension and deposit feeders reached a peak in spring 2014 (Figure 5B). In terms of

260    abundance, omnivores were the most dominant feeding guild at L4 (Figure 5C), while the

261    predator/scavenger guild dominated in terms of wet biomass (Figure 5F). The

262    predators/scavengers (Figure 5E) exhibited an increase in abundance in spring 2014,

263    although it was not as dramatic as that recorded for the suspension feeders. The number of

264    taxa mapped into each feeding guild is shown in Table 2. The majority of taxa recorded were

265    predators/scavengers, while sub-surface deposit feeders were represented by only a small

266    number of taxa.
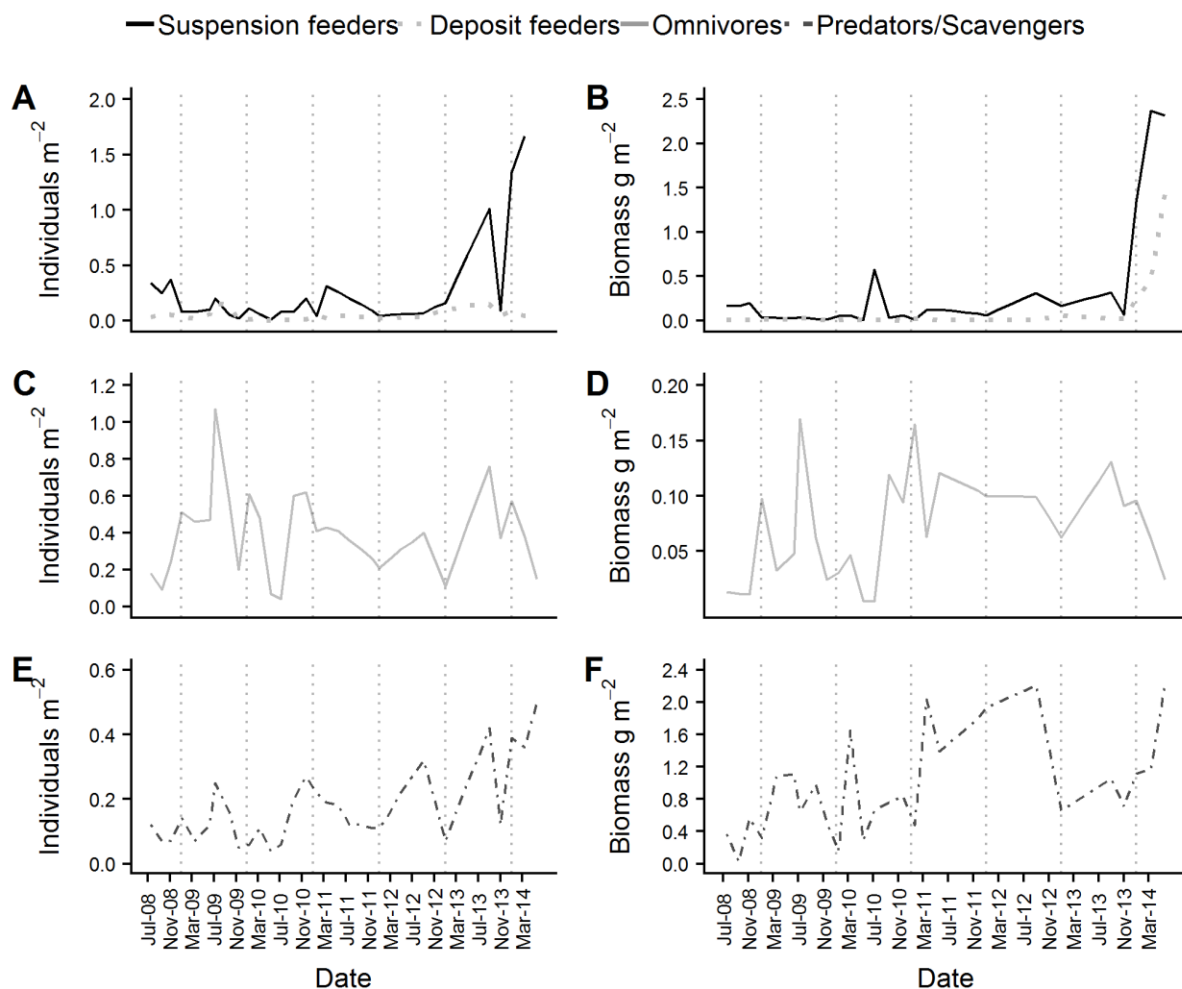


267
268    **Fig. 5.** Abundance (left hand side of the panel) and wet biomass (right hand side of the panel) of the main
269    feeding guilds found at L4. (A) and (B) are suspension and deposit feeders, (C) and (D) are omnivores and (E)
270    and (F) are predators/scavengers. Deposit feeders were split into surface and sub-surface feeders for the
271    purposes of analysis, but were combined for plotting.

