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## Available Benthic Energy Coefficient (ABEC): a generic tool to estimate the food profitability in coastal fish nurseries

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### Abstract :

The benthic production of prey seems to be one of the main drivers among many environmental factors that influence the quality of fish nurseries and potentially limit their carrying capacity. However, the contribution of food availability in the growth and survival of juveniles is still controversial. The Available Benthic Energy Coefficient (ABEC) aims to assess the trophic profitability of benthic invertebrate prey; this concept reflects the combination of energy richness and availability of prey. A value of the coefficient was associated with each prey species. This value was calculated from the product of 4 components: (1) mass energy, (2) productivity, (3) regeneration, and (4) accessibility. Thus, this coefficient is expressed as a quantity of energy per unit of weight and per year. From this coefficient, it is simple to calculate the annual production of profitable energy for the fish community in a delimited nursery; it only needs information about the biomass of benthic invertebrates via a standard sampling method. This tool appears to be decisive in properly estimating the carrying capacity of such a fish nursery. Prey classifications based on taxonomy or trophic guilds are widely used in predator-prey studies; comparison with a classification based on ABEC highlighted the energetic heterogeneity of these groups. ABEC can also be used as an index of profitable energy, thereby substituting the usual classifications of prey in trophic studies.

**Keywords :** Predator-prey relationship, Secondary production, Prey availability, Demersal fish, Nursery habitat, Carrying capacity, Bioenergetics

## 29 INTRODUCTION

30 Coastal habitats are used as nurseries by many species and are thus considered essential for  
31 achieving the life cycle of several demersal and benthic fishes (e.g. *Solea solea* or *Pleuronectes*  
32 *platessa*)(Peterson et al. 2000, Beck et al. 2001, Fulford et al.2011). Among the many environmental  
33 factors (e.g.depth, sediment, predation, food availability) that influence the quality of a nursery habitat  
34 and thus potentially limit its carrying capacity, the production of potential prey in the benthos seems to  
35 be one of the main drivers (Gibson 1994, Wouters & Cabral2009). However, the relative contribution of  
36 food availability to the growth and survival of juveniles is still widely discussed (Le Pape &  
37 Bonhommeau2013). Some authors suggest that predation pressure from the fish community has no  
38 (or relatively little) impact on the biomass of benthic fauna (e.g. Gee et al. 1985, Shaw & Jenkins  
39 1992). Thus, food availability would not be a limiting factor for the juveniles in these nursery habitats  
40 (Ross 2003, Hampel et al. 2005, Vinagre & Cabral 2008). However, other authors posit that fish  
41 communities regulate the distribution of benthic fauna in estuarine and coastal ecosystems. Food  
42 availability in such habitats would thus be a limiting factor (Nash & Geffen 2000, Craig et al. 2007,  
43 Nash et al. 2007).

44 Studies that arrive at these contradictory conclusions use different methodologies; some are based on  
45 analysis of negative density-dependent growth, which reflects competition for food (e.g. van der Veer  
46 & Witte 1993, Craig et al. 2007); others directly test the hypothesis that the quantity of available food  
47 determines the carrying capacity (hereafter called the 'trophic carrying capacity') by comparing fish  
48 demand for food with the food supply (e.g. Collie 1987, Vinagre & Cabral 2008). To test this  
49 hypothesis, we suggest that an energetic approach, developed at the fish community scale (unlike the  
50 previously cited studies), would provide a suitable framework to estimate the trophic carrying capacity  
51 of nurseries and thus determine the relative importance of food availability in these habitats. Prior to  
52 any assessment of the trophic carrying capacity, it seems essential to energetically quantify the food  
53 available to the fish community. Food availability can be estimated using generic tools that should  
54 consider life history traits of benthic invertebrates to relevantly quantify the benthic energetic supply  
55 available to fish species.

56 Most predator-prey studies describe benthic prey as a simple quantity of dry mass or gross energy  
57 (Collie 1985, Pihl 1985, Vinagre & Cabral 2008). However, according to optimal foraging theory  
58 (Emlen 1966, MacArthur & Pianka 1966), a predator must be 'energetically' penalised to account for  
59 the energy it invests to obtain its prey. The term 'profitability' was first introduced by Charnov (1976) to  
60 describe this concept of energetic gain in combination with the energy demand of foraging. It is now  
61 commonly used in experimental and modelling studies through the E/T ratio (energy benefit/searching  
62 and handling time) (e.g. Werner et al. 1983, Lai et al. 2011, Visser & Fiksen 2013). However, the time  
63 investment of a predator is not directly observable given the technical constraints of large-scale *in situ*  
64 surveys. Following optimal foraging theory, a predator tends to maximise this ratio; thus, the variation

65 in predation rates among prey species is expected to reflect this E/T ratio, i.e. the predators' interest in  
66 the prey species studied. Assuming that biological and behavioural features of benthic invertebrates  
67 (e.g. burrowing, diving) make them more or less accessible to fish, and thus available and interesting  
68 as potential prey, it is possible to relate the variation in predation rate to these features. A coefficient of  
69 'interest' is therefore associated with these features. Consequently, the gross energy provided by prey  
70 can be weighted by this penalising component within an energetic tool to properly reflect the prey's  
71 level of interest (to the fish) as a food source.

72 This study aimed to develop the 'Available Benthic Energy Coefficient' (ABEC), a generic energetic  
73 tool in which the profitability of prey is defined as a combination of its energy supply (i.e. energetic  
74 gain) and its accessibility to predators (i.e. energetic penalty). We developed and applied ABEC using  
75 data from a coastal case study, the Bay of Vilaine located in the northern Bay of Biscay, France. The  
76 development of ABEC raised 3 main issues which are thoroughly assessed in this study: (1) finding a  
77 method to calculate the annual estimated energy of prey using a '1-time' observation of biomass from  
78 scientific surveys, (2) defining relevant criteria (generic and consistent with empirically known  
79 predator-prey relationships) for assigning any benthic prey species to an accessibility class, and (3)  
80 developing and fitting coefficients for each accessibility class. These coefficients are key components  
81 of ABEC, as they weight the energy supplied by prey to a predator.

## 82 **MATERIALS AND METHODS**

### 83 **Study site**

84 The Bay of Vilaine (Fig. 1) is one of the most productive nursery grounds in the Bay of Biscay (Le  
85 Pape et al. 2003). It has been studied for more than 30 yr, producing valuable knowledge about its fish  
86 (Nicolas et al. 2007, Kopp et al. 2013) and benthic invertebrate (Le Bris & Glemarec 1995,  
87 Brind'Amour et al. 2009, 2014) communities. Given such data and a knowledge-rich context, the bay  
88 constitutes a relevant framework for developing a tool for benthic invertebrate prey energetics. The  
89 study area covers the subtidal grounds located from 5 to 30 m in depth. It is mostly covered by  
90 sediments with high proportions of fine particles (diameter <63  $\mu\text{m}$ ), between 40 and 80% for sandy  
91 muds and above 80% for muds (Le Bris & Glemarec 1995).

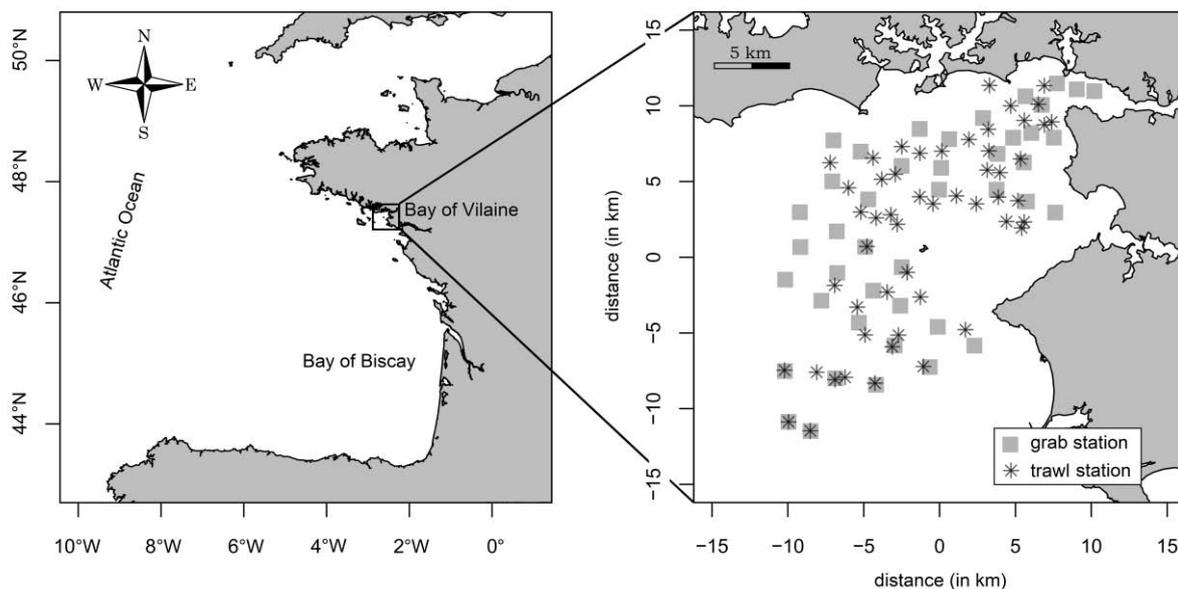
### 92 **Sampling protocol**

#### 93 ***Benthic invertebrate sampling***

94 Benthic macrofauna of the Bay of Vilaine were sampled using a van Veen grab (van Veen 1933)  
95 during the late summer (September) of 2008 (Fig. 1). Once aboard, grab samples were immediately  
96 rinsed with a 1 mm mesh on the boat deck and then collected in zipper bags and fixed with formalin to

97 a final concentration of 7%. In the laboratory, samples were rinsed with water and then fractionated  
 98 using a column of 5 successive sieves of different mesh sizes (from 16 to 1 mm square mesh).

99 The benthic invertebrates from each mesh size were stored in a 70% ethanol solution and identified to  
 100 species level whenever possible, or to higher taxa, then weighed. A total of 160 taxa were identified.  
 101 The 3 replicates performed in each of the 42 sampling stations were pooled, and density of benthic  
 102 invertebrate fauna was estimated given a grab-sampled area of 0.1 m<sup>2</sup> (Gallardo 1965, Eleftheriou &  
 103 McIntyre 2005).



104

105 *Fig. 1. Location of the Bay of Vilaine in the Bay of Biscay, France, and sampling stations (trawls and grabs).*  
 106 *Symbols indicate mean coordinates of each haul*

### 107 **Gut content data**

108 Along with the grab sampling, the Bay of Vilaine was also sampled using a 2.9 m wide and 0.5 m high  
 109 beam trawl, with a 20 mm stretched mesh net in the cod end. Each haul was performed at stations  
 110 displaying homogeneous sediment and water depth and lasted 15 min, covering a surface area  
 111 between 4500 and 5000 m<sup>2</sup>. A total of 52 hauls were conducted. Each haul was weighed, and fish  
 112 were identified, counted and weighed by species. We selected the 5 most numerically dominant  
 113 species within the fish community and kept them for gut content analyses: 4 flatfish species  
 114 (*Buglossidium luteum*, *Dicologlossa cuneata*, *Pleuronectes platessa*, *Solea solea*) and 1 demersal  
 115 species (*Trisopterus luscus*). These species are representative of the fish community that feeds on  
 116 benthic macroinvertebrates (they correspond to 80% of the total biomass of this community). A total of  
 117 426 guts sampled from 18 stations were removed and fixed with formalin at 10%, then rinsed with  
 118 water for ultimate dissection. All benthic invertebrates from stomachs and intestines were stored in a

119 70% ethanol solution to be identified to species level whenever possible, or to higher taxa. A total of  
120 114 taxa were identified.

