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1 Potential marine benthic colonisers of offshore wind farms in
2 the English Channel: a functional trait-based approach

3
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12
13 **Highlights**

- 14 • Communities of hard substrates in English Channel differed from those of offshore
15 wind farms and oil and gas platforms.
16 • 157 taxa have been identified as potential colonisers of Dunkirk's offshore wind farms
17 • Functional profiles of potential colonisers were created based on the categories of
18 functional traits represented most in each community.
19 • Communities of young offshore wind farms (< 3 y) and hard substrates had similar
20 functional volumes, while that of oil and gas platforms was the smallest.
21
22
23

24 **Abstract**

25 Offshore wind farms (OWFs) have gained attention as a promising alternative to conventional
26 energy sources. However, their installation and operation may have multiple ecological
27 impacts on the marine environment, including the “reef effect”. The reef effect is the
28 colonisation of [wind turbines and other artificial substrates](#) by benthic organisms, which has a
29 major impact on marine biodiversity as it changes community assemblages and ecosystem
30 functioning. We conducted a two-step study to predict the reef effect of a future OWF
31 (Dunkirk, northern France). First, we explored similarities between colonisers of existing
32 OWFs and those of other hard substrates (oil and gas platforms (O&GP) and hard substrates
33 in the English Channel (HSEC)). We then analysed functional traits to determine a trait
34 profile of potential colonisers of Dunkirk’s OWF. Statistical analyses revealed that OWF and
35 O&GP communities were more similar to each other than to that of HSEC. Comparing the
36 three communities revealed that they shared 157 taxa, which could be potential colonisers of
37 Dunkirk’s future OWF. The functional profile revealed that OWF colonisers were species
38 ranging from 10–100 mm in size, with gonochoric reproduction, pelagic and planktotrophic
39 larvae, a life span of less than 2 years or 5–20 years, were sessile, and were carnivores or
40 suspension feeders. Functional trait analysis revealed that during their intermediate stage of
41 development, OWF benthic communities have a functional richness and diversity (0.68 and
42 0.53, respectively) similar to those of HSEC communities (0.54 and 0.50, respectively).
43 However, based on using O&GP as a long-term view of the colonisation of OWFs, functional
44 richness and diversity could decrease during the climax stage (0.07 and 0.42, respectively).

45 **Keywords:** offshore wind farms, colonisation; benthic species; biological traits; functional
46 diversity; English Channel.

47 **1. Introduction**

48 It is now evident that greenhouse gas emissions from human activities are responsible for
49 global warming. According to the Sixth IPCC report, total net anthropogenic greenhouse gas
50 emissions continued to increase from 2010–2019, as did cumulative net emissions since 1850.
51 Mean annual emissions from 2010–2019 were higher than those in previous decades (IPCC,
52 2022). To reduce greenhouse gas emissions and meet the demand for energy, renewable
53 energy became a relevant alternative and continues to develop.

54 In the context of the European Green Deal, which aims to make Europe a climate-
55 neutral continent by 2050, the European Union has set several targets to transition energy use,
56 such as having 32.5% of renewable energy in total energy consumption and reducing
57 greenhouse gas emissions 40% by 2030. [In Europe and around the world, such as China and](#)
58 [the United States of America, the development of offshore wind turbines is a response to the](#)
59 [need for renewable energy in the energy mix \(de Castro et al., 2019\).](#) The influence of this
60 type of infrastructure on the marine environment is complex from technical, legal, societal,
61 and environmental [points of view](#) for all stakeholders. This renewable source of marine
62 energy must be integrated into ecosystems that are already subject to multiple human
63 disturbances (e.g. climate change, overexploitation of resources, pollution). Installing and
64 operating OWFs ([Offshore Wind Farms](#)) can have many ecological impacts on the marine
65 environment, including wildlife populations, habitats, water quality, and nutrient cycles
66 (Degraer et al., 2020; Galparsoro et al., 2022). For example, noise [pollution](#) and sea bottom
67 destruction can occur immediately during installation of OWFs, whereas other ecological
68 impacts can occur over longer periods, such as the colonisation of benthic species on new
69 structures, known as the "reef effect" (Wilhelmsson and Malm, 2008).