272

273 **Table 2:** The number of taxa mapped into each feeding guild, and their percent contribution to the total
274 number of species recorded at station L4 between July 2008 – May 2014.

| Feeding guild | Number of taxa | % of total number of species recorded |
|---|---|---|
| Suspension feeders | 39 | 27.2 |
| Surface deposit feeders | 19 | 13.3 |
| Sub-surface deposit feeders | 8 | 5.6 |
| Omnivores | 25 | 17.5 |
| Predators/scavengers | 52 | 36.4 |
| **Total** | **143** | **100** |

275

276 **Overall structure of the epibenthic community**

277 There was some structure apparent in the overall means of the community abundance and

278 wet biomass series. Abundance increased from January to reach a peak in May, before

279 declining again over the summer. There was a second, smaller increase apparent in

280 September, and abundance then decreased steadily through the winter (Figure 6A). Wet

281 biomass peaked in March, and remained fairly high over the spring before declining from

282 May onward. There was a second, smaller increase in community wet biomass in September

283 (Figure 6B). The first peak in abundance can be attributed to an increase in abundance of

284 molluscs (Figure 6E) which, when added to an already high abundance of crustaceans

285 (Figure 6I), raised community abundance to ~1.2 individuals m$^{-2}$. While mollusc abundance

286 dropped sharply after the May maximum (Figure 6E), the decline in community abundance

287 was more gradual, due to an increase in the abundance of crustaceans (Figure 6I), and

288 numbers of polychaetes and echinoderms remaining relatively high (Figure 6C and G). This

289 increase in crustacean abundance, which reached its maximum in September, was the

290 primary contributor to the second community abundance peak (Figure 6A). The biomass

291 maximum in March was predominantly caused by a sharp increase in biomass of

292     echinoderms (Figure 6H), and polychaetes (Figure 6D). Both molluscs and crustaceans

293     (Figure 6F and J) reached a biomass peak in May, ensuring that community biomass

294     remained high throughout the spring (Figure 6B).
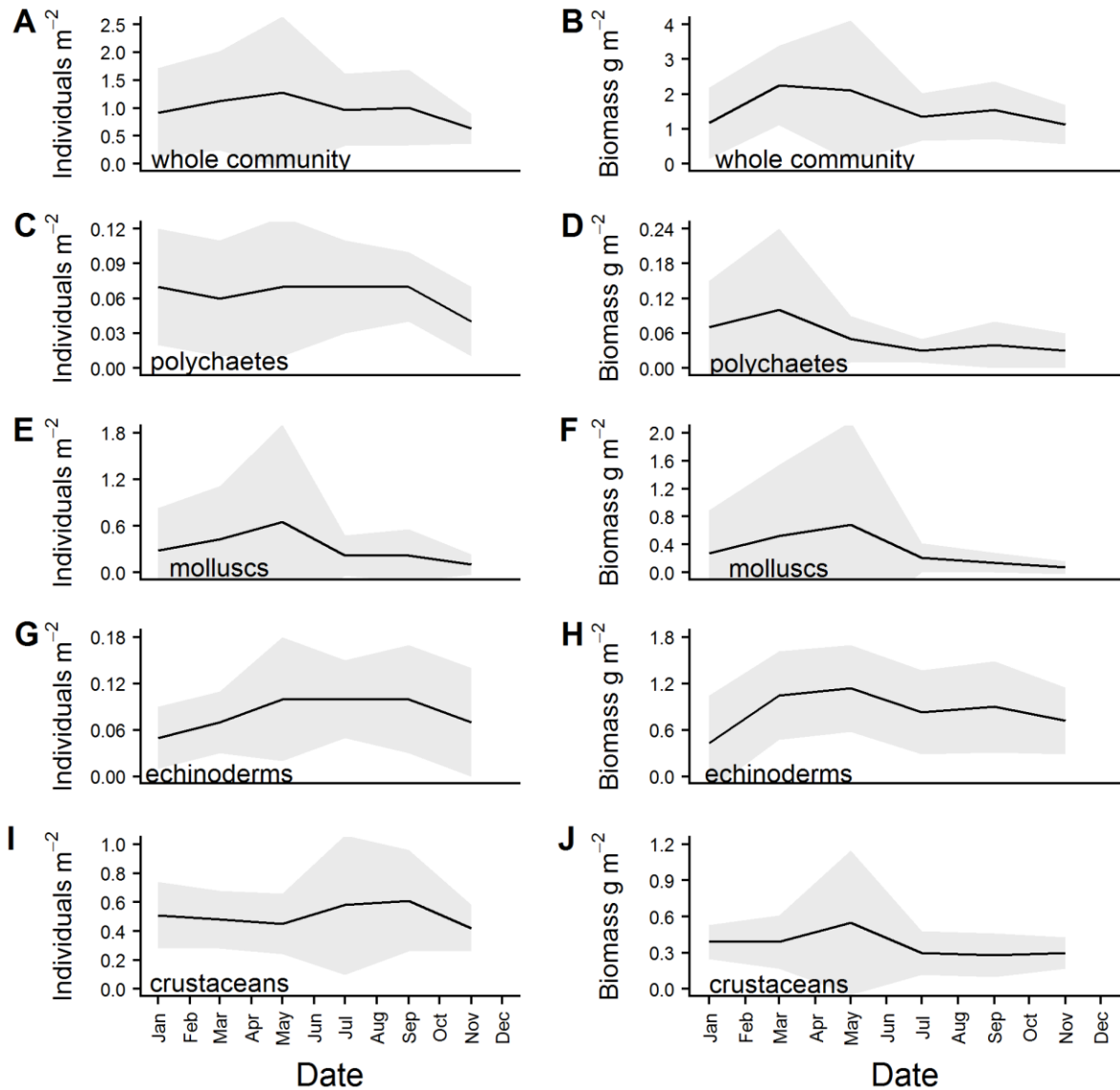