121 Prey from gut contents were partially damaged by the digestion process; thus, the identification  
122 resolution was generally lower than that in the grabs. To improve identification of prey in gut contents,  
123 we compared prey taxa from the gut to the corresponding grab taxa; for instance, if arms of the genus  
124 *Ophiura* (*Echinodermata*) were observed in gut contents and the species *Ophiura ophiura* was found  
125 only in the associated grabs, the genus was identified to the *O. ophiura* species. When no prey from  
126 the grab closely matched those from the gut, nothing was changed, and the prey was identified at the  
127 lowest level possible. These modifications corresponded to 3% of the total abundance of prey.

### 128 ***Selection of potential prey***

129 A taxon was considered as potential prey if its relative abundance and occurrence reached an  
130 arbitrary threshold of 1% in the gut contents of at least 1 fish species. For taxa poorly identified in the  
131 gut contents, e.g. *Abra* spp., we kept all of the related species (*Abra abra*, *A. nidita*) found in grabs, as  
132 those species represented more than 1/1000 of the total biomass or 0.5/1000 of the total abundance.  
133 This step allowed a large set of potential prey to be retained. Species found mainly in the 16 mm sieve  
134 of the grab sample were rejected, as they were larger than the mouth sizes of the fishes studied  
135 (Wainwright & Richard 1995). Thus, 95 taxa were considered as potential prey of the 5 fish species.  
136 These prey represented 98.9 and 95.7% of the *in situ* abundance and biomass, respectively, of the  
137 benthic fauna.

### 138 **Composition of ABEC, the Available Benthic Energy Coefficient**

139 ABEC aims to estimate the energetic value of benthic invertebrate prey which is profitable for an  
140 assemblage of predators. A value is thus associated with each prey species. The assemblage of  
141 predators considered are fish commonly found in the benthic-demersal community. The ABEC value is  
142 calculated from the product of 4 components: (1) mass energy ( $E$ ); (2) productivity ( $\pi$ ), defined as the  
143 annual production divided by the annual mean biomass and which is a measure of a species' biomass  
144 turnover rate (Dolbeth et al. 2012); (3) a coefficient of regeneration ( $R$ ); and (4) a coefficient of  
145 accessibility ( $A$ ):

$$146 \quad ABEC_i = E_i \times \Pi_i \times R_i \times A_i \quad (1)$$

147 where  $E$  is expressed in  $\text{kJ}\cdot\text{g}^{-1}$ ,  $\pi$  in  $\text{year}^{-1}$ , and  $R$  and  $A$  unitless. Thus, the coefficient corresponds to  
148 a quantity of energy per unit of wet mass and per year for prey species  $i$ .

### 149 ***Mass energy coefficient (E)***

150 Conversion of the wet mass of benthic invertebrates to gross energy quantities was accomplished  
151 using a coefficient of ash-free dry mass divided by the wet mass (AFDM/WM) and an energy

152 conversion factor (energy/AFDM) in  $\text{kJ g}^{-1}$ , taken from a database developed by Brey et al. (2010).  
 153 Individual energy quantities were estimated from the product of both coefficients and individual  
 154 biomasses. Whenever a conversion factor for a studied species was not available or was based on a  
 155 single data point, we used the conversion factor of the closest taxon (e.g. *Ampelisca* for *Ampelisca*  
 156 *spinipes*).

### 157 **Productivity ( $\pi$ )**

158 We retrieved 300 productivity values from 64 published articles or theses (available from the  
 159 corresponding author).  $\pi$  ratios from the literature were used only for taxa identified at the species  
 160 level. Given the variability in  $\pi$  values for a single species, we used mean  $\pi$  whenever at least 5  
 161 values were available from sites with environmental conditions (temperature and depth) similar to the  
 162 studied site. The empirical productivity model built by Brey (2012) was used for the remaining taxa.  
 163 Table 1 displays the input data required to calculate productivity values. Mean body energy was  
 164 calculated from the product of mean body wet mass of each taxon and the associated mass energy  
 165 (Brey et al. 2010). The mean bottom temperature used was computed from the MARS 3D model  
 166 (Huret et al. 2013) using data from the Bay of Vilaine. The mean temperature in 2008 was  $13.9^{\circ}\text{C}$  at  
 167 the bottom and varied in the studied area from  $13.3$  to  $14.5^{\circ}\text{C}$ . Depth was recorded during the  
 168 scientific survey. Mobility and feeding parameters were assessed using different sources: WoRMS  
 169 (WoRMS Editorial Board 2013), MarLIN (MarLIN 2006), and Lincoln (1979). Reliable productivity ratios  
 170 were obtained from the literature for 6 of the 95 selected taxa. The Brey (2012) model was used for  
 171 the remaining 89 taxa.

172 *Table 1. Data required in the Brey model (2012) to provide benthic invertebrate productivity ratios ( $\pi$ ) of these*  
 173 *taxa (89 of 95 selected taxa) for which suitable  $\pi$  values were not available from the literature*

<b>Numerical resolution</b>	<b>Variable</b>
Quantitative	Body mass [kJ]
	Temperature [ $^{\circ}\text{C}$ ]
	Depth [m]
Qualitative	Taxon [ <i>Mollusca/Annelida/Crustacea/Echinodermata</i> ]
	Mobility [infauna/sessile/crawler/facultative swimmer]
	Feeding [herbivore/omnivore/carnivore]

174

175

176 **Coefficient of regeneration (*R*)**

177 Productivity data gathered from the literature did not consider the regeneration process of benthic  
 178 species. However, according to de Vlas (1985), production associated with somatic regeneration can  
 179 be as high as the classical growth production; this was observed notably for the bivalve *Macoma*  
 180 *balthica* and the polychaete *Arenicola marina*. Based on Clavier (1984), Brey (2001), Skold et al.  
 181 (1994), and Bourgoïn & Guillou (1994), regeneration due to fish cropping on the polychaete  
 182 *Euclymene oerstedii* and the echinoderms *Amphiura filiformis* and *Acrocorda brachiata* was estimated  
 183 at 20, 15, and 18%, respectively, of the annual production. Bowmer & Keegan (1983) reported that  
 184 *Amphiura filiformis* bodies regenerated at an average of 25%, a value which was roughly consistent  
 185 with previous results and confirms the phenomenon for this species.

186 Given the dearth of information in the literature regarding regeneration rates, we extrapolated the  
 187 available data on species for which we knew cropping by fish occurred but for which no data were  
 188 available (half the species in the sample). This was done by following the precautionary principle. In  
 189 concrete terms, the production of polychaetes and echinoderms with long arms was raised by 20 and  
 190 15%, respectively (i.e. the minimum value in the literature). Since only 1 value was available for  
 191 bivalve species with a developed siphon, we arbitrarily assumed half of this value, i.e. 50%. In all  
 192 cases, these values were most likely underestimated (de Vlas 1985). A coefficient for regeneration  
 193 was calculated by adding 1 to the regeneration rate (i.e.  $R = 1 + \text{regeneration rate}$ ). The product of this  
 194 coefficient and the productivity equalled effective productivity. For instance, for *Amphiura filiformis*,  
 195 given that  $\pi = 0.73$  and the regeneration rate = 15%, effective productivity =  $\pi \times R = 0.73 \times (1 + 0.15)$   
 196 = 0.84.

197 **Coefficient of accessibility of prey (*A*)**

198 The combination of the first 3 components along with the biomass provides the gross energy annually  
 199 produced by a community of prey. However, as mentioned in the 'Introduction', the catch rate of prey  
 200 varies among prey species, based on their accessibility to predators. The term 'accessibility' is related  
 201 here to predator and prey abilities and behaviours (i.e. capture and avoidance). We hypothesise that  
 202 accessibility reflects the availability of prey. We thus associated an accessibility level with each prey  
 203 species and then computed a coefficient for each accessibility level which reflected predator  
 204 investment. In practice, this was achieved by (1) defining 2 categories of prey accessibility and  
 205 associating all prey species with one or the other, (2) computing predation rates by comparing the *in*  
 206 *situ* composition of benthic invertebrates (i.e. grab samples) with that observed in the guts of the  
 207 studied fish species, and (3) modelling the predation rate as a function of accessibility. The  
 208 accessibility coefficients fitted from the model were then standardised for use as the accessibility  
 209 component of ABEC (i.e. *A*).

210 **Accessibility categories**

211 Benthic prey species were categorised into 2 groups of accessibility (hardly or easily accessible),  
 212 according their ability to avoid benthic-demersal predators. The grouping criteria were based on either  
 213 location within the sediment or morphological and behavioural features. Species found above or just  
 214 beneath the sediment surface were considered 'easily accessible': Bivalvia species with a short siphon  
 215 (e.g. *Cerastoderma edule*), surface-living Crustacea (e.g. *Diastylis bradyi*), Echinodermata (e.g. *O.*  
 216 *phiura*), and Gastropoda (e.g. *Philine aperta*). Species buried more deeply were considered 'hardly  
 217 accessible': Bivalvia species with a developed siphon (e.g. *Abra alba*), subsurface-living  
 218 Echinodermata (e.g. *Am phiura filiformis*), Gastropoda (e.g. *Turitella communis*), and sedentary  
 219 Polychaeta (e.g. *Lagis koreni*). Species with the ability to quickly shelter in the sediment were also  
 220 considered 'hardly accessible': tube-dwelling crustaceans (e.g. *Haploops niraе*) and errant  
 221 polychaetes (e.g. *Nephtys* sp.) that have the ability to escape because of their burying capacity.

## 222 Computation of accessibility coefficients

223 For each prey species found in the stomach contents of a predator (i.e. fish), the predation rate was  
 224 computed in 2 steps. (1) The abundance of an invertebrate species caught by the studied fish species  
 225 (representative of the fish community) was estimated for each sampling station as follows:

$$226 \text{ prey total abundance} = \sum_{j \in N \text{ fish species}} \overline{\text{prey}}_j * \text{fish}_j \quad (2)$$

227 where  $\overline{\text{prey}}_j$  is the mean number of a prey species, computed from the gut contents of all fish  
 228 individuals of a species  $j$  captured in a sampling station, and  $\text{fish}_j$  is the abundance of the fish species  
 229  $j$  observed at the same sampling station. Therefore, *prey total abundance* is the sum of all the prey  
 230 caught by the studied fish species at each sampling station. (2) We computed the predation rate as  
 231 the ratio of the total abundance of prey over the density of prey found in the grab samples (i.e. the *in*  
 232 *situ* density of prey):

$$233 \text{ predation rate} = \frac{\text{prey total abundance}}{\text{in situ grab prey density}} \quad (3)$$

234 The predation rate as defined here assumes that each predator can potentially eat all the prey. Each  
 235 grab was associated with adjacent sampling stations if it was located within a 3 km radius, the  
 236 maximum area potentially prospected daily by a juvenile given their swimming ability (Riley 1973,  
 237 Gibson et al. 1998, Burrows et al. 2004, Vinagre et al. 2006).

