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## Surprisingly diversified macrofauna in mobile gravels and pebbles from high-energy hydrodynamic environment of the 'Raz Blanchard' (English Channel)

Foveau Aurélie <sup>1,\*</sup>, Dauvin Jean-Claude <sup>1</sup>

<sup>1</sup> Normandie Univ., UNICAEN, UNIROUEN, Laboratoire Morphodynamique Continentale et Côtière, UMR CNRS 6143 M2C, 24, rue des Tilleuls, F-14000 Caen, France

\* Corresponding author : Aurélie Foveau, email address : [aurelie.foveau@ifremer.fr](mailto:aurelie.foveau@ifremer.fr)

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### Abstract :

Our study concerns the sampling of patches of mobile gravel and pebbles at 14 stations (25 to 66 m water depth) in an area of hard bottom located in the 'Raz Blanchard' (between Cap de La Hague in France and Alderney in the Channel Islands, UK). The samples collected from these benthic habitats with scattered fauna were sieved on 1-mm mesh and subjected to meticulous sorting, revealing the presence of a highly diversified mobile fauna. The epifauna and vagile macrofauna (>1 mm) account for 140 taxa (120 species, 17 genera and three other levels of identification). Amphipods and polychaetes dominate the taxonomic richness, while crustaceans represent 75% of the fauna. Among these taxa, two species are new for the English Channel marine fauna. Biological Traits Analysis (BTA) indicates that the species show adaptation to such strong hydrodynamic conditions, owing to their small size which allows them to live in interstitial environments and on biological substrates, and which can locally modify the hydrodynamic conditions.

### Highlights

► The Raz Blanchard is an area of high-energy hydrodynamics with a hard and irregular seabed. ► The fauna in these particular benthic habitats is highly diversified. ► The fauna is dominated by crustaceans and polychaetes. ► The fauna is small-sized and interstitial. ► Two species are new for the English Channel.

**Keywords** : Amphipods, Polychaetes, Taxonomic richness, Hard bottom, High-energy environments

## 40 1. Introduction

41

42 The English Channel is characterized by the presence of strong tidal currents which in  
43 some places exceed 3 m/s. The sedimentation of fine particles is impossible in such areas with  
44 strong hydrodynamics, and the sea bed is covered by pebbles and blocks, and sometimes  
45 outcrops of bedrock (Larsonneur et al., 1982). This is the case off the northern coast of  
46 Cotentin and south of the Isle of Wight, where there are projects for the installation of tidal  
47 stream turbines (SEEDA, 2007; Thiébot et al., 2015). Nevertheless, several authors (see  
48 Cabioch, 1968; Retière, 1979; Brown et al., 2002, 2004a, b; Diesing et al., 2009; Coggan and  
49 Diesing 2011, 2012) have described the presence of patches of mobile sediment on hard-  
50 bottoms in high-energy environments in the western and central parts of the English Channel.  
51 In these rocky areas, it is not feasible to sample benthic fauna with grabs since the mobile  
52 coarse sediment covers very small patches. Therefore, sampling is only possible with  
53 equipment such as the Rallier du Baty dredge, which can be used when sediment patches are  
54 encountered (mainly gravels and pebbles) (Cabioch, 1968; Retière, 1979).

55 In such coarse sediments, the grains are smooth, clean and lack any fixed fauna,  
56 reflecting the important role of bed load transport in such high-energy environments, which  
57 are very well oxygenated to a depth of several decimetres beneath the seabed. These  
58 sediments are described as very poor in fauna, in particular when sieving is carried out with a  
59 2 mm mesh (Cabioch, 1968; Retière, 1979).

60 The French Public Body ADEME (Agence de l'Environnement et de la Maîtrise de  
61 l'Energie) supports various Research and Development ("R&D") projects in the domain of  
62 renewable energy, including tidal turbines. In this context, the research project Pile & Tide  
63 was financed by the ADEME and our laboratory was placed in charge of investigating the  
64 benthic habitats in the Raz Blanchard area (seabed composition and benthic communities).

65 Describing or measuring the functioning of ecosystems is difficult. As it encompasses  
66 many phenomena (Hooper et al., 2005), the overall functioning of an ecosystem is complex  
67 and involves many factors relating to the chemical, physical and biological components of the

68 system. The use of multiple variables offers an appropriate approach to describe the  
69 functioning of entire ecosystems (Duffy and Stachowicz, 2006). Biological Traits Analysis  
70 (BTA) is a tool developed for this purpose, which takes into account the biological  
71 characteristics of benthic species (life-history, morphological and behavioural aspects) to  
72 analyse the functioning of benthic communities (Verissimo et al., 2012). BTA has been  
73 applied to marine ecosystems (see for example Bremner et al., 2006) or in freshwater  
74 environments (see Menezes et al., 2010). Even if BTA requires further improvement, previous  
75 research can provide information on the general relationships between traits, species and their  
76 environment. This method appears to be useful in two domains: (1) assessing the effects of  
77 human activities and subsequent management strategies and (2) making predictions about  
78 future changes (Bremner, 2008).

79 The main objectives of this paper are 1) to describe the main characteristics of the  
80 representative fauna collected in such high-energy hydrodynamic environments and 2) to  
81 present the main biological traits of life of fauna adapted to coarse mobile sediment habitats.

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## 83 **2. Materials and methods**

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### 85 *2.1 Study site*

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87 The Raz Blanchard is located in the western part of the English Channel to the North of  
88 the Normand-Breton Gulf, occupying an area with the strongest tidal currents in Europe. It is  
89 situated in a strait between the north-western tip of the Cotentin (Cap de La Hague, France)  
90 and the island of Alderney (UK). At its northern limit, the Raz Blanchard is between 2 and 5  
91 nautical miles wide, being situated on a line joining the lighthouses of Mannez on Alderney  
92 and La Hague on the Cotentin. To the south, it is delimited by a line between the Schôle bank  
93 and the Cap de Flamanville, to the west by a line between Mannez lighthouse and the Schôle  
94 bank and to the east by a line between the Cap de Flamanville and the 'Basse-Bréfort' buoy  
95 (Fig. 1). The water depth is comprised between 25 and 66 m.

96 The sea bed is complex, made up of a substratum composed of granite and calcareous  
97 rocks of Cambrian, Silurian and Cretaceous age (Boillot, 1964; Hommeril, 1967). The  
98 surficial sediments, where they exist, are composed of gravel and pebbles (Hommeril, 1967;  
99 Larsonneur et al., 1982).