295
296   **Fig. 6.** Overall means for community and major phyla abundance (left hand side of panel) and wet biomass
297   (right hand side of panel), calculated from data for each sampling month (Jan, Mar, May, Jul, Sept, Nov) pooled
298   across the whole time series. Shaded grey area represents standard deviation of the mean.

299

300     Average individual body mass of the whole community reached a maximum in March, and

301     then decreased steadily over the summer, before increasing again from September (Figure

302    7A). Polychaete (Figure 7A) individual body mass exhibited a similar pattern, although the

303    decline after March was much steeper. Peaks in body mass for crustaceans and molluscs

304    (Figure 7A) were reached in May, again with a decrease over the summer, and an increase

305    beginning in September. Echinoderms (Figure 7B) reached a maximum in March, and body

306    mass remained high into May before declining. There was a subsequent increase in

307    echinoderm body mass although it started earlier than in other taxa, in July.
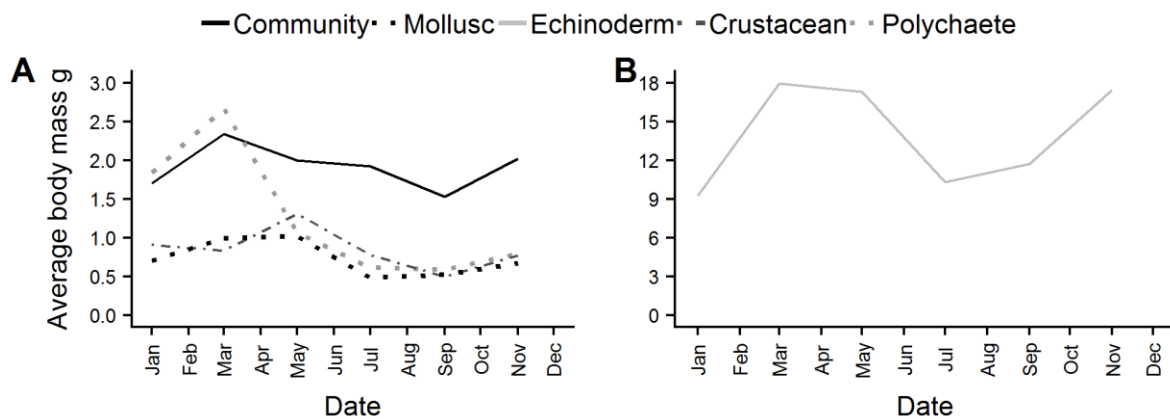


308
309    **Fig. 7.** Average individual body mass of the whole epibenthic community, molluscs, polychaetes and
310    crustaceans (A), and echinoderms (B).