238 Using the following generalised linear model, we tested the hypothesis that the accessibility level of  
 239 prey has an effect on the predation rate and quantified the coefficients related to each accessibility  
 240 class. We used the Gaussian family and  $\log_{10}$  link function; the intercept term was removed because  
 241 the aim was to assess the effect of each accessibility level and not to assess how these accessibility  
 242 levels are distributed around the mean predation rate:

$$243 \log_{10}(\text{predation rate}) \sim \text{accessibility} \quad (4)$$

244 As previously mentioned, prey accessibility was defined in 2 categories (hardly or easily accessible).  
 245 The model was deemed relevant if (1) the accessibility variable had a significant effect (as tested with  
 246 an ANOVA) and (2) its estimates were consistent with the assumption that ‘hardly accessible’ prey had  
 247 a lower predation rate than ‘easily accessible’ prey. As the model was developed using log10-  
 248 transformed data, both predictions of predation rate, which directly corresponded to both estimates of  
 249 the accessibility categories, were exponentially transformed using the correction of Laurent to obtain  
 250 unbiased predicted values (Laurent 1963). The normality assumption was tested using the Wilks-  
 251 Shapiro test.

252 We standardised both estimates by dividing them by the highest estimate of the 2 accessibility  
 253 categories, i.e. the ‘easily accessible’ category. This standardization provided generic coefficients of  
 254 accessibility. Therefore, the ABEC accessibility coefficient of a prey species corresponded to the  
 255 standardized estimate of the accessibility category  $k$  to which it belonged:

$$256 \quad A_k = \frac{\text{accessibility estimate}_k}{\text{"easily accessible" estimate}} \quad (5)$$

### 257 **Variability in ABEC composition within the prey community**

258 To represent and identify patterns of variation in ABEC components between prey taxa, Principal  
 259 Component Analysis (PCA) was performed in R environment (R Development Core Team 2012) using  
 260 the package FactoMineR (Lê et al. 2008). Values of each component and ABEC were detailed for the  
 261 7 most abundant species.

### 262 **Comparison of prey classifications**

263 Groups of benthic prey are commonly used as explanatory biotic variables in habitat models or in the  
 264 description of predator–prey relationships (Nicolas et al. 2007, Brind’Amour et al. 2009, Kopp et al.  
 265 2013). These groups, most often based on taxonomic classification or trophic guilds, are useful, as  
 266 they reduce the number of variables to include in a model. However, they often have little relevance in  
 267 terms of energetic gain. In this study, we proposed a substitute to the usual classifications (i.e. trophic  
 268 guilds and taxonomy) of benthic prey. This new energetic classification used ABEC as an index to  
 269 define groups of prey based on the energy they may provide. It was calculated as follows. Once ABEC  
 270 was calculated for the 95 prey taxa, hierarchical ascendant classification of these prey species was  
 271 performed using the Euclidean distance with the Ward classification algorithm (Ward 1963). The  
 272 classification algorithm is simple: each species starts in its own group (95 groups initially), and pairs of  
 273 groups are merged iteratively following a similarity criterion (Euclidian distance). The best partition was  
 274 identified using the inertia based criterion of the Hierarchical Clustering on Principal Components  
 275 (HCPC) function developed in the R package FactoMineR (Le et al. 2008). The partition displaying the  
 276 lowest value was used to assess the best number of groups corresponding to the most compact ABEC  
 277 values. Concurrently, species were attributed to categories following their taxonomy and trophic guilds

278 (WoRMS Editorial Board 2013). Comparison between the 3 classifications (ABEC, trophic guilds, and  
 279 taxonomy) was done using boxplots and by computing Mantel correlations (Mantel 1967) on  
 280 classifications matrix transformed with the Jaccard similarity coefficient (Jaccard 1901).

## 281 **Application of the ABEC in the Bay of Vilaine nursery ground**

282 Scientific surveys in the Bay of Vilaine were conducted in March and September 2008, corresponding  
 283 to the beginning and end, respectively, of the main period of macrobenthic production at this latitude.  
 284 This peak in production is mainly due to the increase in temperature during summer and is associated  
 285 with an increase of biomass (e.g. *Lagis koreni* [Nicolaidou 1983, Elkaim & Irlinger 1987]; *Ampelisca*  
 286 *brevicornis* [Klein et al. 1975]; *Hediste diversicolor* [Gillet & Torresani 2003]; *Abra alba* [Hily & Le Bris  
 287 1984]; *Cerastoderma edule* [de Montaudouin & Bachelet 1996]). Thus, the biomasses recorded during  
 288 these periods were considered as minima ( $B_{min}$ ) and maxima ( $B_{max}$ ) for most prey species.  $\pi$  ratios,  
 289 and consequently ABEC, need to be applied to values of annual mean biomass ( $\bar{B}_{in\ situ}$ ) to provide an  
 290 value of production. Therefore, we estimated  $\bar{B}_{in\ situ}$  as the mean biomass between the two sampling  
 291 periods. As  $B_{min}$  were missing for several species, but  $B_{max}$  were recorded for all of the species, we  
 292 estimated  $\bar{B}$  using a simple linear regression between  $\bar{B}_{in\ situ}$  and  $B_{max}$  for the species for which we  
 293 had all the data, and we used the coefficient of regression ( $\alpha$ ) to predict  $\bar{B}_{pred}$  for all the benthic  
 294 species.

$$295 \quad \bar{B}_{pred} = \alpha \times B_{max} \quad (6)$$

296 ABEC was calculated for all of the prey species sampled in the Bay of Vilaine. Values of the coefficient  
 297 are expressed in  $\text{kJ g}^{-1} \text{yr}^{-1}$ . The product of ABEC along with the predicted annual mean biomass of  
 298 prey (a wet mass expressed in g) provided an estimate of the production (in  $\text{kJ yr}^{-1}$ ) available for the  
 299 fish community. The production assessment is thus based on 2 assumptions: (1) The production peak  
 300 and consequently the dynamic of the biomass and density are synchronized among species; this  
 301 assumption is coherent with the literature observing a peak of production in summer (cf. references  
 302 above). (2) The body mass dynamic is also similar among species and allows us to get productivity  
 303 values from Brey's model. This latter assumption is supported by the adequacy between outputs of  
 304 Brey's model and productivity ratios collected in the review (cf. 'Discussion: Reliability of core data').

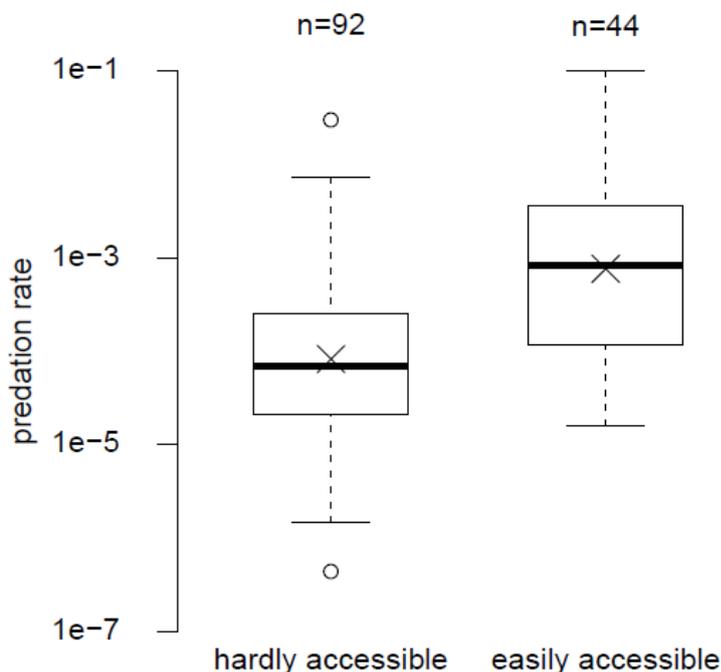
305 To illustrate the contribution of each component to the final coefficient (ABEC) and to compare the  
 306 spatial distributions of profitable production and biomass, we successively added each ABEC  
 307 component over the annual mean biomass. We tested whether the distribution of the available energy  
 308 production values (estimated using ABEC) corresponded to the distribution of gross biomass values  
 309 using analyses accounting for spatial correlation. A linear model between these 2 variables, in which  
 310 the autocorrelation structure was considered via latitude and longitude, was built using the function  
 311 'gls' from the 'nlme' package (Pinheiro et al. 2013). All computations and statistical analyses were  
 312 done using R (R Development Core Team 2012).

## 313 RESULTS

### 314 Fitted accessibility coefficients

315 Predation rates were estimated for 60% of the taxa identified in gut contents. Around 30% of the  
 316 remaining taxa are rarely caught by predators; they represent less than 14% of the abundance of prey  
 317 items ingested. Though these taxa were observed in the study site, they were absent in the grab  
 318 stations associated with the trawl stations involved; the distance between grab and trawl samples was  
 319 sometimes >1 km, which could explain this lack of information. Only a few taxa (around 10%) that  
 320 occurred in gut contents were never sampled in the grab. These taxa were very small benthic  
 321 invertebrates (meiofauna) or highly mobile suprabenthic invertebrates of the Crangonidae family,  
 322 representing less than 3% of the prey items.

323 Coefficients of accessibility were applied to the 95 prey taxa. The standardised coefficients were 0.11  
 324 and 1.00 for the 'hardly accessible' and 'easily accessible' prey categories, respectively (Fig. 2).  
 325 Differences between the 2 values (ANOVA: p-value < 0.001) clearly underlined the disparity between  
 326 the 2 prey categories. The accessibility effect explained 20% of the variation in predation rate.