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## 2.2 Field investigation

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A total of 38 stations were visited during three sampling campaigns: (1) 28-29 April 2015; (2) 19-23 October 2015 and (3) 1-2 April 2016 (Fig. 1). Dredges were towed along the bottom for 5 minutes (except in cases where the gear was hauled off the bottom for security reasons). Out these stations, 20 dredges were unsuccessful and only 14 yielded a sufficient volume of sediment for the purposes of study. In the remaining four cases, the sample was of insufficient size to be studied. The sampling depth is comprised between 25 to 66 m. Nevertheless, the volume of sediment sampled at the 14 successful stations varied from 0.5 L to 32 L. For marine sediments sampled with the Rallier du Baty dredge, Cabioch (1968) and Retière (1979) estimated that a minimum sediment volume of 30 L is required to obtain a representative sample of the species and benthic communities in the English Channel. Only three sampling stations yielded a sediment volume  $\geq 30$  L (Table 2), with one sample having a volume of 15 L and the 10 others having small volumes between 0.5 and 2 L. Fig. 2 illustrates the types of sampled sediment; i.e. gravels and pebbles with or without sessile epifauna. The number of empty dredges and the low volume of sediment collected highlight the difficulties of sampling on such types of seabed. Samples were sieved through a 1-mm circular mesh and preserved in formalin solution and then in 70 % ethanol after the sorting step. In this particular area (where few (if any) benthic samples have been collected), we sieved our samples through 1-mm circular mesh in the laboratory. For coarser sediments collected in the English Channel, it is common practice to sieve through 2-mm circular mesh on board the oceanographic vessel (see Foveau, 2009 and Lozach, 2011 for examples). In the present study, to ensure an adequate definition of this poorly known benthic community, we favoured the use of a 1-mm sieve.

Species determination was carried out in the laboratory using a binocular microscope and relevant literature (see collection of the Synopsis of the British Fauna, for example). In the present study, mainly the vagile epifauna and infauna are taken into account. However, due to the high relevance of some fixed species (number of collected individuals, natural heritage value or engineer species), we added three species to the analysis (*Musculus discors*, *Spirobranchus triqueter* and *Sabellaria spinulosa*).

### 135 2.3 Diversity

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137 Due to the small number of successful dredges, we consider samples from all fourteen  
138 stations where dredge sampling recovered sediment and macrobenthic fauna. All the data used  
139 for the calculations were normalized to the same sampling volume. The diversity indices, *i.e.*  
140 taxonomic richness (number of taxa), Shannon index ( $H'$ , using log<sub>2</sub> base and expressed in  
141 bits because this measure of diversity is derived from information theory) and Pielou's  
142 evenness ( $J$ ) are calculated from the collected fauna. A  $k$ -dominance curve is plotted to  
143 illustrate the quantitative distribution of the individuals among the taxa.

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### 145 2.4 Biological Traits of Life

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147 Biological Traits Analysis (BTA) is carried out on the recorded species as an alternative to  
148 studying the relative taxon composition (Bremner et al., 2003, 2006). Ten Biological Traits  
149 (BT) selected here cover different aspects of the life history, morphology and behaviour of  
150 each taxon: position on the substratum, habit, feeding mode, adult mobility, bioturbation, size,  
151 life span, developmental mechanisms, substratum preferences and ecological groups (Table  
152 1). Each trait is divided into modalities (49 across the 10 studied traits) (Table 1). The  
153 significance of the selected BTs with regard to benthic functioning is discussed in Garcia  
154 (2010), Verisissimo et al. (2012) and Bolam and Eggleton (2014).

155 Information for assigning taxa to functional traits is obtained from various sources  
156 including the PhD thesis of Garcia (2010), the WORMS site (<http://www.marinespecies.org>;  
157 accessed on 15 September 2016), the UK Marlin site (<http://www.marlin.ac.uk/biotic/>;  
158 accessed on 15 September 2016), scientific journals and the scientific expertise of the authors.  
159 When reliable information is missing, data are considered from the phylogenetic nearest  
160 neighbour taxa. The resulting 'traits by station' data matrix is then submitted to multivariate  
161 analysis.

162 The Biological Traits Analysis is performed following the approach of Rigolet et al.  
163 (2014). The fuzzy coded 'species by trait' matrix is computed using a Fuzzy coded multiple  
164 analysis (FCA). The FCA output (coordinates of taxa on the first axes) is used to plot a  
165 dendrogram using Ward's linkage method based on Euclidean distances (Ward, 1963).  
166 Clusters of species exhibiting similar traits are then defined by selecting a given partitioning  
167 level. Finally, a biological profile is created for each cluster, showing for each trait the  
168 proportion of modalities exhibited by the cluster (Usseglio-Polatera et al., 2000).

### 169 3. Results

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#### 171 3.1 Main characteristics of the sampled fauna

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173 A total of 4,748 individuals are recorded from the 14 sampling stations. From  
174 standardized data expressed in terms of numbers of individuals per 1 L of sediment, we obtain  
175 a mean value of 170 ind/L, while the numbers per station varies from 8.5 at station PT4 to 484  
176 at station PT10 (Table 2). One mollusc taxon (*Musculus discors*) makes up more than 1,000  
177 individuals among the collected fauna, while three amphipods (*Elasmopus thalyae*,  
178 *Gammaropsis maculata* and *Maerella tenuimana*) account for > 300 individuals, five other  
179 taxa > 100 individuals and 42 other taxa  $\geq$  10 individuals. The eight dominant species  
180 represent 67% of the collection, while the amphipods represent 47 % and the polychaetes 13  
181 %. Among the eight dominant species, there are seven crustaceans (five amphipods, one  
182 decapod and a Mysidae) and only one mollusc. The total number of taxa is 140, with 120  
183 species, 17 genera and 3 taxa at a higher level of identification. Two zoological groups  
184 dominate: the crustaceans (69 taxa), which comprise the amphipods (33 species), and the  
185 polychaetes (48 taxa), including the Syllidae (14 taxa) (Fig. 3).

186  $H'$  is comprised between 0.25 (PT14) and 5.24 bits (Moul2), *i.e.* ranging from a poorly  
187 diversified to an extremely diverse community, with a mean value of 3.13 bits, *i.e.* the  
188 sampled community can be considered as very diverse.

189  $J'$  ranges between 0.08 (PT14) and 0.83 (PT4), *i.e.* station PT14 is dominated by one  
190 species and there is a large variation in community structure between species.  $J'$  shows a  
191 mean value of about 0.69, *i.e.* the specimens are spread evenly between the different species.

192 The K-dominance curve (Fig. 4) shows the cumulative species abundance plotted  
193 against the log of species rank. It can be seen that the K-dominance curve has a typical  
194 sigmoidal shape indicating a balanced community of macroinvertebrates. Thus, no dominance  
195 of a single species can be observed, which means that the diversity increases along with the  
196 abundance of the macroinvertebrates.