311

312    Overall monthly means of larval abundance show that the highest numbers of benthic

313    larvae are recorded in the water column in July/August (Figure 8A). While all four major

314    phyla contribute to this peak in abundance, it is largely attributable to high abundances of

315    molluscs (Figure 8C) and echinoderms (Figure 8D). Different classes of mollusc appear to

316    have different spawning times at L4, with gastropod larvae abundances (grey dotted line,

317    Figure 8C) in the water column peaking slightly earlier than bivalve larvae (grey dashed line,

318    Figure 8C). Polychaete larvae exhibited two peaks, in March and June (Figure 8B), while

319    decapod larvae abundances peaked in March/April (Figure 8E), and remained relatively high

320    throughout the summer, before declining steadily from July. Much of the initial peak in

321    decapod larval abundance can be attributed to brachyuran larvae (grey dotted line, Figure

322    8E), although this declines after April.
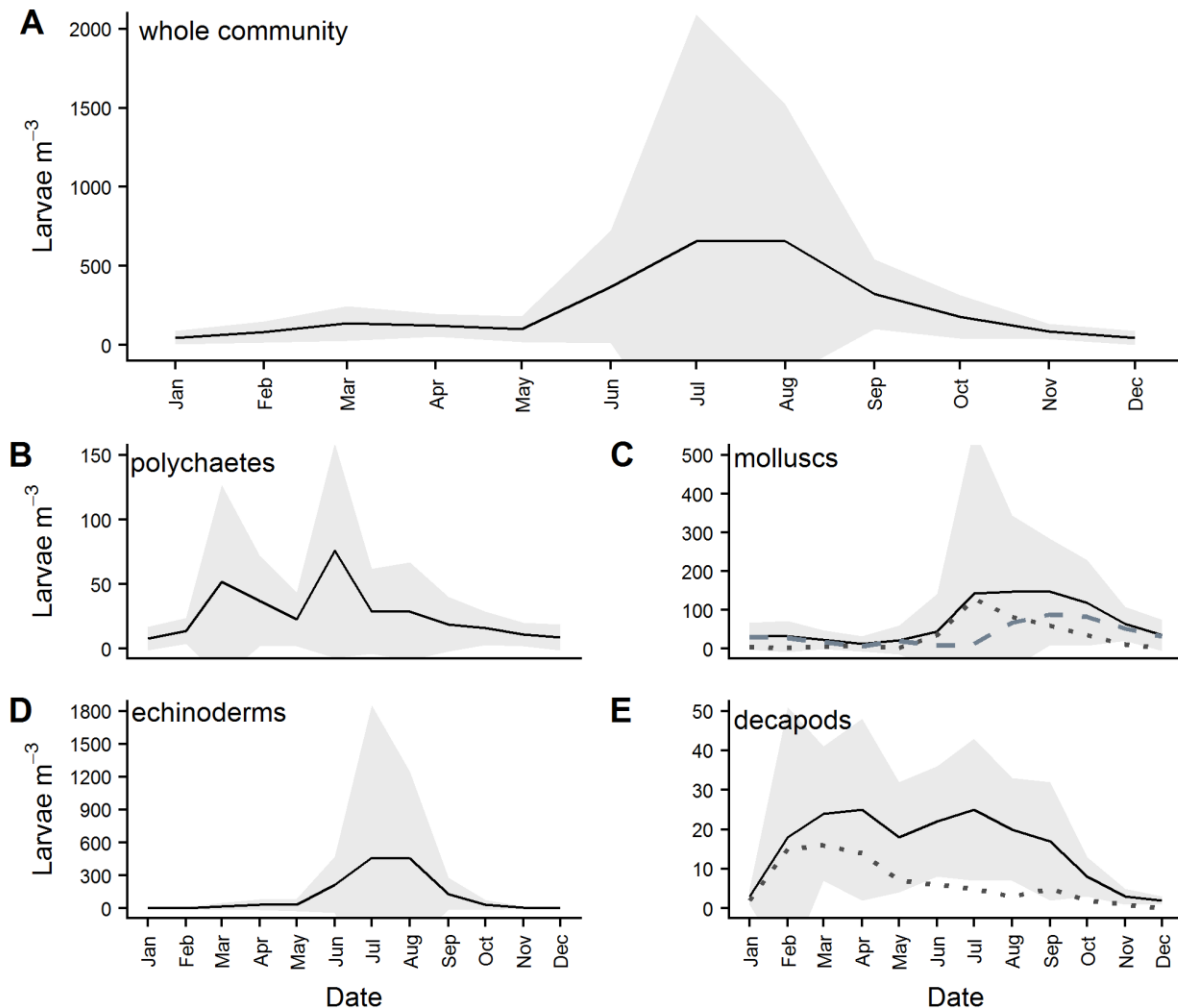


323
324    **Fig. 8.** Overall monthly mean abundances of benthic larvae in the water column for (A) the four major benthic
325    phyla combined, (B) polychaetes, (C) molluscs, (D) echinoderms and (E) decapod crustaceans. Means were
326    calculated for each month from data pooled across the whole time series. The grey dotted line in panel (C) is
327    the abundance of gastropod larvae present, while the grey dashed line is the abundance of bivalve larvae. The
328    grey dotted line in panel (E) is the abundance of brachyuran larvae present. Grey shading represents standard
329    deviation from the mean calculated for the phyla.