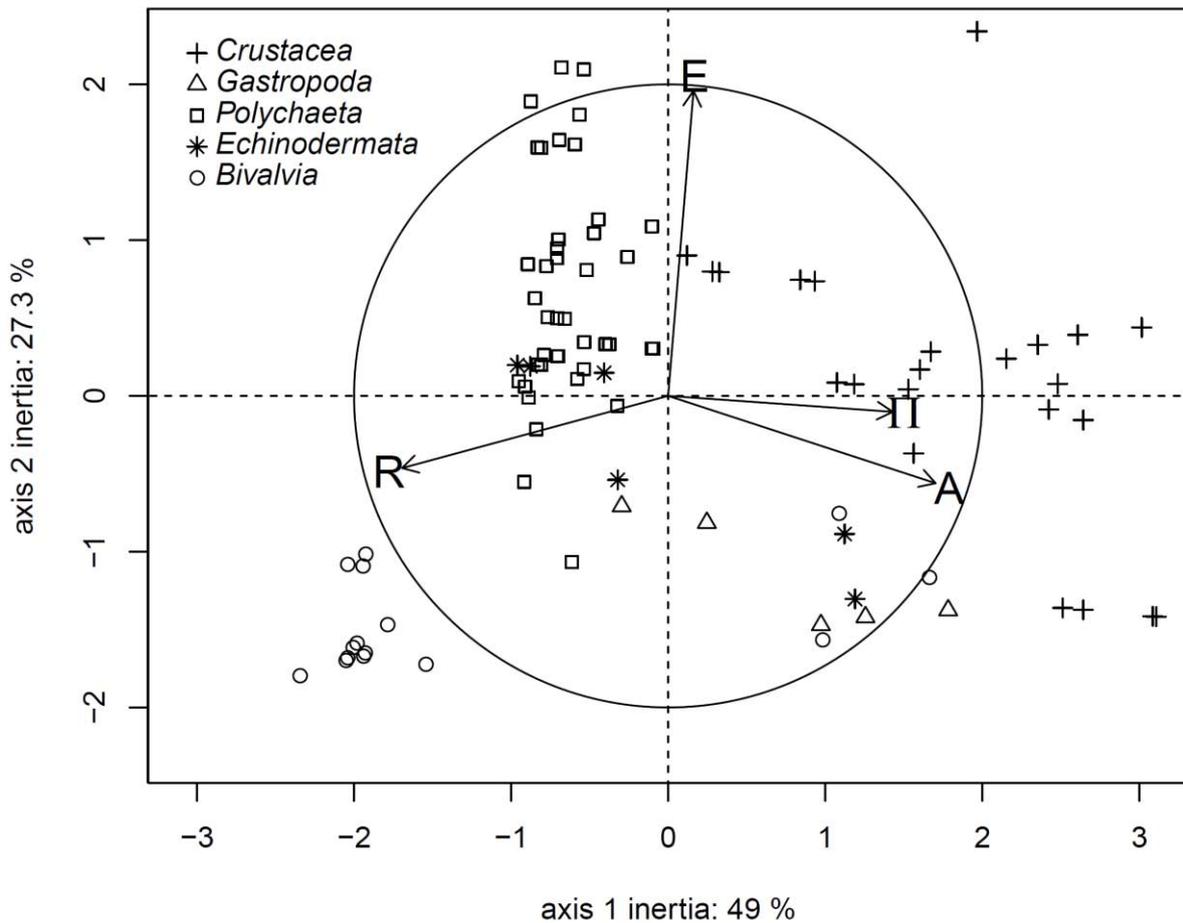


327

328 *Fig. 2. Distribution of log<sub>10</sub>-transformed predation rates for each accessibility category, displayed as Tukey*  
 329 *boxplots; the thick line and the cross indicate median and mean rates, respectively; the bottom and top of the*  
 330 *boxes indicate the first and third quartiles, respectively; the ends of the whiskers are the lowest and highest data*  
 331 *values within the 1.5 interquartile range of the lower quartile and the upper quartile, respectively; the dots are*  
 332 *outliers. Mean rates correspond to the estimates of the model. After standardisation, they are used as*  
 333 *accessibility coefficients*

334 **Diversity of ABEC composition within the prey community of the Bay of Vilaine**

335 The first 2 axes of the PCA accounted for 76% of ABEC variance. The 4 variables structuring ABEC  
 336 represented on the first PCA plane were weakly correlated with each other (Fig. 3). Axis 2 was highly  
 337 correlated with mass energy (*E*), whereas axis 1 was associated with the 3 other variables; the  
 338 regeneration coefficient (*R*) was negatively correlated with accessibility (*A*). The positions of prey  
 339 along axis 2 highlighted that polychaetes contained more energy than echinoderms (Student's *t*-test: *p*  
 340 < 0.001) and species with shells (gastropods and bivalves) (for both Student's *t*-tests: *p* < 0.001).  
 341 Furthermore, crustaceans had higher productivity and were generally more accessible than the other  
 342 groups (Student's *t*-test: *p* < 0.001). Detailed data for the 7 most representative species (Table 2)  
 343 seemed to indicate that ABEC values were weakly associated with taxonomic groups, except for  
 344 echinoderms. Thus, combination of the 4 components of ABEC smoothed the previously observed  
 345 trend. All ABEC values are detailed in the Appendix.



346  
 347 *Fig. 3. Principal Component Analysis (PCA) displaying prey taxa projection on the 4 Available Benthic Energy*  
 348 *Coefficient (ABEC) components (A: accessibility E: mass energy, R: regeneration, π: productivity). Prey taxa are*  
 349 *classified in taxonomic groups. The correlation circle of variables is displayed to help interpret the axes*  
 350

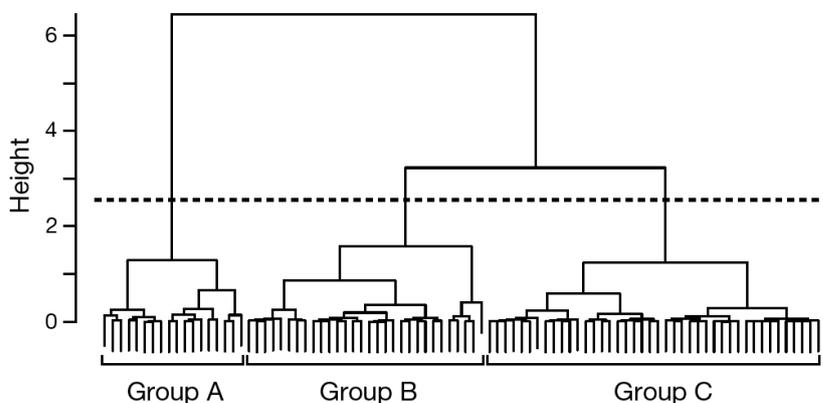
351 Table 2. Component values of ABEC for the 7 main species of the Bay of Vilaine

species	taxonomic group	mass energy (kJ.g <sup>-1</sup> )	productivity (year <sup>-1</sup> )	regeneration	accessibility	ABEC (kJ.g <sup>-1</sup> .year <sup>-1</sup> )
<i>Haploops nirae</i>	Crustacea	3.64	2.87	1.00	0.11	1.15
<i>Owenia fusiformis</i>	Polychaeta	5.18	1.69	1.20	0.11	1.16
<i>Sternaspis scutata</i>	Polychaeta	3.13	1.60	1.20	0.11	0.66
<i>Acrocnida brachiata</i>	Echinodermata	2.99	0.44	1.15	0.11	0.17
<i>Amphiura filiformis</i>	Echinodermata	2.99	0.73	1.15	0.11	0.28
<i>Cerastoderma edule</i>	Bivalvia	1.06	0.82	1.00	1.00	0.87
<i>Abra alba</i>	Bivalvia	1.11	1.92	1.50	0.11	0.35

352

353 **Comparison of prey classifications**

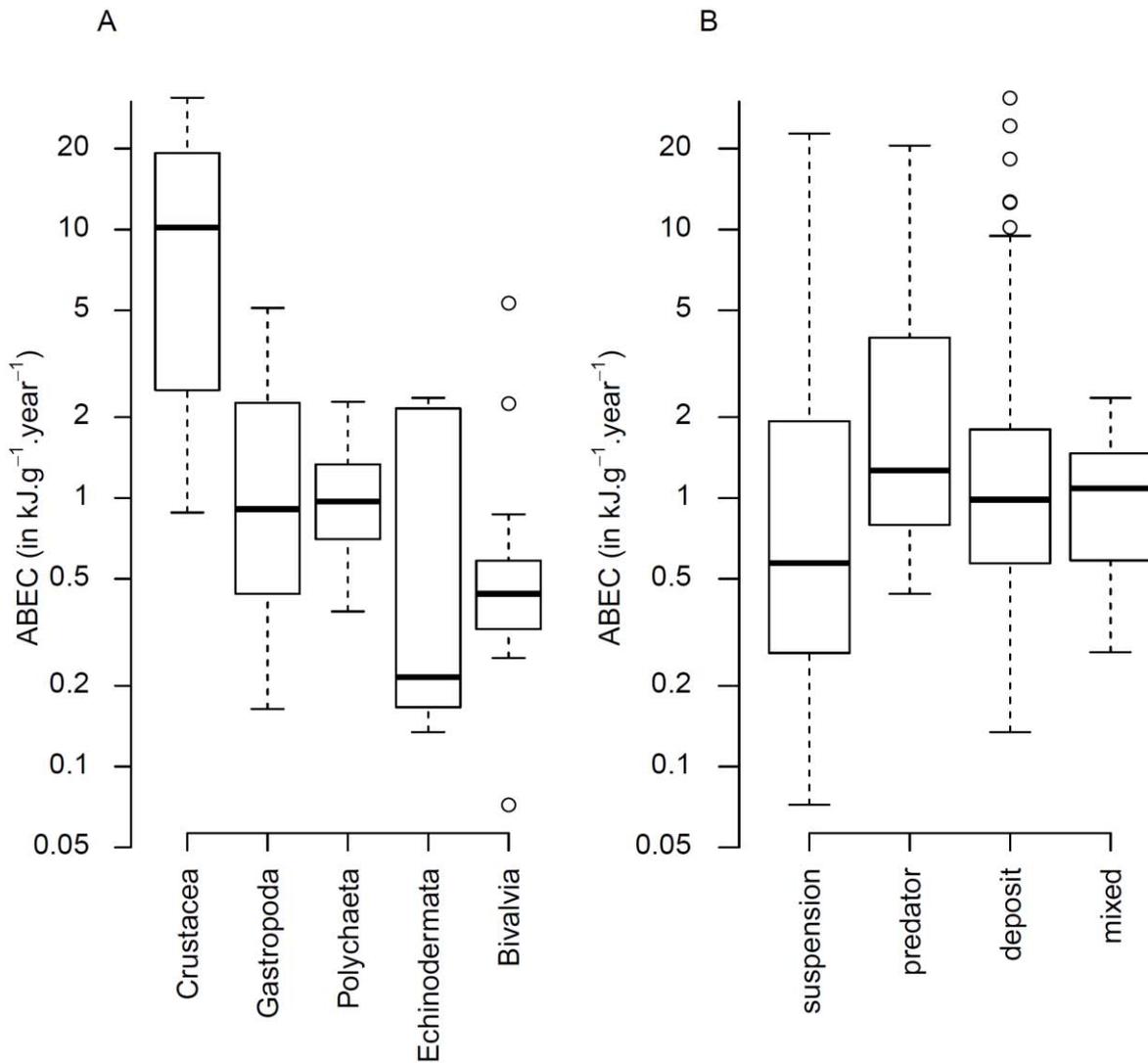
354 Classification analyses on ABEC values suggested 3 groups of prey (Fig. 4). Group A (ABEC > 3.00  
 355 kJ m<sup>-2</sup> yr<sup>-1</sup>) corresponded to easily accessible prey species with high effective productivity;  $\pi \times R =$   
 356 4.9 vs. 2.0 and 2.7 for groups B and C, respectively. Group B (ABEC < 0.75 kJ m<sup>-2</sup> yr<sup>-1</sup>) was  
 357 characterised by hardly accessible prey species with low mass energy coefficients:  $E = 2.2$  kJ g<sup>-1</sup>, on  
 358 average, vs. 3.1 and 3.6 kJ g<sup>-1</sup> for groups A and C, respectively. Group C (ABEC from 0.75 to 3.00 kJ  
 359 m<sup>-2</sup> yr<sup>-1</sup>) included both hardly and easily accessible prey.