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#### 198 3.2 Biological Traits of Life

199 The first two axes of the FCA account for more than 80 % of the variability in biological  
200 trait composition (Fig. 5A). Correlation of traits along a given axis is relatively poor for the  
201 different axes used in this analysis.

202 Cluster analysis allows us to divide the stations into three groups; group 1 (PT9, PT10  
203 and PT14) is characterized by larger number of sessile epifauna species (fixed) that do not  
204 bioturbate, showing small size and direct larval development, with medium life-span and  
205 corresponding to sub-surface deposit-feeders. These species have an affinity with coarser  
206 sediment (pebbles) and are sensitive to disturbance. Group 3 is only observed at one station  
207 (PT29), being characterized by infaunal species, which are in most cases tolerant of  
208 disturbance, showing very small size and with a short life-span, corresponding to tube- or  
209 burrow-dwellers with diffusive activity (bioturbation) and characterized by direct larval  
210 development. These species have a preference for coarse mixed sediments and are mostly  
211 non-specific deposit-feeders. Group 2 clusters together all the other stations, and is made up  
212 of various species lacking any particular biological trait that can be discriminated by FCA  
213 (Figs. 5B and C).

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## 215 **4. Discussion**

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### 217 *4.1 General characteristics of the sampled fauna*

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219 The benthic fauna recorded in this study area belongs to an extremely diverse community,  
220 without dominance of any particular species. The major groups of this fauna are made up of  
221 crustaceans, especially the amphipods, as well as polychaetes, in particular the Syllidae.

222 Before performing a biological traits analysis, much time and effort is needed to  
223 collate relevant data on species and ensure the availability of this information (Verissimo et  
224 al., 2012). In the present study, we succeeded in compiling a large and comprehensive  
225 database. Moreover, the large number of traits considered here lead to a more informative  
226 analysis (Bremner et al., 2006). The more commonly selected traits are “trophic groups” (for  
227 the description of community functioning) and “body size” (that gives an idea of the physical  
228 and life-history traits of species) (Paganelli et al., 2012). In the present study, we choose to  
229 add some traits that have been previously disregarded (because of a lack of information in the  
230 literature, Bremner et al., 2003; Paganelli et al., 2012), such as “larval development” or “life-  
231 span”, because we consider they are ecologically relevant. As with previous results obtained  
232 by Bremner et al. (2003, 2006), Marchini et al. (2008) or Paganelli et al. (2012), the benthic  
233 community studied here is governed by traits related to lifestyle and behaviour of the species  
234 (trophic group, adult mobility, bioturbation, life habits and substratum affinity). Traits related  
235 to life-cycle properties (larval development and life-span) are moderately well correlated with

236 FCA axes. This might be due to the dominance of single modalities, such as direct larval  
237 development (but well adapted for an area of high-energy hydrodynamics) or short life-span.  
238 The biological traits highlighted by this analysis of the Raz Blanchard benthic fauna are as  
239 follows: species of small size, belonging to the epifauna but living preferentially in burrows or  
240 tubes in coarse sediments (granules, pebbles and blocks), which participate in bioturbation of  
241 the site. The species may be mobile, probably to allow escape during periods of strong  
242 currents, and are mostly deposit-feeders (specialized or not) with a short life-span and  
243 showing a direct larval development. Finally, most of the sampled species are considered as  
244 sensitive to disturbance.

245 Gravels and coarse sand in the English Channel are known to have a diversified fauna, as  
246 observed in the Bay of Morlaix (1-mm mesh sieving) (Dauvin, 1988a, b). The mean value of  
247 diversity index  $H'$  in the Bay of Morlaix is lower than the mean value observed for coarse  
248 sediments in the eastern basin of the English Channel (mean value of 3.13 bits observed in the  
249 Raz Blanchard as compared to 4.33 bits in the English Channel; Foveau, 2009). The mean  
250 diversity index obtained for this site is comparable to values observed during the  
251 VIDEOCHARM surveys (Lozach, 2011). In areas with such strong hydrodynamic conditions,  
252 we might assume that food availability could be poor, with constant removal of fine-grained  
253 sediment that would cause abrasion on the species or prevent their settlement (Gray, 2002;  
254 Bigot, 2006). Thus, we would expect that this habitat is unable to support a rich community.  
255 For this reason, the species richness found in this area is considered as “surprisingly” diverse.

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#### 257 *4.2 New species for the western part of the English Channel*

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259 A total of 350 individuals of the amphipod *Elasmopus thalyae* Gouillieux & Sorbe, 2015  
260 were collected from eight stations (Table 2). This species was first described on soft and hard  
261 bottoms in Arcachon Bay (France), and is found in the Raz Blanchard on three main  
262 substrates: gravel, pebbles and hard bottoms with sessile epifaunal turf (Foveau and Dauvin,  
263 2017). This finding represents the northernmost localization of the species, which has been  
264 probably previously confused with the Mediterranean species *Elasmopus rapax* Costa 1853.

265 The amphipod *Jassa herdmani* (Walker, 1893) was previously known to exist only in  
266 the eastern part of the English Channel along the Opal coast (Dauvin, 1999). The present  
267 study is the first report of this species (13 individuals from four stations ranging from 40 to 64  
268 m depth) in the western part of the English Channel.



269 The tanaid *Zeuxo holdichi* (Bamber, 1990) was first described from Arcachon Bay by  
270 Bamber in 1990. This species has been recorded in Belgium and in the Netherlands since  
271 2006 and in Germany since 2012, in coastal areas, on and between shells, on sediments, as  
272 well as on red seaweeds. This species is found in the Raz Blanchard at two gravelly stations  
273 (one specimen from each, at water depths of 51 to 64 m), which represent one of the few  
274 subtidal locations of this species, most of the other identified sites being intertidal. It is the  
275 first report of occurrence in high-energy environments. *Z. holdichi* remains rare at most of the  
276 sampled locations, except at Luc-sur-Mer where the species is particularly abundant, although  
277 this occurrence remains enigmatic (Foveau et al., submitted).

278 The syllid species *Prosphaerosyllis chauseyensis* Olivier, Grant, San Martín, Archambault  
279 & McKindsey, 2012 was recently described from a coarse sand intertidal habitat of the  
280 Chausey Islands (Olivier et al., 2012). A single individual was recorded at station PT9 at 50 m  
281 depth. This represents the deepest location of the species in the northern part of the Normano-  
282 Breton Gulf. The syllid *Syllis columbretensis* (Campoy, 1982) is known to range from the  
283 southern part of the Bay of Biscay to the eastern part of the Mediterranean Sea, and is  
284 recorded in the English Channel offshore Dieppe-Le Tréport on coarse sand (Pezy et al., in  
285 press). Many specimens were recorded during the monitoring of an artificial reef in the  
286 eastern Bay of Seine (Luc-sur-Mer beach, Foveau et al., 2015). A total of three individuals, all  
287 collected at station PT1, confirms the presence of this species in the English Channel.