70 The reef effect is the colonisation of wind turbines and other artificial substrates (e.g.
71 OWFs, shipwrecks, harbours, oil and gas platforms) by benthic [species](#), which has a large

72 influence on marine biodiversity (Svane and Petersen, 2001; Petersen and Malm, 2006;
73 Kerckhof et al., 2010; Langhamer, 2012; Dannheim et al., 2020; [Degraer et al., 2020](#)). During
74 the operational phase, wind turbine foundations and their scour protection layers create new
75 habitats that are quickly colonised, mainly by larvae of benthic species such as gastropods,
76 bivalves, crustaceans, and polychaetes (Wilhelmsson and Malm, 2008; [Zupan et al., 2023](#)).
77 Installing an OWF modifies local marine habitats, which implies changes in community
78 assemblage due to the installation of artificial hard substrates on natural soft sediment
79 (Kerckhof et al., 2010, 2019; Dannheim et al., 2020). The OWF increases the rapid and
80 abundant colonisation of benthic marine species via larval dispersal, as most of these species
81 have a benthopelagic life cycle. [At first, the scientific community thought that the new
82 community followed the same temporal dynamics as a colonised natural habitat](#) (Kerckhof et
83 al., 2010, 2019). First, the pioneer stage of early colonisers lasts for 2 years after the turbines
84 are installed. The early colonisers are opportunistic, and the species composition depends on
85 the type of foundation (Kerckhof et al., 2019). Next, an intermediate stage, 3–5 years after
86 installation, has high species richness (Kerckhof et al., 2019; Degraer et al., 2020). Finally,
87 the climax stage, 6 years after installation, has biomass dominated by mussels and anemones
88 (Kerckhof et al., 2019; Degraer et al., 2020). [But a recent study challenges this theory,
89 discussing the unstable nature of the community even after 11 years](#) (Zupan et al., 2023). The
90 [difficulty of understanding and anticipating succession at the community level could be
91 overcome by both longer-term and large-scale research, where biological interactions are
92 included into the analysis.](#)

93 Colonisers can influence the diversity of the community (Walker and Chapin, 1987;
94 Connell and Slatyer, 1997). Some species can help increase its species richness, such as the
95 filter-feeding blue mussel (*Mytilus edulis*), which is considered positive engineer that
96 facilitates establishment of other species (Connell and Slatyer 1977; Kerckhof et al., 2019).

97 Conversely, other species are considered negative engineers, such as the plumose anemone
98 (*Metridium senile*), which inhibits establishment of other species by predated their free-
99 swimming larvae (Connell and Slatyer 1977; Kerckhof et al., 2019). This biofouling provides
100 an additional food resource for higher trophic levels within the local marine food web. For
101 example, the foundation of a wind turbine can contain up to 2 t of mussels (Shields and
102 Payne, 2014), which in turn attracts predators. On some OWF, such as a Belgian OWF in the
103 North Sea, the climax community is dominated by the plumose anemone and the blue mussel
104 (i.e. ‘[slimeification](#)’ or ‘mytilisation’, respectively) (Krone et al., 2013; Kerckhof et al., 2019).

105 Installing an OWF can influence species richness of the local community assemblage
106 as well as ecosystem functioning. In the past few decades, the development of trait databases
107 (e.g. FishBase, Polytraits, Arctic Traits) has supported the development of the functional trait-
108 based approach in ecology (Martini et al., 2021). Instead of understanding and classifying
109 species based only on their taxonomy, it does so based on their functional traits, including
110 morphological (e.g. maximum body size), life-history (e.g. mode of reproduction, life span),
111 physiological (e.g. maximum growth rate, feeding regime) and behavioural (e.g. mobility),
112 which determine their role and impact in an ecosystem. Analysing these traits can increase
113 understanding of mechanisms that underlie community assembly, species interactions, and
114 ecosystem functioning (Naeem and Wright, 2003; Petchey and Gaston, 2006; Nock et al.,
115 2016; Degen et al., 2018).