360

361 Fig. 4. Hierarchical cluster analysis (Ward algorithm) using the Euclidean distance computed on Available Benthic  
 362 Energy Coefficient (ABEC) values of the prey. The number of groups was determined using the inertia-based  
 363 criterion of the Hierarchical Clustering on Principal Components function (Le et al. 2008)

364 Groups of ABEC were weakly correlated with the taxonomic groupings (Mantel  $r = 0.28$ ,  $p$ -value =  
 365 0.001) and were uncorrelated with the trophic guilds (Mantel  $r = -0.01$ ,  $p$ -value = 0.76), confirming the  
 366 trend already observed in Table 2. Furthermore, ABEC calculated by taxonomic groups or trophic  
 367 guilds (Fig. 5) confirmed the Mantel test results: no differences among trophic guilds and significant  
 368 differences among taxonomic groups. The latter corresponded mainly to the Crustacea group, which  
 369 had a mean ABEC value 10 times as high as those of the other groups.



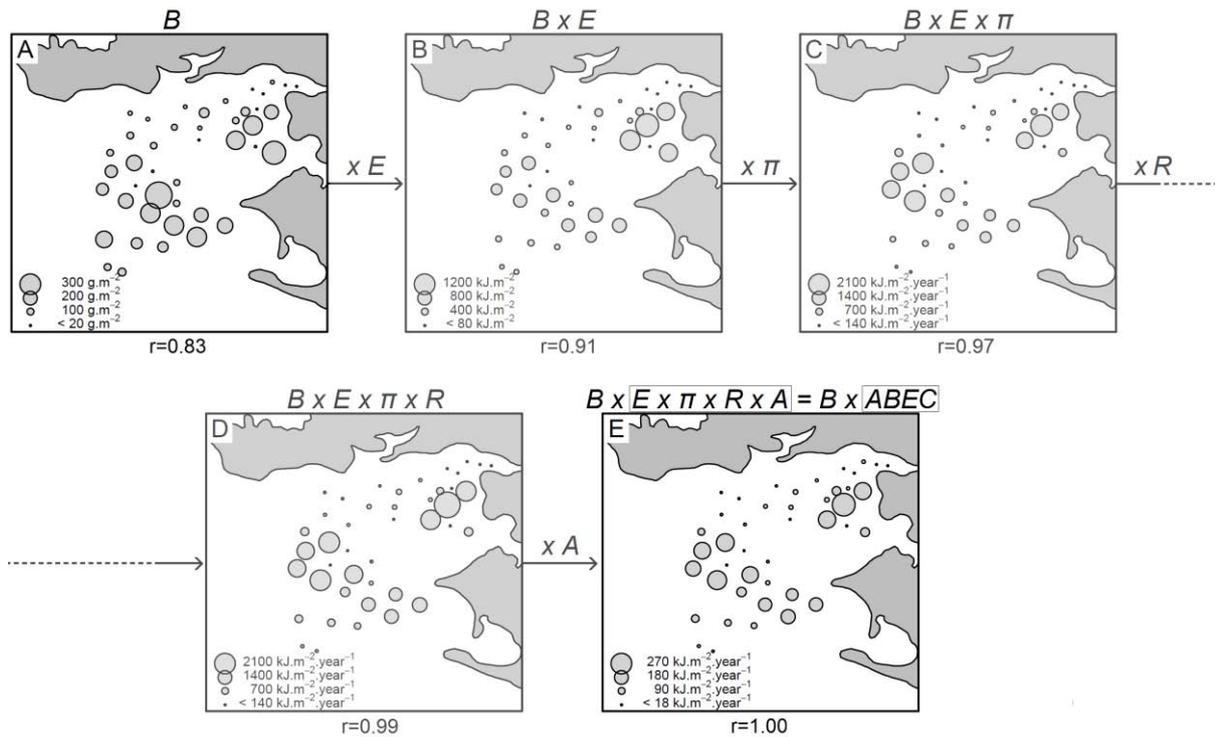
370

371 *Fig. 5. Available Benthic Energy Coefficient (ABEC) values calculated by (a) taxonomic groups and (b) trophic*  
 372 *guilds. Box-plot definitions are given in Fig. 2*

373 **Profitability assessment using ABEC in the Bay of Vilaine**

374 Annual mean biomass was fitted for the 20 species observed in both March and September and  
 375 present in at least 10 sampling stations. The regression coefficient (i.e. slope) was 0.68, explaining  
 376 96% of variation.

377 Fig. 6 presents the steps for calculating the spatial distribution of available energy production for  
 378 benthic-demersal fish predators in the Bay of Vilaine nursery ground in 2008. Fig. 6A corresponds to  
 379 the predicted annual mean biomass, whereas Fig. 6B–E presents the relative contribution of each  
 380 component of ABEC to the total profitable energy.



381

382 Fig. 6. Spatial distribution of (A) biomass (B) and (E) profitable production ( $B \times ABEC$ ); (B, C, D) components of  
 383 ABEC are successively included to display their contribution to the spatial variability; Pearson correlation  
 384 coefficient ( $r$ ) between (E) profitable production and each other panel is given underneath the panel. A:  
 385 accessibility, ABEC: Available Benthic Energy Coefficient, E: mass energy, R: regeneration,  $\pi$ : productivity  
 386

387 Spatial distribution of the biomass of benthic invertebrates identified 2 areas with high biomass  
 388 (eastern and southern parts of the bay) and 2 areas with lower biomass (mouth of the estuary and  
 389 northern part of the bay). Quantitative and qualitative variables based on sediment, organic matter,  
 390 oxygen, temperature, depth, and salinity were tested. None of these explained the spatial variability  
 391 observed. Converting the biomass data (Fig. 6A) into energy (Fig. 6B) reduced the relative contribution  
 392 of the southern part of the bay to the overall energy budget. This was particularly obvious for 5 of the  
 393 stations which had very low energy ( $400 \text{ kJ m}^{-2}$ ) but relatively high biomass ( $>200 \text{ g m}^{-2}$ ). This drop  
 394 in energy was due to the echinoderm *Amphiura filiformis* and the bivalve *Abra alba*, which represented  
 395 50 to 90% of the biomass recorded in these stations. Indeed, echinoderms have a low energy content,  
 396 and most bivalve mass corresponds to the shell (Brey et al. 2010). Multiplying energy values by  
 397 productivity ( $\pi$ ; Fig. 6C) increased the contribution of the western part of the bay, which was  
 398 composed of the crustacean *Haploops nirae* (60 to 95% of the biomass). The contribution of the  
 399 regeneration coefficient uniformly increased the production (Fig. 6D; Pearson  $r = 0.99$  with data in Fig.  
 400 6C). The accessibility coefficient greatly penalised gross energy production but scarcely modified the  
 401 patterns described previously (Fig. 6e; Pearson  $r = 0.99$  with data in Fig. 6D). This illustrates that  
 402 hardly and easily accessible benthic invertebrates were uniformly distributed in the study area.

403 Finally, profitable energy production estimated using ABEC (Fig. 6E) was partially correlated with  
 404 biomass (Pearson  $r = 0.83$ ). Moreover, ABEC provided a more contrasting distribution of available  
 405 food than using biomass alone. Production maxima (Fig. 6E) were located on muds at depths of 15 to  
 406 25 m and sandy muds at depths of 5 to 10 m. These 2 areas were mainly dominated by *Haploops*  
 407 *nirae*-*Owenia fusiformis*-*Abra alba* and *Owenia fusiformis*-*Acro cnida brachiata*, respectively.

## 408 **DISCUSSION**

409 The combination of 3 energy-related components, weighted by the accessibility of prey, provides an  
 410 energetic coefficient that can be computed for any type of marine benthic prey. This coefficient, called  
 411 ABEC, converts the gross biomass of benthic invertebrates into an annual production of profitable  
 412 energy. To the best of our knowledge, it is the first integrated coefficient to be developed that  
 413 assesses the profitability of benthic prey that benefit the fish community. Although other tools can  
 414 assess food preference or prey accessibility (e.g. Ivlev 1961, Strauss 1982, Walters et al. 1997), these  
 415 aspects are not included in the trophic studies that compare food availability and demand (e.g. Collie  
 416 1987, Vinagre & Cabral 2008). ABEC is a relevant tool for estimating the carrying capacity of similar  
 417 nurseries because of 2 features: time integration, by considering annual production instead of a  
 418 temporal snapshot of biomasses, and the weighting of energy supply. The secondary production  
 419 computed provides insights about e.g. recruitment, mortality, size, cohort structure, and growth type.  
 420 Therefore, when compared to biomass, ABEC is a major step towards the assessment of the spatial  
 421 distribution of benthic production. Before extending the use of ABEC to other ecosystems to assess  
 422 the carrying capacity, it seems relevant to validate the calibration of the accessibility component.  
 423 However, because that component is associated with the whole fish community and is independent of  
 424 the predator density (the component is standardized), it is expected to be resilient among various  
 425 ecosystems and potentially usable as is.

### 426 **ABEC: a theoretically-sound and integrated coefficient**

427 The optimal foraging theory, developed by Emlen (1966) and MacArthur & Pianka (1966), states that  
 428 the foraging behaviour of a predator is driven by the maximisation of energy intake per time unit. More  
 429 specifically, it stipulates that a predator that attempts to maximise energy intake ( $E$ ) is penalised by the  
 430 handling ( $H$ ) and searching ( $S$ ) time of its prey [ $E/(H + S)$ ]. This non-random behaviour of a predator  
 431 can be interpreted as a preference for certain prey (Shorygin 1931, Hoar et al. 1979, Floeter &  
 432 Temming 2003). The large variation in predation rates observed between the prey species selected in  
 433 our study corroborates this idea of food preference. However, according to Visser & Fiksen (2013), the  
 434 concept of feeding preference remains abstract and is hardly practical in differentiating *in situ* prey.  
 435 Griffin et al. (2012) suggested using the accessibility of prey, similar to the vulnerability concept of prey  
 436 (Walters et al. 1997, Ahrens et al. 2012), to explain variations in predation intensity. We posit that the  
 437 coefficient of accessibility developed in this study theoretically reflects the 'searching time' of the

438 optimal foraging formula. Specific prey characteristics, such as mobility and position within the  
 439 sediment, could easily be associated with this accessibility concept. In a study conducted in the  
 440 southern North Sea, Hinz et al. (2005) made an initial attempt to relate prey characteristics (position,  
 441 mobility, and palatability) and variation in abundance to the diet of *Limanda limanda*. In the present  
 442 study, we showed that combining 2 prey characteristics (mobility and position) into a unique  
 443 component, accessibility, explains a large part of variability in predation intensity: the prey most  
 444 accessible to benthic-demersal fish correspond mainly to epibenthic species, whereas the least  
 445 accessible ones correspond mainly to species that bury into or live beneath the surface. This concurs  
 446 with several other studies conducted in similar ecosystems or experiments (e.g. Hall et al. 1990,  
 447 Posey et al. 2002). Adding complexity to this 'penalising' component would be an interesting  
 448 perspective. Considering additional accessibility categories is an initial solution; our analyses showed  
 449 that a third category, associated with an intermediate burying level, seems relevant but was not  
 450 significant with the data available (results not shown). Another source of predator energy expenditure  
 451 is handling time; the rigidity of prey bodies could be a reliable proxy (Hinz et al. 2005), but it would  
 452 need to be combined with the existing burying criteria to provide relevant mixed categories.