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#### 289 4.3 Consequences of the presence of mixed benthic habitats for the EUNIS Classification 290 and typology of marine habitats

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292 The macrofauna recorded in the Raz Blanchard during the three sampling campaigns in  
293 2015-2016 corresponds to the EUNIS habitat A4.13 'Mixed faunal turf communities on  
294 circalittoral rock' (EEA, 2006). This habitat type occurs on wave-exposed circalittoral  
295 bedrock and boulders, subject to tidal streams ranging from strong to moderately strong: 'This  
296 complex is characterised by its diverse range of hydroids (*Halecium halecinum*, *Nemertesia*  
297 *antennina* and *Nemertesia ramosa*), bryozoans (*Alcyonidium diaphanum*, *Flustra foliacea*,  
298 *Bugula flabellata* and *Bugula plumosa*) and sponges (*Sycon ciliatum*, *Pachymatisma*  
299 *johnstonia*, *Cliona celata*, *Raspailia ramosa*, *Amphilectus fucorum* (= *Esperiopsis fucorum*),  
300 *Hemimycale columella* and *Dysidea fragilis*) forming an often dense and mixed faunal turf.  
301 Other species found within this complex are *Alcyonium digitatum*, *Urticina felina*, *Sagartia*  
302 *elegans*, *Actinothoe sphyrodeta*, *Caryophyllia smithii*, *Pomatoceros triqueter* (= *Pomatoceros*

303 *triqueter*), *Balanus crenatus*, *Cancer pagurus*, *Necora puber*, *Asterias rubens*, *Echinus*  
304 *esculentus* and *Clavelina lepadiformis*'.

305 As shown in the present study, the substrates and sediment characteristics of the Raz  
306 Blanchard area are highly variable, with the seabed showing a marked topographic  
307 heterogeneity, expressed mainly at a small scale by the presence of sediment patches in an  
308 overall rocky environment. Dauvin (2015) has suggested that the EUNIS habitat typology  
309 should be updated to take account of such variations in bed forms and mixed hard soft-bottom  
310 marine habitats. The investigations carried out by CEFAS on the English side of the Channel  
311 have also underlined the need to consider such mixed soft-hard bottoms (see Brown et al.,  
312 2002, 2004 a, b, 2011; Coggan and Diesing, 2012).

313 Hence, the macrofauna found in soft-bottom enclaves on the hard bottom correspond  
314 to two EUNIS habitats: respectively A5.1 Sublittoral coarse sediment and A5.14 Deep  
315 circalittoral coarse sediment. The first habitat type corresponds to coarse sediments including  
316 coarse sand, gravel, pebbles, shingle and cobbles, which are often unstable due to tidal  
317 currents and/or wave action. These habitats are generally found on the open coast or in tide-  
318 swept channels of marine inlets. The second habitat type corresponds to offshore (deep)  
319 circalittoral environments with coarse sands and gravel or shells, and may cover large areas.  
320 Animal communities in this habitat are closely related to offshore mixed sediments, and  
321 settlement of *Modiolus* larvae may occur in some areas. Consequently, these habitats may  
322 occasionally contain large numbers of juvenile *M. modiolus*. The horse mussel *M. modiolus*  
323 was reported in some parts of the Raz Blanchard during the investigations carried out by  
324 Retière (1979), forming mussel beds in an area which corresponds to the southern limit of this  
325 species in this part of the English Channel. However, this species is not recorded at our  
326 sampling stations and its persistence in this area needs to be confirmed.

327 Described in the French Marine Benthic Habitats classification issued by the National  
328 Museum of Natural History (Paris) by Michez et al. (2015), the benthic habitats identified in  
329 our study correspond to three marine benthic communities:

- 330 1) Very mobile coarse infralittoral sediments with scattered fauna (*Sédiments grossiers très*  
331 *mobiles infralittoraux à faune éparse*);
- 332 2) Circalittoral pebbles under strong hydrodynamic conditions with scattered fauna (*Cailloutis*  
333 *circalittoraux sous fort hydrodynamisme à faune éparse*);
- 334 3) Mobile coastal circalittoral gravel and pebbles with *Spirobranchus triqueter* and Barnacles  
335 and encrusted Bryozoans) (*Galets et cailloutis instables du circalittoral côtier à*  
336 *Spirobranchus triqueter avec Cirripèdes et Bryozoaires encroûtants*).

337 Our study demonstrates that neither the European EUNIS classification nor the French  
338 Marine Benthic Habitats classification are able to reflect the full variability of benthic  
339 assemblages, and that some updates need to be implemented in the future.

340

## 341 **5. Conclusions**

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343 Although the benthic habitats of the Raz Blanchard have not been previously  
344 characterized, the fauna sampled here represents a highly diversified benthic community. The  
345 dominant groups of this community are crustaceans (particularly amphipods) and polychaetes  
346 (particularly Syllidae). The fauna is characterized by small species, living in interstitial  
347 position or as infauna or protected as in the case of erect hydrozoans. The species recorded  
348 here have adapted to this area of high-energy hydrodynamic conditions and hard irregular  
349 seabed. Adaptations may be morphological such as (1) development of a special body form to  
350 reduce friction; (2) reduction of body size, allowing the species to find protection in cracks;  
351 (3) body structures that enable temporary or permanent fixation, leading to improved footing  
352 or a reduction of structures serving for swimming; (4) increased body weight; (5) allocation of  
353 biomass to different organs physiologically conditioned by water flow) or behavioural (such  
354 as spending most of their life cycle within the substratum; mobility in protected areas or  
355 within the sediment; and (6) development of clear morphological adaptations for attachment.  
356 The community described here includes new species for the English Channel, and its  
357 recognition could lead to the implementation of future updates of the EUNIS classification.