116 The functional trait-based approach can address a wide range of ecological issues,
117 including climate change and human impacts. It can be used to compare how functioning
118 differs between assemblages and can highlight initial responses to changes in the functional
119 structure that traditional diversity analysis cannot detect (Mouillot et al., 2013). Installing
120 human-made structures, including OWFs and the structures they are built on (e.g.
121 foundations, cables), may encourage colonisation of species not present in the local soft-

122 bottom marine habitat that have novel functional traits. This could increase functional
123 diversity and change ecosystem functioning by increasing the functional niche space. The
124 functional trait-based approach can help identify which species are colonising these new
125 habitats and how their functional traits may influence the local ecosystem. We considered the
126 future OWF of Dunkirk (northern France) as a case study to predict consequences of
127 installing OWFs in the eastern EC. The Dunkirk OWF (planned for 2028) is particularly
128 interesting because it is located in the transition zone between the eastern French EC, where
129 no OWF currently exists (but seven are planned), and the southern North Sea. Our goal was to
130 identify potential colonisers and their functional trait profiles. To this end, we compared
131 benthic communities in the EC on natural (e.g. rocks, gravel, pebbles) and artificial hard
132 substrates (e.g. shipwrecks, harbours) (HSEC) to those on OWFs in the North Sea and Irish
133 Sea (OWF), and on oil and gas platforms in the North Sea (O&GP). This was done using
134 traditional community-structure analysis and the functional trait-based approach. The
135 objectives of this study were as follows:

- 136 1. Describe the community structure of the three hard-substrates habitats (i.e. HSEC,
137 OWF, and O&GP) and their similarities.
- 138 2. Develop a [traits profile](#) of the species that colonise each of these three habitats,
139 with emphasis on the dominant traits of species that colonise OWFs.
- 140 3. Compare functional characteristics (e.g. functional diversity, species richness) of
141 the three community assemblages to predict the community of the artificial reef
142 created by installing the Dunkirk OWF.