330

331    **Drivers of variation in epibenthic community structure**

332    NMDS ordination revealed no clear seasonal pattern over the course of the time series in

333    either the abundance or wet biomass data, but there were some interannual differences in

334    the abundance data. Analysis of community abundance identified 3 clusters (Figure 9A).

335     Cluster 1 consists of the years 2008, 2013 and 2014. Cluster 2 contains the years 2011 and

336     2012, and cluster 3 contains the years 2009 and 2010. The differences between these three

337     clusters were driven by differences in the relative abundances of the two dominant species.

338     In cluster 1, the gastropod *T. communis* was dominant, whereas in cluster 3 the anomuran

339     crab *Anapagurus laevis* was dominant. Cluster 2 was characterised by a more even

340     community structure, with no single species dominant. There were no clear interannual

341     patterns identified in the biomass data, with most data points falling into a single cluster

342     (Figure 9B). The only months to fall outside this cluster were January 2010 and January

343     2011. This appears to be due to the fact that during these months, the asteroid *M. glacialis*,

344     which dominated the biomass over the course of the time series, was not recorded.
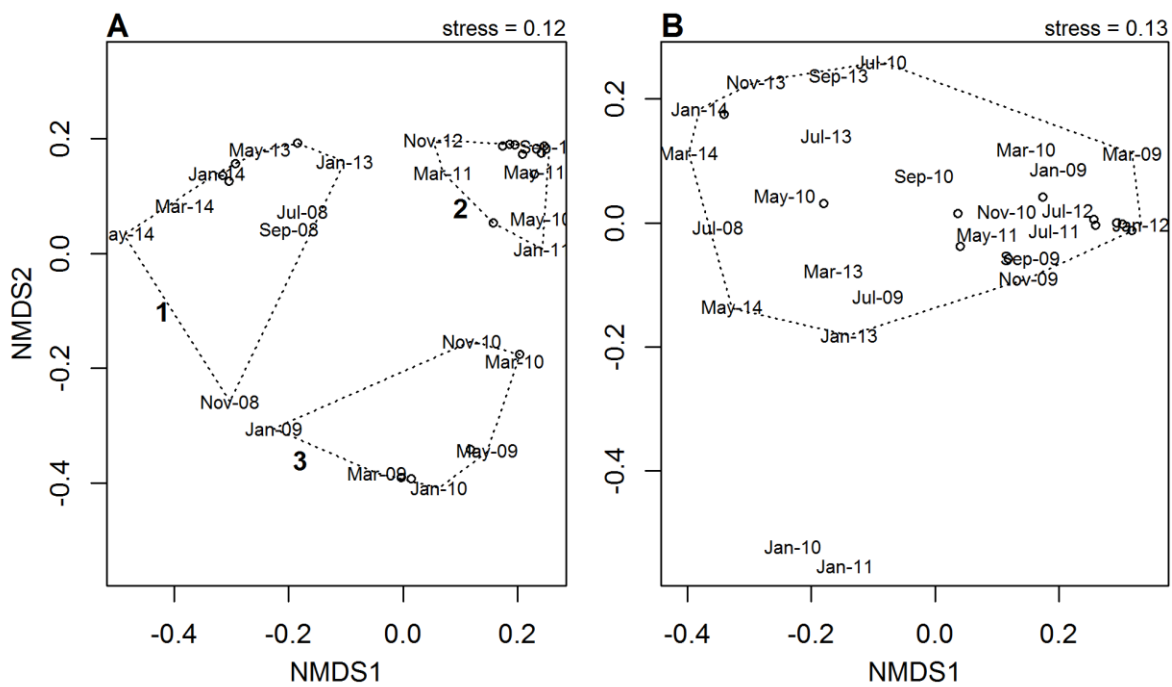


345
346     **Fig. 9.** NMDS ordination of community abundance (A) and wet biomass (B) data over the course of the time
347     series July 2008 – May 2014. Although there is no seasonal pattern evident in either the abundance or wet
348     biomass data, there is some interannual variation in the abundance data, predominantly due to the relative
349     variations in abundance of the dominant species.