358

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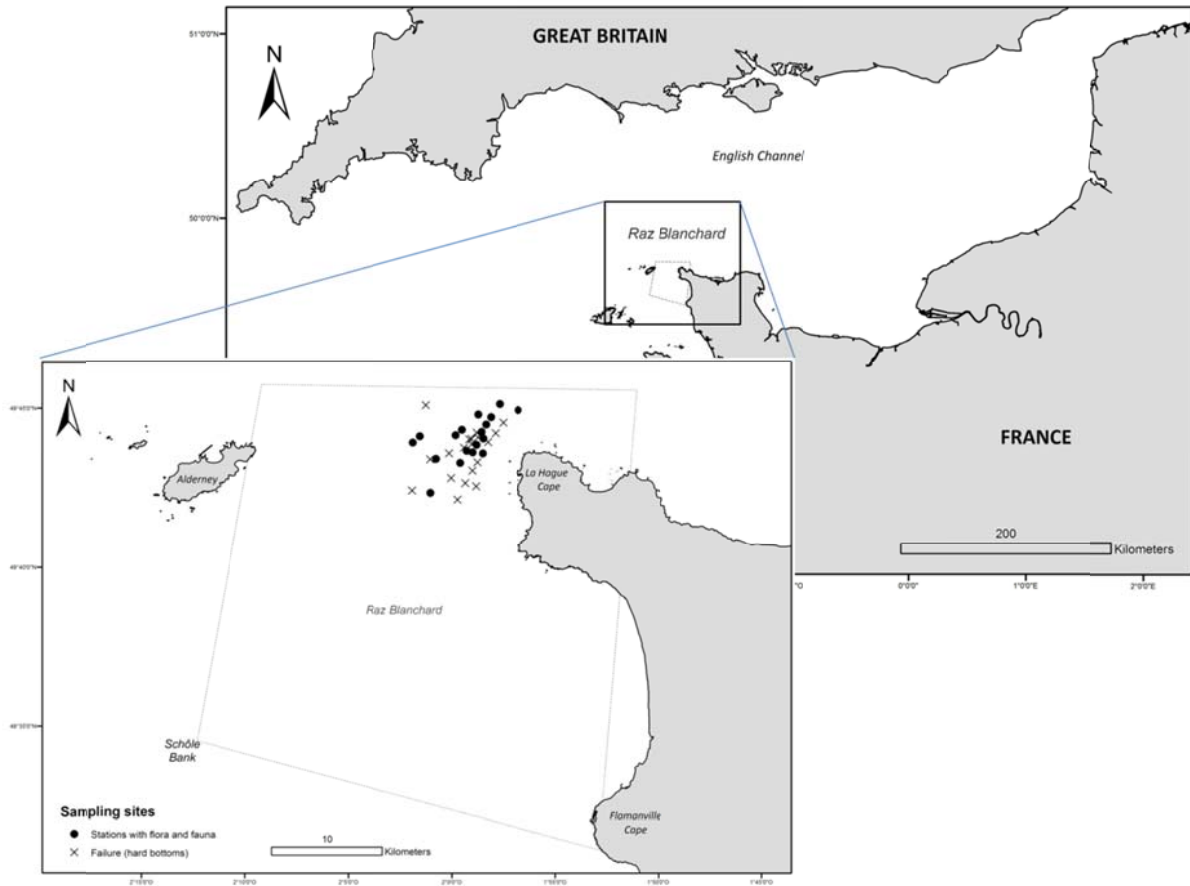
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484 Figure 1. Map of the Raz Blanchard and location of sampling stations.

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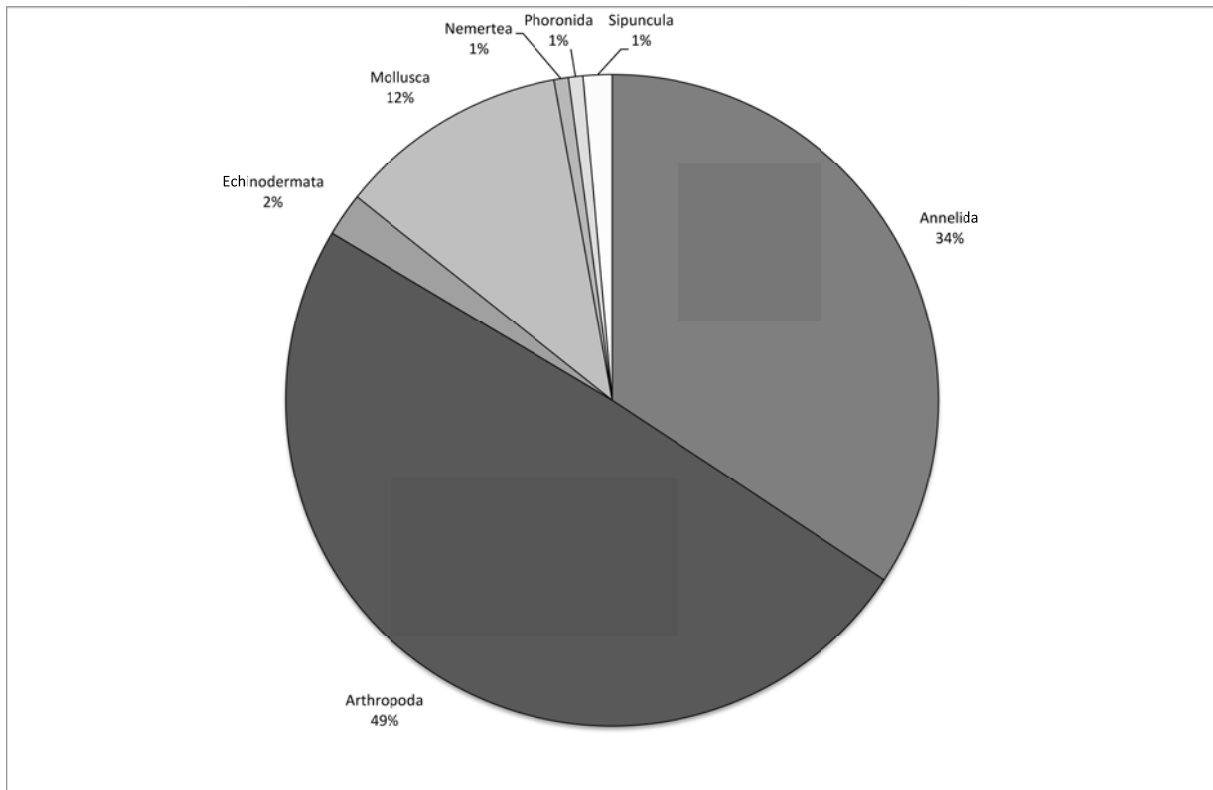




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487 Figure 2. Images of sediments collected from the four main successful dredges (gravel, mix of  
488 gravel and pebbles, pebbles).