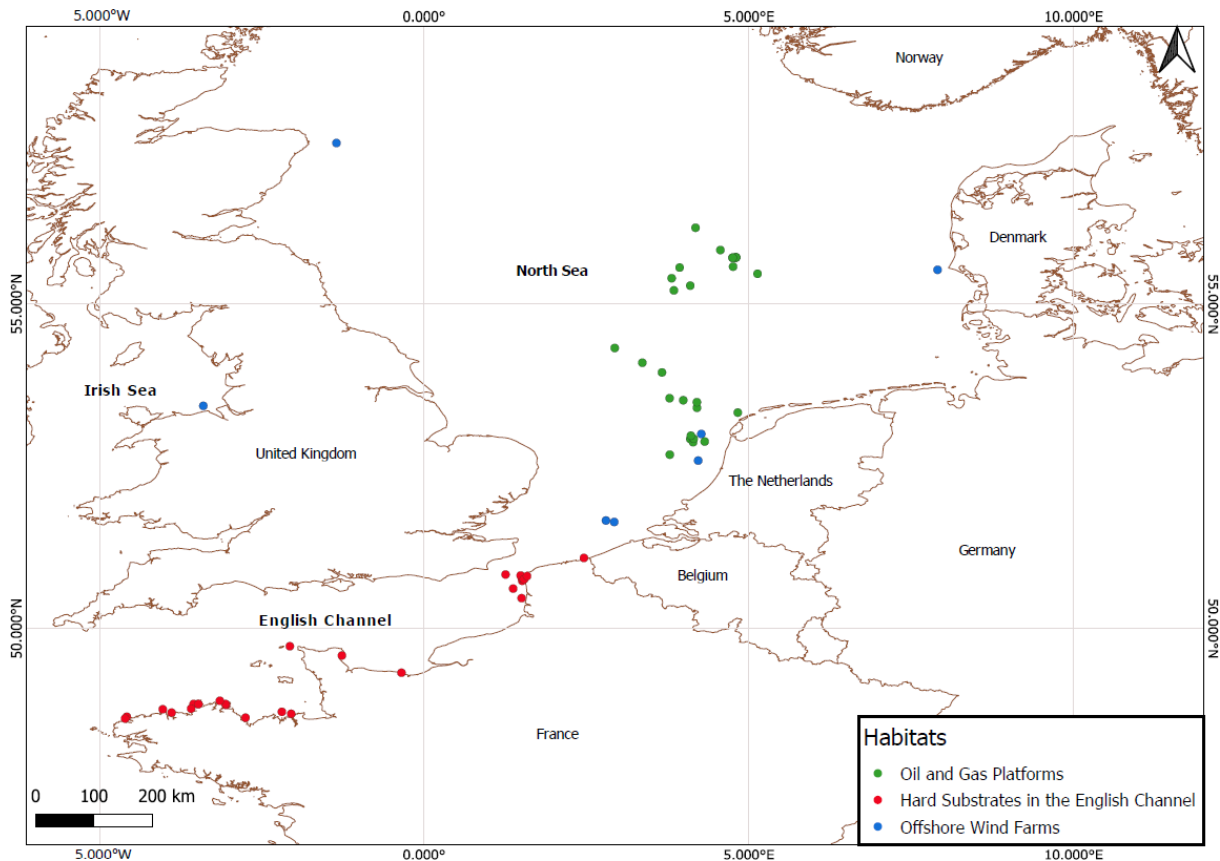
143

144 2. **Material and methods**

145 2.1. Data collection

146 [The first step in the study was to compile the literature on colonisers of the three habitats of](#)
147 [interest \(OWF, O&GP, HSEC\), and to be able to compare their communities with each other.](#)

148 Data on species community composition were collected from the EC, Irish Sea and the North
149 Sea [since](#) the Dunkirk OWF will be located at the transition between these two biogeographic
150 provinces. The literature review identified 7 OWFs (i.e. C Power, Belwind, Egmond aan Zee,
151 Princess Amalia, Horns Rev, Hywind, and NorthHoyle) for which lists of colonising species
152 were available, in 13 references and 1 shared data set (Supplementary Material Table A). For
153 O&GP, 28 platforms had lists of colonisers available in 5 references (Supplementary Material
154 Table A). Finally, for HSEC we identified three types of hard substrates – natural hard
155 substrates (e.g. rocks, gravel, pebbles), artificial reefs, and shipwrecks – using 8 references
156 (Supplementary Material Table A). [A literature review was performed using Google Scholar](#)
157 [and ISI Web of Science, where 28 references have been identified with species lists of](#)
158 [colonisers](#). In these references, species were collected and/or identified via scuba diving, scrape
159 sampling, ROV imagery [and Rallier du Baty dredge](#). We selected only macrofauna (> 1 mm)
160 for our study. We used the WORMS database to verify that all benthic species cited in the
161 literature were identified by the correct species name. A list of species presence (1) or absence
162 (0) was then created and transformed into a data frame for each habitat.



163

164 **Figure 1.** Locations of the three hard substrate habitats (oil and gas platforms, hard substrates
 165 in the English Channel, and offshore wind farms) with a species list found in the literature
 166 (see Supplementary Material Table A for information on the habitats).

167

168 2.2. Community structure analysis

169 We built a list of species for each of the three hard-substrates habitats (OWF, O&GP and
 170 HSEC). As the characteristics of these three habitats are potentially different (age, shore
 171 distance, depth...), we carried out an analysis of the community structure and we made the
 172 hypothesis that OWF and O&GP would have closer characteristics compared to HSEC. To
 173 this end, we combined the three lists into a single presence/absence data set (Supplementary
 174 Material Table B) and calculated a matrix of the Bray-Curtis dissimilarity index using the
 175 *vegdist* function of the *vegan* package of R software (R Core Team, 2022). We then
 176 performed a PERMANOVA (999 permutations, Bray-Curtis dissimilarity index (McArdle
 177 and Anderson, 2001)) on the dissimilarity matrix using the *Adonis* function of the *vegan*

178 package. To illustrate similarities among colonisers of the three habitats, we performed
179 hierarchical ascending classification on the dissimilarity matrix using the Ward method, using
180 the `hclust` function of the *stats* package of R. Finally, we used a Venn diagram to identify
181 which species the three habitats shared in common.