453 The accessibility component used in this study did not modify the dispersion patterns of food in the  
 454 Bay of Vilaine, as hardly and easily accessible prey are homogeneously distributed in the bay.  
 455 However, examples occur where the inaccessibility of a highly profitable and abundant prey (e.g.  
 456 tubicolous species) might strongly decrease the gross energy available for predators. For instance,  
 457 *Haploops nira*, a tubicolous amphipod, represents more than 90% of the total biomass in the Bay of  
 458 Concarneau (Rigolet et al. 2014), but this species is rarely accessible to most fish species and is thus  
 459 absent from most fish diets (H. Le Bris unpubl. data). The way our coefficient is designed, profitable  
 460 energy would be closer to gross energy in areas of sandy sediment, where surface-living fauna,  
 461 notably some amphipods and cumaceans, are usually abundant (i.e. easily accessible prey), as  
 462 observed in coastal ecosystems on the Atlantic coast (Hily 1976, Menesguen 1980, Le Bris &  
 463 Glemarec 1996).

#### 464 **Reliability of core data**

465 Much of the information included in ABEC comes from the literature. The lack of relevant productivity  
 466 data ( $\pi$ ), one of the main components of ABEC, led us to estimate productivity for most prey in the  
 467 study using the model developed by Brey (2012). Other studies also using the Brey model compared  
 468 their results with other empirical models (Cusson & Bourget 2005, Dolbeth et al. 2005) and concluded  
 469 that the former model performed best in a variety of circumstances. Although we do not have any  
 470 productivity values at the scale of the Bay of Vilaine with which to compare, we are fairly confident in  
 471 our estimates. For instance, productivity estimates for 6 species (*Abra alba*, *Cerastoderma edule*,  
 472 *Corophium volutator*, *Macoma balthica*, *Mytilus edulis*, *Nephtys hombergii*) and 3 taxa (*Ampelisca*,  
 473 *Bivalvia*, *Polychaeta*) for which we had a minimum of 5  $\pi$  values from different study sites fell within

474 the range of what is commonly found in the literature. Additionally, Brey (2001) states that the error  
475 associated with estimating the production of a single species generally remains high but decreases  
476 greatly when averaged over multi- species communities, thus making his model well suited for this  
477 study.

478 Regeneration data were available for a few species and were extrapolated to others. This aspect likely  
479 generated uncertainties in ABEC values (Appendix). Assessing the range of these uncertainties is  
480 unfortunately impossible given the paucity of data. However, failing to include regeneration leads to  
481 underestimating benthic production. In our study, aggregating these values at the community scale  
482 smooths these uncertainties. Furthermore, the regeneration component improves production  
483 estimates without modifying the spatial pattern of production (i.e. Pearson  $r = 0.99$  between Fig.  
484 6C,D).

485 Prey biomass in the Bay of Vilaine was estimated using a van Veen grab. This device is one of the  
486 most common tools for collecting and estimating benthic infauna, with a sampling efficiency estimated  
487 at 90% in subtidal zones (Lie & Pamatmat 1965). The remaining 10% mainly concerns highly mobile  
488 suprabenthic organisms (e.g. *Crangon crangon* and *Philocheras trispinosus*) escaping from the grab  
489 and very small organisms (e.g. *Ostracoda* and *Harpacticoida*) that are flushed by the grab mechanism.  
490 In our study, some of the aforementioned taxa were found in the diet of the fish but were absent from  
491 the grab samples. We assume that these missing taxa had only a small impact on the estimated  
492 profitable production of the Bay of Vilaine, as they corresponded to only 3% of the predators' diet.

### 493 **Implications for trophic ecology studies**

494 ABEC was used in the Bay of Vilaine to convert biomass data into annual profitable production for  
495 each prey taxon. This production was then aggregated to obtain the production of the entire directly  
496 usable prey community to calculate the annual quantity of food that is profitable for a set of predators.  
497 When compared to the spatial distribution of biomass, ABEC revealed more heterogeneous food  
498 patterns. Therefore, biomass may not be the best proxy to estimate food spatial distribution on an  
499 annual basis. Nevertheless, discrepancies between biomass and ABEC distributions remained  
500 moderate given the high correlation (Pearson  $r = 0.83$ , Fig. 6). Spatial distributions of biomass and  
501 profitable production in the Bay of Vilaine suggest that the 2 values are most likely produced by  
502 different processes occurring at different temporal scales. Biomasses are observed at a single  
503 moment (a temporal snapshot), whereas profitable production, estimated from ABEC, is calculated on  
504 a yearly basis and by definition integrates productivity rates. The dynamic dimension of ABEC  
505 combined with biomass data provides integrated information about the food supply. Therefore, ABEC  
506 is a good candidate for trophic ecology studies, which require work at an annual time scale. We  
507 believe that ABEC is especially relevant in benthic studies that investigate anthropogenic impact on

508 benthic communities, such as trawling impacts (Hinz et al. 2009) or hypoxia (Gray et al. 2002). ABEC  
509 is also a good candidate to quantify available energetic inputs in bioenergetic studies.

### 510 **A flexible and generic tool**

511 The multi-component structure of ABEC offers a framework that can be easily manipulated and  
512 adapted to other sites that have a different community of prey and/or predators. Applying ABEC to  
513 another site requires knowing the biomass of the prey community and readjusting the productivity  
514 model, as productivity varies with the temperature of the site. However, prey accessibility categories  
515 were defined according to widespread morphological or behavioural traits available in the literature,  
516 and the associated accessibility coefficients were fitted to predation pressure data measured at the  
517 scale of the predator community (i.e. benthic-demersal fish); therefore, they are not specific to a unique  
518 fish species. Consequently, ABEC could be used to compare the quantity of food available from  
519 different nursery grounds even if benthic invertebrate communities differ. Additionally, given that  
520 biomass data are available on a yearly timescale, ABEC could also be used as an indicator of  
521 changes in benthic production.

522 The mean distance between 2 grab stations in our study is nearly 3 km. The high spatial variability of  
523 profitable production between some adjacent stations suggests that a finer sampling resolution would  
524 have been more appropriate. For instance, sampling on a 1 km grid would have been suitable given  
525 the relative continuity observed. The Bay of Vilaine is characteristic of an open shallow and muddy  
526 estuarine area under the influence of freshwater runoff (Gilliers et al. 2006) and is composed of  
527 benthic communities commonly found in other estuarine ecosystems (Brind'Amour et al. 2014).  
528 Therefore, we believe that the optimal spatial resolution suggested here would also be appropriate for  
529 other coastal nurseries. Alternatively, the sampling design in areas with more heterogeneous  
530 substrates, such as the continental shelf, would likely require increasing the sampling effort and/or  
531 stratifying the sampling protocol to better describe such ecosystems.

### 532 **An energetic classification of benthic invertebrate prey**

533 Taxonomic groups were not distinguished by ABEC, except for crustaceans. This can be explained by  
534 their high productivity and high accessibility for most of them. Conversely, the absence of correlation  
535 between ABEC and trophic guilds was somewhat expected. There are no functional reasons that  
536 would explain why a filter feeder, feeding mainly on particulate organic matter, would be of higher (or  
537 lower) energetic value than a deposit feeder, feeding on microphytobenthos (Grall et al. 2006). We  
538 argue that ABEC values accurately reflect profitability of the prey community. Nevertheless, analysing  
539 invertebrate communities with ABEC classification in habitat models would provide a trophic variable  
540 that contains information about energetic aspects of the prey community.

541

542 **CONCLUSION**

543 The generic architecture of ABEC, when combined with biomass data, is able to properly quantify the  
 544 profitable production of prey for fish communities in nurseries. Hopefully, it will help to resolve debates  
 545 about the influence of the trophic factor on the actual carrying capacity of such essential habitats.

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551 **LITERATURE CITED**

- 552 Ahrens RNM, Walters CJ, Christensen V (2012) Foraging arena theory. *Fish Fish* 13:41–59
- 553 Amara R, Laffargue P, Dewarumez JM, Maryniak C, Lagardere F, Luczac C (2001) Feeding ecology  
 554 and growth of O-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North  
 555 Sea). *J Fish Biol* 58:788–803
- 556 Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern BS, Hays CG,  
 557 Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The Identification, Conservation,  
 558 and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. *Bioscience* 51:633–  
 559 641
- 560 Bourgoin A, Guillou M (1994) Arm regeneration in two populations of *Acrocnida brachiata* (Montagu)  
 561 (Echinodermata: Ophiuroidea) in Douarnenez Bay, (Brittany: France): An ecological significance. *J*  
 562 *Exp Mar Biol Ecol* 184:123–139
- 563 Bowmer T, Keegan BF (1983) Field survey of the occurrence and significance of regeneration in  
 564 *Amphiura filiformis* (Echinodermata: Ophiuroidea) from Galway Bay, west coast of Ireland. *Mar Biol*  
 565 74:65–71
- 566 Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2.  
 567 <http://www.thomas-brey.de/science/>
- 568 Brey T (2012) A multi-parameter artificial neural network model to estimate macrobenthic invertebrate  
 569 productivity and production. *Limnol Oceanogr-Methods* 10:581–589
- 570 Brey T, Mueller-Wiegmann C, Zittier ZMC, Hagen W (2010) Body composition in aquatic organisms -  
 571 A global data bank of relationships between mass, elemental composition and energy content. *J Sea*  
 572 *Res* 64:334–340
- 573 Brind'Amour A, Laffargue P, Morin J, Vaz S, Foveau A, Le Bris H (2014) Morphospecies and  
 574 taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. *Cont Shelf Res* 72:1–9