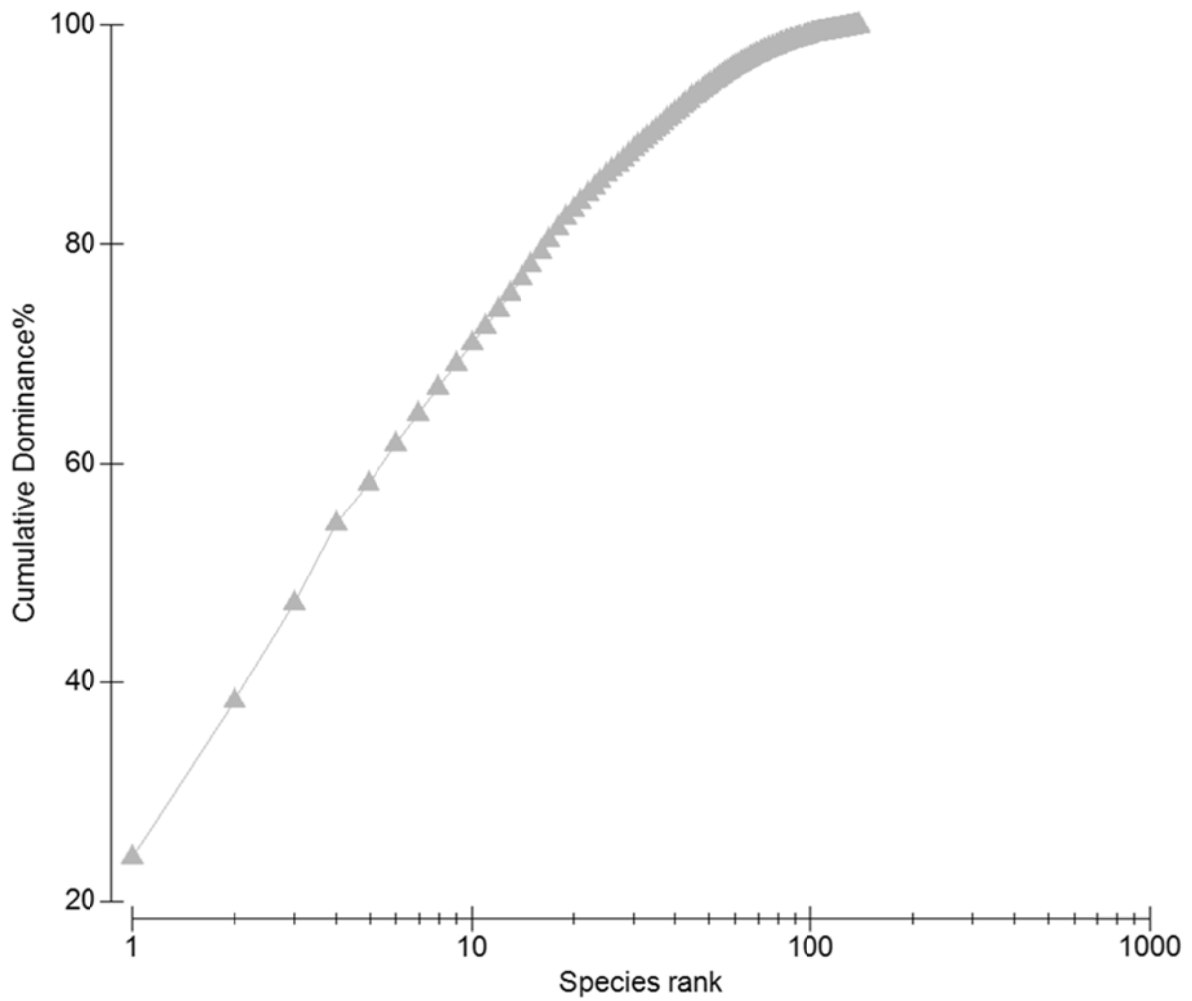
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491 Figure 3. Distribution of the collected taxa in terms of main faunal groups.

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494 Figure 4.  $k$ -dominance curve of the total number of individuals recorded at the 14 stations.

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500 Table 1. Biological traits and modalities of species selected for biological traits analysis

Biological trait	N°	Modality	Definition
Larval development	1	Planctotrophic	Planktonic larvae feeding on plankton
	2	Lecithotrophic	Planktonic larvae feeding on yolk
	3	Direct development	No planktonic larvae
Life span	1	Short	< 2 years
	2	Medium	2-5 years
	3	Long	> 5 years
Mobility	1	Swimmer	Adults actively swim in water column
	2	Walker	Adults capable of extensive movement at sediment surface
	3	Crawler	Adults with limited movements at sediment surface
	4	Burrower	Endofauna that moves in the sediment
	5	Sessile	Non-mobile adults (attached, limited to a tube or a burrow)
	6	Burrower & Swimmer	Benthic burrower species with nycthemeral migrations
	7	Walker & Swimmer	Benthic walker species with nycthemeral migrations
Living position	1	Epifauna	Live at the surface of the sediment
	2	Endofauna	Live in the sediment
Habit	1	Tube-dweller	Adults builds tube
	2	Burrow-dweller	Adults live in burrows (temporary or permanent)
	3	Free-living	Adults not limited by a structure
	4	Fixed	Adults live fixed on the substratum
Bioturbation	1	No bioturbation	Do not induce sediment displacement
	2	Surface deposition	Surface displacement
	3	Upward conveyor	Displacement of particles from depth to surface
	4	Downward conveyor	Displacement of particles from surface to depth
	5	Diffusive mixing	Small-scale displacement
Trophic groups	1	Non-specific deposit feeder	Feeds on particles at sediment surface and within the sediment
	2	Surface deposit feeder	Feeds on particles at sediment's surface
	3	Sub-surface deposit feeder	Feeds on particles within the sediment
	4	Suspension feeder	Feeds on particles within the water column
	5	Carnivorous	Feeds on live prey
	6	Omnivorous	Generalist feeder
	7	Mixtes	Feeds on particles in the water column and at sediments' surface
Ecological groups (AMBI)	1	Sensitives	Only present in unpolluted areas
	2	Indifferent	Always present at low densities
	3	Tolerant	More abundant in slightly enriched areas
	4	Second-order opportunists	Present in unbalanced conditions
	5	First-order opportunists	Proliferate in reduced sediment
Substratum affinity	1	Mud	Particles <63µm are present or dominant
	2	Sandy mud	50% to < 90% sand, mud remainder
	3	Muddy sand	10% to < 50% sand; mud remainder
	4	Fine clean sand	> 90% sand, median 0.125 to < 0.25 mm
	5	Coarse clean sand	> 90% sand, median 0.500 to < 1 mm
	6	Mixed sediments	Mix of different sediments
	7	Granules	Particles between 1 and 2 mm
	8	Pebbles, rocks and hard substratum	Particles between 2 and 64 mm
	9	Biological substratum	Adults live on living organisms
Maximal size	1	Very small	< 10 mm
	2	Small	10 to 20 mm
	3	Medium	21 to 100 mm
	4	Large	> 100 mm

501

502

503 Table 2. List of taxa recorded from the 14 stations classified by phylum. Total number of  
 504 individuals per station, number of taxa, Shannon diversity index (H'), Pielou's evenness  
 505 (J) and volume of sediment in each dredge are given at bottom of table.