350

351    All significant results of the cross correlation analysis are shown in Table 3. There was no

352    significant relationship between total community abundance and any of the explanatory

353    environmental variables. Community wet biomass correlated with both phytoplankton

354    carbon and temperature, with a 6 month lag in both cases.  If both carbon and temperature

355    are left in the linear model as explanatory variables, the model fit improves and both terms

356    remain significant. There was no significant interaction effect detected between carbon and

357    temperature. Of the four major phyla, only echinoderm biomass exhibited significant

358    relationships with any of the explanatory environmental variables, correlating with

359    temperature with a 6 month lag. Both mollusc and echinoderm abundance were correlated

360    with larval abundance. Mollusc abundance was correlated with total mollusc larval

361    abundance and gastropod larval abundance with a 4.5 year lag in each case. Echinoderm

362    abundance is correlated with echinoderm larval abundance with a lag of 3 years.


363    Analysis of the community when grouped into feeding guilds (suspension feeders, surface

364    and sub-surface deposit feeders, omnivores and predators/scavengers) showed a

365    relationship between predator/scavenger biomass and phytoplankton carbon with a 6

366    month lag (Table 3).  As with community wet biomass, this group also exhibited a

367    relationship with temperature, again with a six month lag. If both of these terms are left in

368    the model, they remain significant and the overall fit improves (Table 3). There was no

369    significant interaction effect detected however. This analysis also showed a relationship

370    between phytoplankton carbon and surface-deposit feeder abundance, with an immediate

371    response from the surface-deposit feeders to phytodetrital input (Table 3).


372
373
374

375 **Table 3.** Significant models identifying relationships between the epibenthic community and environmental
376 variables. In those models where two predictors were included, the significance value for the whole model has
377 been given in the column for $R^2$, and the significance value for individual predictors has been given in the
378 coefficients column.

| Response variable | Predictor | lag | $R^2$ ($p$) | Coefficient ($p$) |
|---|---|---|---|---|
| Community biomass | phytoplankton carbon | 6 months | 0.4 (0.0001) | 0.1 |
| Community biomass | temperature | 6months | 0.43 (0.0001) | 0.18 |
| Community biomass | carbon + temperature | 6months | 0.6 (<0.0001) | Carbon = 0.1(0.003) Temperature = 0.14 (0.002) |
| Echinoderm biomass | temperature | 6 months | 0.37 (0.0003) | 0.11 |
| Predator/scavenger biomass | phytoplankton carbon | 6 months | 0.32 (0.0006) | 0.1 |
| Predator/scavenger biomass | temperature | 6 months | 0.38 (0.0003) | 0.13 |
| Predator/scavenger biomass | carbon + temperature | 6 months | 0.53 (<0.0001) | Carbon = 0.09 (0.02) Temperature = 0.12 (0.002) |
| Surface-deposit feeder abundance | phytoplankton carbon | 0 months | 0.42 (0.02) | 0.09 |
| Mollusc abundance | mollusc larvae | 4.5 years | 0.81 (0.001) | 0.21 |
| Mollusc abundance | gastropod larvae | 4.5 years | 0.61 (0.01) | 0.17 |
| Echinoderm abundance | echinoderm larvae | 3 years | 0.58 (0.002) | 0.1 |

379

## DISCUSSION

381 Time series data (collected every other month during the period July 2008 – May 2014) for

382 benthic epifauna at Station L4 were analysed to establish patterns in community

383 abundance, wet biomass and composition, and to link any observed patterns to

384 environmental variables. A clear response to the input of organic material from

385 phytoplankton blooms was detected, with sediment surface living deposit feeders showing

386 an immediate increase in abundance, while predators and scavengers responded later, with

387    an increase in biomass. An inter-annual change in community composition was also

388    detected, as the community shifted from one dominated by the anomuran *Anapagurus*

389    *laevis* to one dominated by the gastropod *Turitella communis.*

390    There is some evidence for benthic-pelagic coupling at Station L4, demonstrated by the

391    correlation between surface-deposit feeder abundance and phytoplankton carbon. This

392    pattern has been previously observed in the macro-infauna at L4, with deposit feeders

393    rapidly responding to phytodetrital input with an increase in abundance, while predators

394    and scavengers responded more slowly with an increase in biomass (Zhang et al., 2015).