182 2.3. Functional trait-based approach

183 After comparing the communities structure between the three hard-substrates habitats, we
184 compared the functional traits of the main colonisers of these three habitats in order to
185 explore whereas it follows the same trend. Based on Degen and Faulwetter (2019), seven
186 biological traits were selected: one morphological trait (i.e. maximum body size), four life-
187 history traits (i.e. mode of reproduction, type of larval development, mode of larval
188 dispersal, and life span), and two behavioural traits (i.e. mobility and feeding regime of
189 juveniles/adults) (Table 1). Some functional traits give information on the state of the
190 community (successional stage and stability) such as maximum body size and longevity.
191 Other functional traits such as the mode of reproduction, the type of larva and its diet give
192 insights into their potential dispersal strategy and then, colonisation abilities of artificial
193 substrates at a larger scale. Each trait was divided into 3–5 categories, resulting in 27
194 categories (Table 1). The biological traits were obtained from the literature (Supplementary
195 Material Table C) and from databases (e.g. Polytraits, Marlin, Biotic, Encyclopedia of
196 life). We used a fuzzy coding approach to allocate each species to the categories of a given
197 biological trait (Chevenet et al., 1994), attributing 0 or 3 when a species had no affinity or
198 complete affinity, respectively, with a category. A species could have affinities with
199 multiple categories for a given trait, but the sum of all categories always equalled 3. We then
200 created a data set that contained the main species in each habitat with their fuzzy coded
201 biological traits. Due to the large number of species, an occurrence index (I_r) was
202 calculated for each habitat:

203
$$Ir = \frac{\text{Number of references in which the species was cited}}{\text{Total number of references}} \times 100 \quad (1)$$

204

205 A species was selected for functional trait-based analysis when it was cited in at least 30% of
206 the references for the targeted habitat. Overall, 68, 56, and 28 species were included in the
207 biological trait matrix for HSEC, OWF, and O&GP, respectively (Supplementary Material
208 Table D). All trait matrices were at the species level and double-checked for accuracy.

209 To test for independence between trait categories and habitats (HSEC, OWF,
210 O&GP), the fuzzy code values for each category were summed and then transformed into a
211 percentage. This is repeated for each of the three habitats (Bolam et al., 2017; Zhulay et al.,
212 2021). Percentage values were used to test the independence using a Chi² test on R.
213 Significant differences were assessed using Pearson's Chi² post-hoc test in R. In order to
214 obtain a functional profile, we calculated a cumulative score of the functional categories
215 with a threshold greater than or equal to 50%, thus identifying the most represented
216 functional categories for each of the three habitats.

217 2.4. Functional diversity and structure

218 To take the functional trait approach a step further, trait diversity and community structure
219 were studied using statistical tools. Two functional diversity indices were calculated to
220 better understand the functional characteristics of each habitat's community. First, the mean
221 functional richness (FRic) was estimated as the percentage of the functional volume of each
222 habitat's community derived from a multidimensional functional space (Mouchet et al.,
223 2010), which revealed how much of the functional niche space was filled by the species
224 present (Degen et al., 2018). The second index was Rao's quadratic entropy (RaoQ), which
225 measures trait dissimilarity and ranges from 0 (i.e. low functional diversity: species in the
226 community have similar functional trait profiles) to 1 (i.e. high functional diversity: species
227 in the community have unique functional trait profiles) (Botta-Dukát, 2005). The two

228 functional indices were calculated using the dbFD function of the *FD* package (Laliberté and
229 Legendre, 2010) of R. The functional spaces were constructed using principal coordinate
230 analysis (PCoA), which encapsulated unique trait combinations of species by substrate
231 (Laliberté and Legendre, 2010), performed on species-by-trait and habitats-by-species data
232 sets (Supplementary Materials E and F).

233 To visualise which trait influenced the functioning of each hard substrate, we
234 performed multiple factor analysis (MFA) (Escofier and Pagès, 1994) of species using trait
235 data sets in which species were grouped by habitat (Supplementary Material G). MFA is a
236 modified PCoA that can consider categorical data and thus gives equal weight to traits that
237 have different numbers of categories (McLean et al., 2021). Associations between traits and
238 substrates were assessed based on the contributions of trait values to the two first axes. MFA
239 was performed using the MFA function of the *FactoMineR* package of R. Principal
240 component analysis was then performed using data from the MFA to obtain a correlation
241 circle of the functional traits using the *fviz_contrib* function of the *factoextra* package of R.
242 Finally, the functional space of each habitat was plotted using the coordinates of the species
243 in the overall functional space provided by the MFA.

244 The overlap of functional polygons between the three hard-substrates habitats was
245 calculated using a Monte Carlo method, usually performed to study niche regions (Swanson
246 et al., 2015). The Bayesian probabilistic method estimates size and pairwise polygon overlap
247 without considering sample size (e.g. number of main species per habitats in our study).
248 Overlaps were estimated from the species coordinates of the two first axes of the PCoA for
249 each of the main species. Average overlap between functional polygons with 95% Bayesian
250 intervals based on 10,000 iterations in bivariate dimension. The analyses were performed
251 using the *nicheROVER* package (Lysy et al., 2021) of R.