Phylum	Taxa	Moul2	PT1	PT4	PT9	PT10	PT11	PT14	PT16	PT17	PT29	PT32	PT33	PT34	PT35
Annelida	<i>Amblyosyllis sp.</i>	0	1	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Autolytinae</i>	38	0	0	0	0	0	0	0	0	0	6	1	8	3
	<i>Boccardia polybranchia</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Branchiomma bombyx</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Cirratulus cirratus</i>	5	0	0	0	0	1	0	0	0	0	0	0	0	3
	<i>Eumida sanguinea</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Eunoe nodosa</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Euphrasine foliosa</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Eupolyornia nebulosa</i>	27	0	0	0	0	0	0	0	0	0	0	1	0	6
	<i>Eurysyllis tuberculata</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Glycera lapidum</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Haplosyllis spongicola</i>	1	0	0	1	4	0	0	0	0	0	0	0	0	1
	<i>Harmothoe spp.</i>	11	0	0	0	0	0	0	0	0	1	0	0	0	2
	<i>Jasmineira elegans</i>	74	1	0	0	0	0	0	0	0	0	0	0	0	26
	<i>Lanice conchilega</i>	1	0	0	2	3	1	0	0	1	0	0	0	0	5
	<i>Lepidonotus squamatus</i>	2	0	0	0	2	0	0	0	0	0	0	0	0	2
	<i>Lumbrineris latreilli</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Lysidice ninetta</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Lysidice unicornis</i>	4	0	0	0	0	1	0	0	0	0	0	0	0	5
	<i>Myrianida sp.</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0
	<i>Mysta picta</i>	6	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Odontosyllis fulgurans</i>	0	0	0	0	3	0	0	3	0	0	0	0	0	0
	<i>Pherusa plumosa</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Phaloe sp.</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Polycirrus sp.</i>	2	0	0	3	2	0	0	0	0	0	0	0	0	3
	<i>Polydora ciliata</i>	18	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Polygordius sp.</i>	10	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Polynoe scolopendrina</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Proceraea sp.</i>	4	2	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Prosphaerosyllis chauseyensis</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>Psamathe fusca</i>	0	0	0	2	0	0	1	0	0	0	0	0	0	0
	<i>Pseudopotamilla reniformis</i>	6	1	0	0	2	1	0	0	0	0	0	0	0	6
	<i>Sabella pavonina</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>Sabellaria spinulosa</i>	39	0	0	0	0	0	0	0	0	0	0	0	0	26
	<i>Schistomeringos sp.</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Sphaerosyllis bulbosa</i>	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Spio martinensis</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Spirobranchus triquetter</i>	2	1	0	0	0	0	0	0	0	0	1	0	0	0
	<i>Syllis armillaris</i>	28	0	0	1	0	1	0	0	0	0	0	0	0	0
	<i>Syllis columbretensis</i>	0	3	0	0	0	0	0	0	0	0	0	0	0	0
<i>Syllis gracilis</i>	5	4	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Syllis hyalina</i>	14	0	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Syllis variegata</i>	8	0	0	0	1	0	0	0	0	0	0	0	0	1	
<i>Syllis vittata</i>	0	1	0	0	0	0	0	0	0	0	1	1	19	0	
<i>Thelepus setosus</i>	5	0	0	0	0	0	0	0	0	0	0	0	0	2	
<i>Trypanosyllis (Trypanosyllis) coeliaca</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Trypanosyllis zebra</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Websterinereis glauca</i>	55	1	0	0	1	0	0	0	0	0	0	0	2	17	
Echinodermata	<i>Amphipholis squamata</i>	17	0	0	0	0	0	0	0	0	1	0	11	2	
	<i>Asterina gibbosa</i>	6	0	0	0	0	0	0	0	0	1	0	3	5	
	<i>Ophiotrix fragilis</i>	7	0	0	5	2	0	0	0	1	2	0	7	1	
Mollusca	<i>Acanthochitona crinita</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	
	<i>Aeolidia papillosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	
	<i>Berthella plumula</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Buccinum undatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Emarginula rosea</i>	2	0	0	0	0	0	0	0	0	0	0	0	1	
	<i>Gibbula cineraria</i>	2	1	0	0	0	0	0	0	0	0	0	1	4	
	<i>Jujubinus montagui</i>	4	2	0	0	0	0	0	0	0	0	0	0	1	
	<i>Musculus discors</i>	35	24	8	156	309	17	478	18	28	1	17	19	23	
	<i>Nucella lapillus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	
	<i>Ocenebra erinacea</i>	13	0	0	0	0	0	0	0	0	0	0	0	8	
	<i>Onchidoris bilamellata</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	
	<i>Pleurobranchus membranaceus</i>	4	0	0	0	0	0	0	0	0	0	0	0	1	
	<i>Rissoa parva</i>	11	11	0	1	0	1	0	1	1	0	2	5	6	
	<i>Sphenia binghami</i>	5	0	0	0	0	0	0	0	0	0	0	1	4	
<i>Tricolia pullus</i>	10	6	0	2	0	1	0	0	0	0	1	1	1		
<i>Tritonia hombergii</i>	0	0	0	0	0	0	0	0	0	0	0	0	1		
Nemertea	<i>Tubulanus sp.</i>	16	0	0	0	1	0	0	0	0	0	3	5	0	
Phoronida	<i>Phoronis sp.</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	
Sipuncula	<i>Golfingia (Golfingia) vulgaris vulgaris</i>	7	0	0	0	0	0	0	0	0	0	0	1	2	
	<i>Phascolion (Phascolion) strombus strombus</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	

507 Table 2 (continued). List of taxa recorded from the 14 stations classified by phylum. Total  
 508 number of individuals per station, number of taxa, Shannon diversity index ( $H'$ ), Pielou's  
 509 evenness ( $J$ ) and volume of sediment in each dredge are given at bottom of table.