395    While many studies have concluded that benthic communities can be structured by

396    phytodetrital input over both short-term and decadal scales (Buchanan, 1993, Clare et al.,

397    2017, Dauwe et al., 1998, Frid et al., 2009a, Frid et al., 2009b, Josefson et al., 1993, Wieking

398    & Kröncke, 2005) clear responses to organic input from benthic fauna can be difficult to

399    detect (Graf et al., 1982, Reiss & Kröncke, 2004). The "food bank" hypothesis suggests that

400    large reserves of labile organic matter in sediments can sustain benthic communities at

401    constant levels of abundance on a year round basis, and clear responses to phytodetrital

402    input are difficult to detect as a consequence (Kędra et al., 2012, Mincks et al., 2005,

403    Włodarska-Kowalczuk et al., 2016). This appears not to be the case at Station L4, which is

404    fairly impoverished in terms of organic matter content, with organic carbon contributing

405    only 0.4% to total sediment mass (Zhang et al., 2015). It is possible that this comparatively

406    low sediment carbon content results in the epibenthic community at L4 being food limited,

407    and so the seasonal pulses of phytodetrital input elicit measurable responses. Furthermore,

408    spring bloom sedimentation in temperate areas can often occur when bottom water

409    temperatures are low, and benthic faunal responses are limited as a result. Weeks can pass

410    before water temperature increases enough to allow for macrofaunal feeding (Lopez &

411    Levinton, 2011). It is possible that the particular hydrographic conditions in the Western

412    English Channel, where bottom water temperatures fluctuate less than in other temperate

413    systems, result in early spring temperatures high enough for the surface-deposit feeders in

414    the L4 community to respond immediately.

415    Interestingly, there was no apparent decrease in diversity associated with the sedimentation

416    of the spring bloom. In macrofaunal communities, enriched sediments are typically rapidly

417    colonised by a few opportunist, fast-reproducing species (Widbom & Frithsen, 1995) which

418    can take advantage of the fresh organic matter, generally resulting in a reduction in diversity

419    (Chamberlain et al., 2001, Widdicombe & Austen, 2001). As noted above, epibenthic

420    surface-deposit feeders did show an immediate increase in abundance with the arrival of

421    phytodetritus, but rarefied richness values for May (post sedimentation) are generally equal

422    to or higher than values for March (pre-bloom). It is possible that these values are indirect

423    evidence of predation. Predation is thought to play a key role in marine sedimentary

424    systems, due in part to the lack of clear evidence for competitive exclusion (Peterson, 1979,

425    Woodin, 1999). While detection of predation is challenging, and numerous studies have

426    found no consistent regulatory role (Thrush, 1999), it has been suggested that epibenthic

427    predators can equalise numbers and increase evenness by preying preferentially on

428    numerically dominant species (Quijón & Snelgrove, 2005). Given the fact that L4 community

429    wet biomass is predominantly represented by predators and scavengers, there is a

430    possibility that opportunistic deposit feeders are prevented from becoming dominant after

431    sedimentation of the spring bloom by the feeding of the predator/scavenger group. This

432    pattern in the regulation of benthic community structure has been noted before (Posey et

433    al., 1995), with those authors concluding that the presence or absence of predation may

434    alter the visible response of the benthos to organic enrichment. While there was no direct

435    evidence of predator-prey interactions (e.g. a clear relationship between deposit-feeder and

436    predator/scavenger abundance or biomass, as defined by Lotka-Volterra type models)

437    detected in this study, the patterns in species richness observed would seem to support the

438    proposal that epibenthic predators can be of major influence in benthic communities

439    (Quijón & Snelgrove, 2005), and may diminish or counterbalance the changes in prey

440    species that result from phytodetrital input.

441    A relationship between community wet biomass and both bottom-water temperature and

442    phytoplankton carbon was detected at Station L4, although there was no significant

443    interaction between the two predictors and their effects on biomass. This leads us to

444    propose that temperature and phytoplankton carbon primarily influence biomass at

445    different times of the year. Community wet biomass peaks in March/May, driven

446    predominantly by an increase in biomass of echinoderms and molluscs. Individual body

447    mass curves for these two phyla show an identical pattern, with a maximum also being

448    reached in March/May. It is possible that this is representative of the development of the

449    gonads in preparation for spawning. Several studies have found that ripe gonads in these

450    two phyla can make a significant contribution to body mass (Alunno-Bruscia et al., 2011,

451    Barker & Nichols, 1983, Berthelin et al., 2000, Freeman et al., 2001, Nichols & Barker, 1984a,

452    Nichols & Barker, 1984b). This view would appear to be supported by the increase in

453    benthic larvae (of which mollusc and echinoderm larvae are recorded in the highest

454    numbers) in the water column from May onwards, while community, mollusc and

455    echinoderm biomass decreases after May, perhaps indicating spent individuals. We suggest

456    that this pre-spawning biomass is influenced by temperature. Several studies have noted

457    the role of temperature in triggering gonad development in marine invertebrate species

458    (Aktaş et al., 2003, Balogh et al., 2018, Herrmann et al., 2009, Sastry, 1966, Sastry & Blake,