252 The functional diversity indices and MFA visualisation were repeated on trait

253 matrices by removing species with direct development (trait L3, Table 1) due to their
 254 absence from the main species list of O&GP colonisers (but not from the entire species list)
 255 but not in HSEC and OWF species' lists.

256 **Table 1.** The biological traits and their categories used in the functional trait-based approach
 257 to identify the main species colonising hard substrates

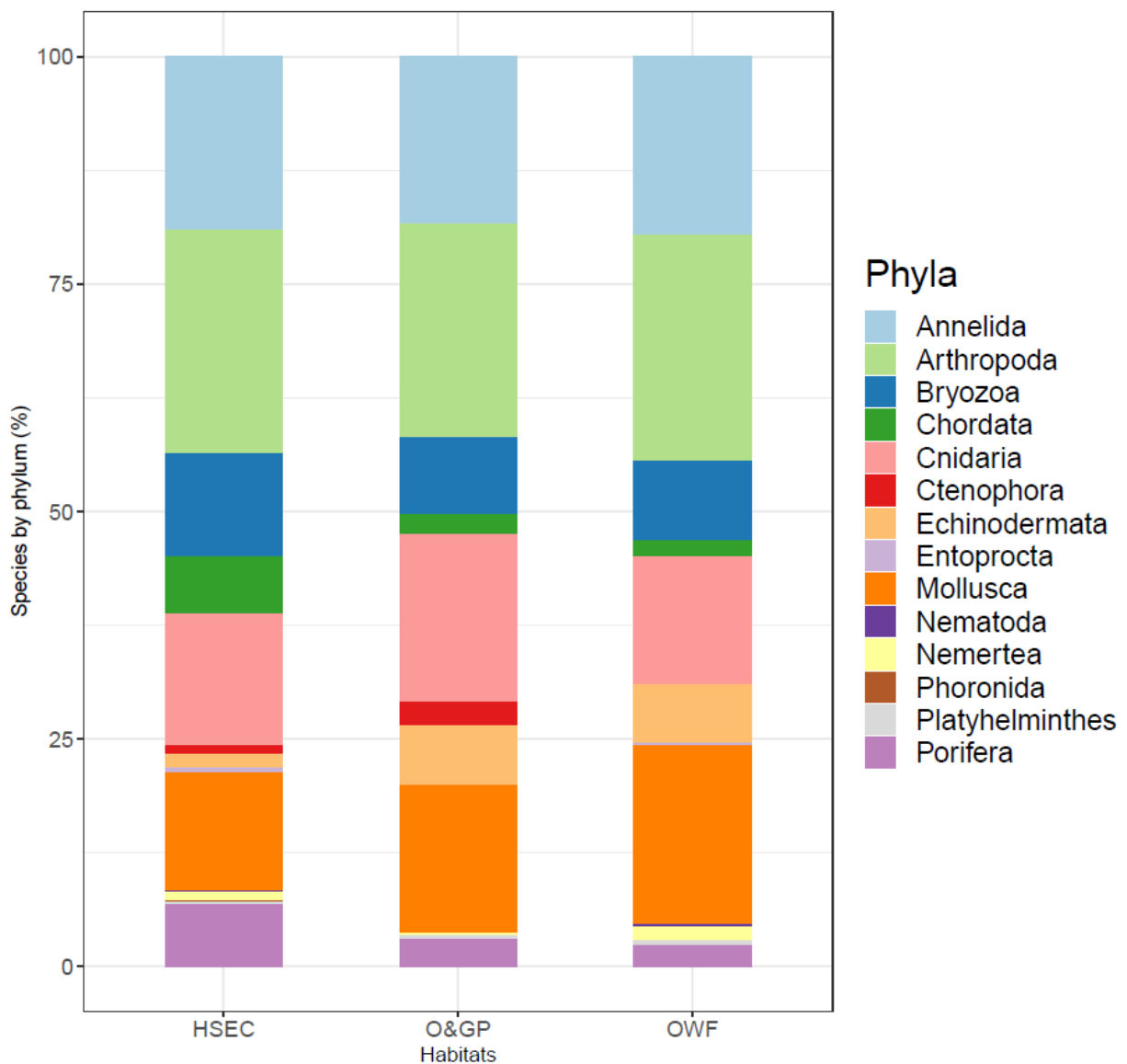
Biological trait	Category	Definition
Maximum body size	S1	Small (< 10 mm)
	S2	Small–medium (10-50 mm)
	S3	Medium (50-100 mm)
	S4	Medium–large (100-300 mm)
	S5	Large (> 300 mm)
Reproduction	R1	Asexual (e.g. budding, fission)
	R2	Gonochoric
	R3	Hermaphrodite
Larval development	L1	Pelagic
	L2	Benthic
	L3	Direct (no larval stage)
Larval diet	LD1	Planktotrophic
	LD2	Lecithotrophic
	LD3	Direct (no larval stage)
Life span	A1	Short (< 2 years)
	A2	Short–medium (2–5 years)
	A3	Medium–long (5–20 years)
	A4	Long (> 20 years)
Mobility	MO1	Sessile
	MO2	Burrower
	MO3	Crawler
	MO4	Swimmer
Feeding habit	FH1	Deposit feeder
	FH2	Suspension feeder
	FH3	Herbivore
	FH4	Opportunist/Scavenger
	FH5	Carnivore