Phylum	Taxa	Moul2	PT1	PT4	PT9	PT10	PT11	PT14	PT16	PT17	PT29	PT32	PT33	PT34	PT35
	<i>Abludomelita gladiosa</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Abludomelita obtusata</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Achelia echinata</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>Achelia hispida</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Ampelisca spinipes</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Amphilocheidae</i>	0	0	0	0	5	0	0	0	0	0	0	0	0	0
	<i>Amphioe rubricata</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>Anapagurus hyndmanni</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Animocera docus semiserratus</i>	0	0	0	0	0	0	1	0	58	0	0	0	0	0
	<i>Anthurus gracilis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Apherusa bispinosa</i>	0	0	0	0	0	0	1	0	0	1	1	0	0	0
	<i>Apherusa jurinei</i>	0	2	0	1	11	2	4	0	2	0	0	0	0	0
	<i>Astacilla longicornis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Axius stirhynchus</i>	0	0	1	2	10	2	0	0	0	0	0	0	0	0
	<i>Badotria scorpioides</i>	11	0	0	0	0	0	0	0	0	0	0	0	7	0
	<i>Cancer pagurus</i>	0	0	1	4	45	1	1	2	4	5	4	3	1	2
	<i>Caprella penantis</i>	13	18	1	0	1	0	0	7	1	0	0	6	3	1
	<i>Caprella tuberculata</i>	1	8	0	2	0	0	2	0	0	1	0	0	0	0
	<i>Cirolana cranchi</i>	1	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Colomastix pusilla</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Cyathura carinata</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0
	<i>Dexamine spinosa</i>	0	0	0	0	0	0	1	0	0	0	3	0	0	0
	<i>Dynamene bidentata</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Dyopedos porrectus</i>	1	0	2	0	5	1	0	0	0	3	3	12	4	
	<i>Elasmopus thalyae</i>	9	2	2	0	2	0	0	3	0	327	0	2	3	0
	<i>Erichthonius punctatus</i>	0	0	0	0	0	0	0	0	1	0	0	1	0	0
	<i>Eurydice spinigera</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	<i>Euryome aspera</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Galathea squamifera</i>	1	0	0	0	0	0	1	0	0	0	0	0	2	0
	<i>Gammaropsis maculata</i>	9	0	0	0	0	0	0	0	413	0	0	0	0	0
	<i>Gnathia dentata</i>	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Gnathia maxillaris</i>	0	0	0	0	0	0	0	0	0	1	0	3	0	0
	<i>Inachus sp.</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Arthropoda	<i>Iphimedia minuta</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Janira maculosa</i>	10	1	0	0	2	0	0	0	1	1	0	4	0	0
	<i>Jassa falcata</i>	8	1	0	0	2	0	0	1	1	44	2	4	6	0
	<i>Jassa herdmani</i>	0	0	0	6	3	1	0	0	3	0	0	0	0	0
	<i>Leptocheirus hirsutimanus</i>	0	0	0	1	0	0	0	0	0	129	0	0	0	0
	<i>Leucothoe sp.</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Liljeborgia pallida</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>Liocarcinus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Macropodia sp.</i>	0	0	0	0	0	0	0	5	0	0	0	0	0	0
	<i>Maerella tenuimana</i>	0	0	0	0	0	0	3	0	675	0	0	0	0	0
	<i>Metopa alderi</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	<i>Metopa tenuimana</i>	0	3	0	0	0	0	0	0	1	0	0	0	0	0
	<i>Microdeutopus anomalus</i>	0	0	0	6	0	0	0	0	0	0	0	0	0	0
	<i>Monocorophium sextonae</i>	11	1	0	0	0	0	0	0	0	0	0	0	1	0
	<i>Mysida</i>	42	4	0	0	0	2	0	1	7	0	3	22	17	18
	<i>Natotropic swammerdamei</i>	40	3	1	1	7	2	2	0	0	2	2	2	25	0
	<i>Othomaera othonis</i>	0	0	0	0	0	0	0	3	0	0	0	0	5	0
	<i>Pagurus sp.</i>	0	0	0	2	0	0	0	0	2	0	0	0	0	0
	<i>Palaemon serratus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Pandalina brevirostris</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	1
	<i>Parapleustes bicuspis</i>	0	0	0	8	5	0	0	1	0	0	0	0	0	0
	<i>Phtisica marina</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	<i>Pilumnus hirtellus</i>	8	0	0	0	1	0	0	0	0	1	1	4	0	0
	<i>Pinnotheres pisum</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Pisa sp.</i>	0	0	2	5	35	3	0	0	6	0	0	0	0	0
	<i>Pisidia longicornis</i>	66	1	0	2	0	0	0	0	3	0	0	97	4	
	<i>Processa sp.</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>Pseudoparatanaeis batei</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Sinelobus stanfordi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Socarnes erythrophthalmus</i>	0	0	0	36	0	0	0	0	0	0	0	0	0	0
	<i>Stenothoe marina</i>	0	0	0	0	2	1	0	0	0	0	0	0	0	0
	<i>Tryphosa nana</i>	1	0	0	0	0	0	0	0	166	0	0	2	0	0
	<i>Tryphosella sarsi</i>	1	0	0	0	0	0	5	0	0	0	0	0	0	0
	<i>Unciola crenatipalma</i>	3	0	0	0	0	0	0	0	0	0	0	1	0	0
	<i>Vaunthompsonia cristata</i>	0	0	0	2	11	0	0	0	1	0	0	0	0	0
	<i>Zeuxo holdichi</i>	0	0	0	1	1	0	0	0	0	0	0	0	0	0
	<b>Total number of individuals</b>	<b>781</b>	<b>107</b>	<b>18</b>	<b>255</b>	<b>484</b>	<b>39</b>	<b>491</b>	<b>53</b>	<b>64</b>	<b>1830</b>	<b>53</b>	<b>82</b>	<b>431</b>	<b>60</b>
	<b>Number of taxa</b>	<b>82</b>	<b>29</b>	<b>8</b>	<b>28</b>	<b>33</b>	<b>17</b>	<b>9</b>	<b>16</b>	<b>15</b>	<b>18</b>	<b>21</b>	<b>20</b>	<b>68</b>	<b>19</b>
	<b>H' (log2)</b>	<b>5.24</b>	<b>3.93</b>	<b>2.50</b>	<b>2.40</b>	<b>2.33</b>	<b>3.18</b>	<b>0.25</b>	<b>3.29</b>	<b>2.90</b>	<b>2.43</b>	<b>3.64</b>	<b>3.44</b>	<b>4.81</b>	<b>3.54</b>
	<b>J</b>	<b>0.82</b>	<b>0.81</b>	<b>0.83</b>	<b>0.50</b>	<b>0.46</b>	<b>0.78</b>	<b>0.08</b>	<b>0.82</b>	<b>0.74</b>	<b>0.58</b>	<b>0.83</b>	<b>0.80</b>	<b>0.79</b>	<b>0.83</b>
	<b>Volume per station (L)</b>	<b>30</b>	<b>2</b>	<b>≤0.5</b>	<b>30</b>	<b>&lt;1</b>	<b>≤0.5</b>	<b>≤0.5</b>	<b>≤0.5</b>	<b>≤0.5</b>	<b>30</b>	<b>≤0.5</b>	<b>≤0.5</b>	<b>15</b>	<b>≤0.5</b>