- 575 Brind'Amour A, Rouyer A, Martin J (2009) Functional gains of including non-commercial epibenthic  
576 taxa in coastal beam trawl surveys: A note. *Cont Shelf Res* 29:1189–1194
- 577 Burrows MT, Gibson RN, Robb L, Maclean A (2004) Alongshore dispersal and site fidelity of juvenile  
578 plaice from tagging and transplants. *J Fish Biol* 65:620–634
- 579 Cabral HN (2000) Comparative feeding ecology of sympatric *Solea solea* and *S-senegalensis*, within  
580 the nursery areas of the Tagus estuary, Portugal. *J Fish Biol* 57:1550–1562
- 581 Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–136
- 582 Clavier J (1984) Production due to regeneration by *Euclymene oerstedii* (Claparède) (Polychaeta:  
583 Maldanidae) in the maritime basin of the Rance (Northern Brittany). *J Exp Mar Biol Ecol* 75:97–106
- 584 Collie JS (1985) Life history and production of three amphipod species on Georges Bank. *Mar Ecol*  
585 *Prog Ser* 22
- 586 Collie JS (1987) Food-Consumption by Yellowtail Flounder in Relation to Production of Its Benthic  
587 Prey. *Mar Ecol Prog Ser* 36:205–213
- 588 Craig JK, Rice JA, Crowder LB, Nadeau DA (2007) Density-dependent growth and mortality in an  
589 estuary-dependent fish: an experimental approach with juvenile spot *Leiostomus xanthurus*. *Mar Ecol*  
590 *Prog Ser* 343:251–262
- 591 Curran MC, Able KW (2002) Annual stability in the use of coves near inlets as settlement areas for  
592 winter flounder (*Pseudopleuronectes americanus*). *Estuaries* 25:227–234
- 593 Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic  
594 habitats\*. *Mar Ecol Prog Ser* 297:1–14
- 595 Darnaude AM, Harmelin-Vivien ML, Salen-Picard C (2001) Food partitioning among flatfish (Pisces :  
596 Pleuronectiforms) juveniles in a Mediterranean coastal shallow sandy area. *J Mar Biol Assoc U K*  
597 81:119–127
- 598 de Montaudouin X, Bachelet G (1996) Experimental evidence of complex interactions between biotic  
599 and abiotic factors in the dynamics of an intertidal population of the bivalve *Cerastoderma edule*.  
600 *Oceanol Acta* 19:449–463
- 601 de Vlas J (1985) Secondary production by siphon regeneration in a tidal flat population of *Macoma*  
602 *balthica*. *Neth J Sea Res* 19:147–164
- 603 Dolbeth M, Cusson M, Sousa R, Pardal MA (2012) Secondary production as a tool for better  
604 understanding of aquatic ecosystems. *Can J Fish Aquat Sci* 69:1230–1253
- 605 Dolbeth M, Lillebø AI, Cardoso PG, Ferreira SM, Pardal MA (2005) Annual production of estuarine  
606 fauna in different environmental conditions: An evaluation of the estimation methods. *J Exp Mar Biol*  
607 *Ecol* 326:115–127
- 608 Eleftheriou A, McIntyre A (2005) *Methods for the Study of Marine Benthos*, 3rd edn. Blackwell  
609 Science, Oxford
- 610 Elkaim B, Irlinger JP (1987) Contribution à l'étude de la dynamique des populations de *Pectinaria*  
611 *koreni* Malmgren (polychète) en baie de Seine orientale. *J Exp Mar Biol Ecol* 107:171–197

- 612 Emlen JM (1966) The Role of Time and Energy in Food Preference. *Am Nat* 100:611–617
- 613 Floeter J, Temming A (2003) Explaining diet composition of North Sea cod (*Gadus morhua*): prey size  
614 preference vs. prey availability. *Can J Fish Aquat Sci* 60:140–150
- 615 Fulford RS, Peterson MS, Grammer PO (2011) An ecological model of the habitat mosaic in estuarine  
616 nursery areas: Part I-Interaction of dispersal theory and habitat variability in describing juvenile fish  
617 distributions. *Ecol Model* 222:3203–3215
- 618 Gallardo VA (1965) Observations on the biting profiles of three 0.1 m<sup>2</sup> bottom-samplers. *Ophelia*  
619 2:319–322
- 620 Gee JM, Warwick RM, Davey JT, George CL (1985) Field experiments on the role of epibenthic  
621 predators in determining prey densities in an estuarine mudflat. *Estuar Coast Shelf Sci* 21:429–448
- 622 Gibson R (1994) Impact of Habitat Quality and Quantity on the Recruitment of Juvenile Flatfishes.  
623 *Neth J Sea Res* 32:191–206
- 624 Gibson RN, Pihl L, Burrows MT, Modin J, Wennhage H, Nickell LA (1998) Diel movements of juvenile  
625 plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors  
626 on a microtidal nursery ground. *Mar Ecol Prog Ser* 165:145–159
- 627 Gillet P, Torresani S (2003) Structure of the population and secondary production of *Hediste*  
628 *diversicolor* (O.F. Müller, 1776), (Polychaeta, Nereidae) in the Loire estuary, Atlantic Coast, France.  
629 *Estuar Coast Shelf Sci* 56:621–628
- 630 Gilliers C, Le Pape O, Desaunay Y, Bergeron J-P (2006) Growth and condition of juvenile sole (*Solea*  
631 *solea* L.) as indicators of habitat quality in coastal and estuarine nurseries in the Bay of Biscay with a  
632 focus on sites exposed to the Erika oil spill. *Sci Mar* 70:183–192
- 633 Grall J, Le Loc'h F, Guyonnet B, Riera P (2006) Community structure and food web based on stable  
634 isotopes ( $\delta$  N-15 and  $\delta$  C-13) analysis of a North Eastern Atlantic maerl bed. *J Exp Mar Biol*  
635 *Ecol* 338:1–15
- 636 Gray JS, Wu RS, Or YY (2002) Effects of hypoxia and organic enrichment on the coastal marine  
637 environment. *Mar Ecol Prog Ser* 238:249–279
- 638 Griffin R, Pearce B, Handy RD (2012) Dietary preference and feeding selectivity of common dragonet  
639 *Callionymus lyra* in U.K. *J Fish Biol* 81:1019–1031
- 640 Hall S, Raffaelli D, Basford D, Robertson M (1990) The Importance of Flatfish Predation and  
641 Disturbance on Marine Benthos. *J Exp Mar Biol Ecol* 136:65–76
- 642 Hampel H, Cattrijsse A, Elliott M (2005) Feeding habits of young predatory fishes in marsh creeks  
643 situated along the salinity gradient of the Schelde estuary, Belgium and The Netherlands. *Helgol Mar*  
644 *Res* 59:151–162
- 645 Hily C (1976) *Ecologie benthique des pertuis charentais*. Thèse de doctorat de 3ème cycle, Université  
646 de Bretagne Occidentale
- 647 Hily C, Le Bris H (1984) Dynamics of an *Abra-Alba* Population (bivalve Scrobiculariidae) in the Bay of  
648 Brest. *Estuar Coast Shelf Sci* 19:463–475

- 649 Hinz H, Kroencke I, Ehrich S (2005) The feeding strategy of dab *Limanda limanda* in the southern  
650 North Sea: linking stomach contents to prey availability in the environment. *J Fish Biol* 67:125–145
- 651 Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: chronic effects and  
652 experimental predictions. *Ecol Appl* 19:761–773
- 653 Hoar WS, Randall DJ, Brett JR (1979) *Growth and Bioenergetics*. Academic Press, New York
- 654 Huret M, Sourisseau M, Petitgas P, Struski C, Léger F, Lazure P (2013) A multi-decadal hindcast of a  
655 physical–biogeochemical model and derived oceanographic indices in the Bay of Biscay. *J Mar Syst*  
656 109–110, Supplement:S77–S94
- 657 Ivlev VS (1961) *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven
- 658 Jaccard P (1901) Distribution de la flore alpine dans le bassin des Dranses et dans quelques régions  
659 voisines. *Bull Société Vaudoise Sci Nat* 37:241–272
- 660 Klein G, Rachor E, Gerlach SA (1975) Dynamics and productivity of two populations of the benthic  
661 tube-dwelling amphipod *Ampelisca brevicornis* (Costa) in Helgoland Bight. *Ophelia* 14:139–159
- 662 Kopp D, Le Bris H, Grimaud L, Nerot C, Brind'Amour A (2013) Spatial analysis of the trophic  
663 interactions between two juvenile fish species and their preys along a coastal-estuarine gradient. *J*  
664 *Sea Res* 81:40–48
- 665 Lai Y-T, Chen J-H, Lee L-L (2011) Prey selection of a shell-invading leech as predicted by optimal  
666 foraging theory with consumption success incorporated into estimation of prey profitability. *Funct Ecol*  
667 25:147–157
- 668 Laurent AG (1963) The Lognormal Distribution and the Translation Method: Description and  
669 Estimation Problems. *J Am Stat Assoc* 58:231–235
- 670 Lê S, Josse J, Husson F (2008) FactoMineR: An R package for multivariate analysis. *J Stat Softw*  
671 25:1–18
- 672 Le Bris H, Glemarec M (1995) Macrozoobenthic communities of an oxygen under-saturated coastal  
673 ecosystem: The Bay of Vilaine (Southern Brittany). *Oceanol Acta* 18:573–581
- 674 Le Bris H, Glemarec M (1996) Marine and Brackish Ecosystems of South Brittany (Lorient and Vilaine  
675 Bays) with Particular Reference to the Effect of the Turbidity Maxima. *Estuar Coast Shelf Sci* 42:737–  
676 753
- 677 Le Pape O, Baulier L, Cloarec A, Martin J, Le Loc'h F, Desaunay Y (2007) Habitat suitability for  
678 juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France): A quantitative description using  
679 indicators based on epibenthic fauna. *J Sea Res* 57:126–136
- 680 Le Pape O, Bonhommeau S (2013) The food limitation hypothesis for juvenile marine fish. *Fish Fish*  
681 DOI: 10.1111
- 682 Le Pape O, Chauvet F, Desaunay Y, Guerault D (2003) Relationship between interannual variations of  
683 the river plume and the extent of nursery grounds for the common sole (*Solea solea*, L.) in Vilaine Bay.  
684 Effects on recruitment variability. *J Sea Res* 50:177–185
- 685 Lie U, Pamatmat MM (1965) Digging characteristics and sampling efficiency of 0.1m<sup>2</sup> van Veen grab.  
686 *Limnol Oceanogr* 10:379–384