459    1971), and it is possible that gonad development at L4 is initiated by the high water

460    temperatures recorded in September, with full maturation and spawning occurring the

461    following spring. Gonad development and maturation in some temperate echinoderm &

462    mollusc species has been recorded to take up to six months, which would be in keeping with

463    the six-month lag between peaks in temperature and biomass identified in this study

464    (Bowner, 1982, Kim et al., 2016, Sköld & Gunnarsson, 1996). Although there was no

465    significant interaction between temperature and phytoplankton carbon and their effects on

466    biomass detected in this study, food availability will clearly affect gonad development as it

467    dictates the nutritional status of an individual (Nunes & Jangoux, 2004), and the autumn

468    bloom characteristic of Station L4, along with the carbon from seaweed detritus which

469    contributes to winter organic matter in the area (Queirós et al., 2019) is likely to help fuel

470    gonad development over the winter. In contrast to maximum temperatures, maximum

471    phytoplankton carbon values are generally recorded in April/May, with a response in

472    community biomass seen six months later. It is possible that the relationship between

473    phytoplankton carbon and biomass is indicative of somatic growth, which occurs after

474    spawning has taken place in the spring. The seasonal prioritisation of either sexual or

475    somatic growth in benthic fauna is well documented, particularly in echinoderms (Coma et

476    al., 1998, Greenwood, 1980, Guillou & Michel, 1993, Lozano et al., 1995, Peterson & Fegley,

477    1986). This shift in energetic prioritisation is often related to reproductive effort being

478    concentrated at a time favourable to the survival of offspring, e.g. spawning prior to or

479    coincident with a phytoplankton bloom (Giangrande et al., 1994). The same lagged

480    relationship between biomass, temperature and phytoplankton carbon was also recorded in

481    the predator/scavenger group. The biomass of this feeding guild is dominated by

482    echinoderms (70%), so the postulated relationships outlined above could also be driving the

483    responses of this group.

484    The role of larval supply as a determinant of the structure and dynamics of marine

485    populations (i.e. supply side ecology) has long been discussed (De Wolf, 1973, Lewin, 1986,

486    Thorson, 1950, Underwood & Fairweather, 1989), and there is much evidence to suggest

487    that variations in recruitment can contribute to patterns of abundance and demographics in

488    adult populations of fish (Doherty & Fowler, 1994, Williams, 1980), barnacles (Gaines &

489    Roughgarden, 1985, Scrosati & Ellrich, 2017, Sutherland, 1990), mussels (Scrosati & Ellrich,

490    2017) and bryozoans (Hughes, 1990). We propose that larval recruitment of dominant species

491    is also a key influence on benthic community structure and composition at Station L4. The

492    dramatic increase in community and suspension feeder abundance and biomass in May

493    2014, and the shift in community structure (from one dominated by *Anapagurus laevis* in

494    2009 to one dominated by *T. communis* in 2013/2014) are likely due to the sieve

495    recruitment (the point at which individuals recruited to the population reach a size where

496    they would be retained on the sieve mesh) of the high numbers of gastropod larvae present

497    in the plankton in 2009. Previous studies of benthic recruitment have stressed that sieve

498    recruitment can be far removed in time from actual settlement (Buchanan & Moore, 1986),

499    as many benthic macrofaunal settlers are of meiofaunal size. The lag of 4.5 years identified

500    between mollusc abundance and gastropod larval abundance likely reflects the fact that any

501    newly settled animal needs to reach a size both big enough to be collected by the dredge,

502    and to be retained on the 4mm sieve used in this study.

503 Analysis of the first six years of the epibenthic time series at Station L4 reveals some

504 temporal structure in community abundance and wet biomass, apparently influenced by

505 both bottom water temperature and seasonal phytodetrital input. We suggest that the

506 spring phytoplankton bloom fuels somatic growth, while gonad development and

507 maturation is triggered by warmer water temperature in the autumn, resulting in a pre-

508 spawning biomass peak evident in early spring. Different functional groups within the

509 community were found to respond to the bloom in specific ways, a result that is in keeping

510 with previous studies of the L4 macro-benthos. While benthic faunal responses to changes

511 in water temperatures have been previously recorded in other temperate systems, clear

512 responses to phytodetrital input as seen here are less common. We suggest that the reason

513 we can detect this response is a combination of two factors. 1) The relative impoverishment

514 of the L4 sediment in terms of organic content, indicating a food limited community, and 2)

515 the comparatively small range of bottom water temperatures, resulting in relatively mild

516 winter/early spring conditions and a community that is able to take immediate advantage of

517 bloom sedimentation.

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