- 687 Lincoln RJ (1979) British Marine Amphipoda: Gammaridea. British Museum, London
- 688 MacArthur RH, Pianka ER (1966) On Optimal Use of a Patchy Environment. *Am Nat* 100:603–609
- 689 Mantel N (1967) The Detection of Disease Clustering and a Generalized Regression Approach.  
690 *Cancer Res* 27:209–220
- 691 MarLIN (2006) BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network.  
692 Plymouth: Marine Biological Association of the United Kingdom. [www.marlin.ac.uk/biotic](http://www.marlin.ac.uk/biotic)
- 693 Menesguen A (1980) La macrofaune benthique de la baie de Concarneau: peuplements, dynamique  
694 de populations, predation exercée par les poissons. Thèse de doctorat de 3ème cycle, Université de  
695 Bretagne Occidentale
- 696 Molinero A, Flos R (1992) Influence of Season on the Feeding-Habits of the Common Sole *Solea*  
697 *solea*. *Mar Biol* 113:499–507
- 698 Nash RDM, Geffen AJ (2000) The influence of nursery ground processes in the determination of year-  
699 class strength in juvenile plaice *Pleuronectes platessa* L. in Port Erin Bay, Irish Sea. *J Sea Res*  
700 44:101–110
- 701 Nash RDM, Geffen AJ, Burrows MT, Gibson RN (2007) Dynamics of shallow-water juvenile flatfish  
702 nursery grounds: application of the self-thinning rule. *Mar Ecol Prog Ser* 344:231–244
- 703 Nicolaidou A (1983) Life history and productivity of *Pectinaria koreni* Malmgren (polychaeta). *Estuar*  
704 *Coast Shelf Sci* 17:31–43
- 705 Nicolas D, Le Loc'h F, Desaunay Y, Hamon D, Blanchet A, Le Pape O (2007) Relationships between  
706 benthic macrofauna and habitat suitability for juvenile common sole (*Solea solea*, L.) in the Vilaine  
707 estuary (Bay of Biscay, France) nursery ground. *Estuar Coast Shelf Sci* 73:639–650
- 708 Persson L-E (1981) Were macrobenthic changes induced by thinning out of flatfish stocks in the Baltic  
709 proper? *Ophelia* 20:137–152
- 710 Peterson CH, Summerson HC, Thomson E, Lenihan HS, Grabowski J, Manning L, Micheli F, Johnson  
711 G (2000) Synthesis of linkages between benthic and fish communities as a key to protecting essential  
712 fish habitat. *Bull Mar Sci* 66:759–774
- 713 Pihl L (1985) Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Mar*  
714 *Ecol Prog Ser* 22:169–179
- 715 Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2013) nlme: Linear and  
716 Nonlinear Mixed Effects Models. R Foundation for Statistical Computing
- 717 Posey MH, Alphin TD, Cahoon LB, Lindquist DG, Mallin MA, Nevers MB (2002) Top-down versus  
718 bottom-up limitation in benthic infaunal communities: Direct and indirect effects. *Estuaries* 25:999–  
719 1014
- 720 R Core Team (2012) R: A Language and Environment for Statistical Computing. R Foundation for  
721 Statistical Computing, Vienna, Austria
- 722 Rigolet C, Dubois SF, Thiébaud E (2014) Benthic control freaks: Effects of the tubiculous amphipod  
723 *Haploops niraе* on the specific diversity and functional structure of benthic communities. *J Sea Res*  
724 85:413–427

- 725 Riley JD (1973) Movements of 0-group plaice *Pleuronectes platessa* L. as shown by latex tagging. J  
726 Fish Biol 5:323–343
- 727 Riley JD, Symonds DJ, Woolner L (1981) On the factors influencing the distribution of 0-group  
728 demersal fish in coastal waters. Rapport de Procès Verbal de la Réunion Annuelle du Conseil  
729 International pour l'Exploration de la Mer:223–228
- 730 Rogers S (1994) Population-Density and Growth-Rate of Juvenile Sole *Solea solea* (L). Neth J Sea  
731 Res 32:353–360
- 732 Ross SW (2003) The relative value of different estuarine nursery areas in North Carolina for transient  
733 juvenile marine fishes. Fish Bull 101:384–404
- 734 Shaw M, Jenkins GP (1992) Spatial variation in feeding, prey distribution and food limitation of juvenile  
735 flounder *Rhombosolea tapirina* Günther. J Exp Mar Biol Ecol 165:1–21
- 736 Shi YB, Gunderson DR, Sullivan PJ (1997) Growth and survival of 0(+) English sole, *Pleuronectes*  
737 *vetulus*, in estuaries and adjacent nearshore waters off Washington. Fish Bull 95:161–173
- 738 Shorygin AA (1931) Foods, selective capacity, and food interrelationships of certain Gobiidae of the  
739 Caspian Sea. Zool Zh 18:27–53
- 740 Skold M, Loo L, Rosenberg R (1994) Production, Dynamics and Demography of an *Amphiura*-  
741 *Filiformis* Population. Mar Ecol Prog Ser 103:81–90
- 742 Strauss RE (1982) Influence of Replicated Subsamples and Subsample Heterogeneity on the Linear  
743 Index of Food Selection. Trans Am Fish Soc 111:517–522
- 744 van der Veer HW, Berghahn R, Miller JM, Rijnsdorp AD (2000) Recruitment in flatfish, with special  
745 emphasis on North Atlantic species: Progress made by the Flatfish Symposia.ICES J Mar Sci 57:202–  
746 215
- 747 van der Veer HW, Witte JIJ (1993) The Maximum Growth Optimal Food Condition Hypothesis - a Test  
748 for 0-Group Plaice *Pleuronectes-Platessa* in the Dutch Wadden Sea. Mar Ecol Prog Ser 101:81–90
- 749 van Veen J (1933) Onderzoek naar het zandtransport von rivieren. Ing 48:151–159
- 750 Vinagre C, Cabral HN (2008) Prey consumption by the juvenile soles, *Solea solea* and *Solea*  
751 *senegalensis*, in the Tagus estuary, Portugal. Estuar Coast Shelf Sci 78:45–50
- 752 Vinagre C, França S, Cabral HN (2006) Diel and semi-lunar patterns in the use of an intertidal mudflat  
753 by juveniles of Senegal sole, *Solea senegalensis*. Estuar Coast Shelf Sci 69:246–254
- 754 Visser AW, Fiksen O (2013) Optimal foraging in marine ecosystem models: selectivity, profitability and  
755 switching. Mar Ecol Prog Ser 473:91–101
- 756 Wainwright P, Richard B (1995) Predicting Patterns of Prey Use from Morphology of Fishes. Environ  
757 Biol Fishes 44:97–113
- 758 Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from  
759 trophic mass-balance assessments. Rev Fish Biol Fish 7:139–172
- 760 Ward JH (1963) Hierarchical Grouping to Optimize an Objective Function. J Am Stat Assoc 58:236–  
761 244

762 Werner EE, Mittelbach GG, Hall DJ, Gilliam JF (1983) Experimental Tests of Optimal Habitat Use in  
763 Fish: The Role of Relative Habitat Profitability. *Ecology* 64:1525

764 WoRMS Editorial Board (2013) World Register of Marine Species. <http://www.marinespecies.org>

765 Wouters N, Cabral HN (2009) Are flatfish nursery grounds richer in benthic prey? *Estuar Coast Shelf*  
766 *Sci* 83:613–620

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## 768 APPENDIX

769 Appendix 1. ABEC values for all prey taxa in the Bay of Vilaine. These values are estimates and  
770 include uncertainties that are not quantified.

Taxa	ABEC (in $\text{kJ}\cdot\text{g}^{-1}\cdot\text{year}^{-1}$ )
<i>Abludomelita obtusata</i>	30.96
<i>Abra alba</i>	0.35
<i>Abra nitida</i>	0.34
<i>Acanthocardia echinata</i>	2.25
<i>Acrocnida brachiata</i>	0.14
<i>Ampelisca</i>	1.87
<i>Ampelisca spinimana</i>	2.00
<i>Ampelisca spinipes</i>	1.09
<i>Ampharete acutifrons</i>	1.49
<i>Amphiura filiformis</i>	0.24
<i>Aphrodita aculeata</i>	0.53
<i>Apseudopsis latreillii</i>	24.40
<i>Asthenognathus atlanticus</i>	0.88
<i>Bivalvia</i>	0.34
<i>Bodotria scorpioides</i>	12.71
<i>Brachyura</i>	16.90
<i>Capitella capitata</i>	1.81
Capitellidae	1.79
<i>Capitomastus minima</i>	1.37
<i>Caprella</i>	20.26
<i>Cerastoderma edule</i>	0.87
<i>Cerebratulus</i>	0.36
<i>Chaetopterus variopedatus</i>	0.63
<i>Chaetozone setosa</i>	1.58
<i>Corbula gibba</i>	0.25
<i>Corophium volutator</i>	2.40
<i>Cylichna cylindracea</i>	0.44
<i>Diastylis</i>	12.58
<i>Diastylis bradyi</i>	10.18
<i>Diastylis rathkei</i>	9.47
<i>Diopatra neapolitana</i>	0.74
<i>Euclymene lumbricoides</i>	0.84
<i>Euclymene oerstedii</i>	0.83
Gammaridae	20.54
Gastropoda	5.11
<i>Glycera</i>	1.32
<i>Glycera convoluta</i>	0.84
<i>Glycera unicornis</i>	0.62

<i>Gnathia maxillaris</i>	20.23
<i>Golfingia (Golfingia) elongata</i>	0.45
<i>Haploops nirae</i>	1.15
<i>Heteromastus filiformis</i>	1.33
<i>Inachus dorsettensis</i>	10.58
<i>Kurtiella bidentata</i>	0.57
<i>Labidoplax digitata</i>	0.17
<i>Labioleanira yhleni</i>	0.51
<i>Lagis koreni</i>	0.46
<i>Lanice conchilega</i>	0.98
<i>Leptopentacta elongata</i>	0.13
<i>Liocarcinus holsatus</i>	2.66
<i>Liocarcinus navigator</i>	3.96
<i>Liocarcinus pusillus</i>	8.06
<i>Lumbrineris gracilis</i>	1.65
<i>Lumbrineris latreilli</i>	1.27
<i>Macoma balthica</i>	0.27
<i>Mactra stultorum</i>	0.44
<i>Magelona alleni</i>	1.05
<i>Maldane glebifex</i>	0.70
<i>Melinna palmata</i>	1.51
<i>Mytilus edulis</i>	5.32
<i>Nassarius reticulatus</i>	0.91
<i>Nemertea</i>	1.63
<i>Neoamphitrite edwardsi</i>	0.49
<i>Nephtys cirrosa</i>	0.89
<i>Nephtys hombergii</i>	0.97
<i>Nephtys hystricis</i>	0.79
<i>Nereis zonata</i>	0.68
<i>Notomastus latericeus</i>	0.44
<i>Nucula nitidosa</i>	0.31
<i>Ophiura albida</i>	2.16
<i>Ophiura ophiura</i>	2.36
<i>Orbinia cuvierii</i>	0.38
<i>Owenia fusiformis</i>	1.16
<i>Paguridae</i>	7.28
<i>Phascolion (Phascolion) strombus</i>	0.57
<i>Phaxas pellucidus</i>	0.60
<i>Pherusa monilifera</i>	0.88
<i>Pherusa plumosa</i>	0.82
<i>Philine aperta</i>	2.26
<i>Pholoe minuta</i>	1.25
<i>Photis longicaudata</i>	18.36
<i>Pisidia longicornis</i>	22.75
<i>Pista cristata</i>	1.02
<i>Polititapes virgineus</i>	0.07
<i>Polychaeta</i>	1.12
<i>Scalibregma inflatum</i>	0.97
<i>Schistomeringos rudolphii</i>	2.28
<i>Sipunculus (Sipunculus) nudus</i>	0.30
<i>Spiochaetopterus costarum</i>	1.39
<i>Spiophanes bombyx</i>	1.86
<i>Spisula subtruncata</i>	0.55
<i>Sternaspis scutata</i>	0.66
<i>Terebellides stroemii</i>	0.99
<i>Thyasira flexuosa</i>	0.54
<i>Turritella communis</i>	0.16