258

259 **3. Results**

260 3.1. Community structure analysis of hard substrates

261 The literature review of colonisers identified 384, 265, and 559 species for OWF, O&GP, and
262 HSEC, respectively (Supplementary Material Table B). A total of 14 phyla were represented,
263 of which 4 dominated (i.e. $\geq 58\%$ of species in each habitat): Arthropoda, Annelida,
264 Mollusca, and Cnidaria (Fig. 2).

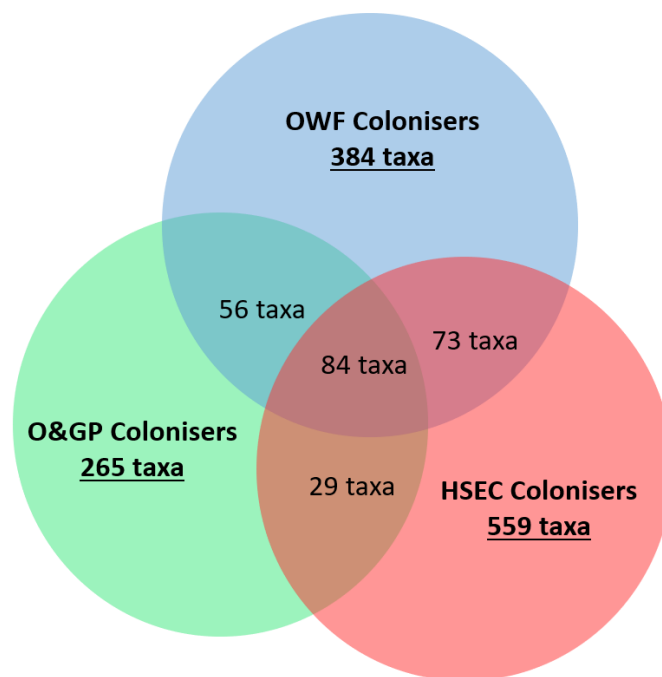


265

266 **Figure 2.** Percentage of each species colonising the three habitats, by phylum. (HSEC: hard
267 substrates in the English Channel, O&GP: oil and gas platforms, and OWF: offshore wind farms)
268

269 The PERMANOVA revealed that habitat had a significant ($P < 0.05$) effect on species
270 communities (Supplementary Material H). The hierarchical classification showed that the
271 community of HSEC (Height = 0.741) differed from those of O&GP and OWF (Height =
272 0.576), which were more similar to each other.

273 The Venn diagram indicated 84 species in common among all three habitats, with OWF
274 and HSEC having the most ($n = 73$) and HSEC and O&GP having the fewest ($n = 29$) (Fig.
275 3).



276
277 **Figure 3.** Venn diagram of the taxa shared among the substrates for all species
278 inventoried (HSEC: hard substrates in the English Channel, O&GP: oil and gas platforms,
279 and OWF: offshore wind farms)

280

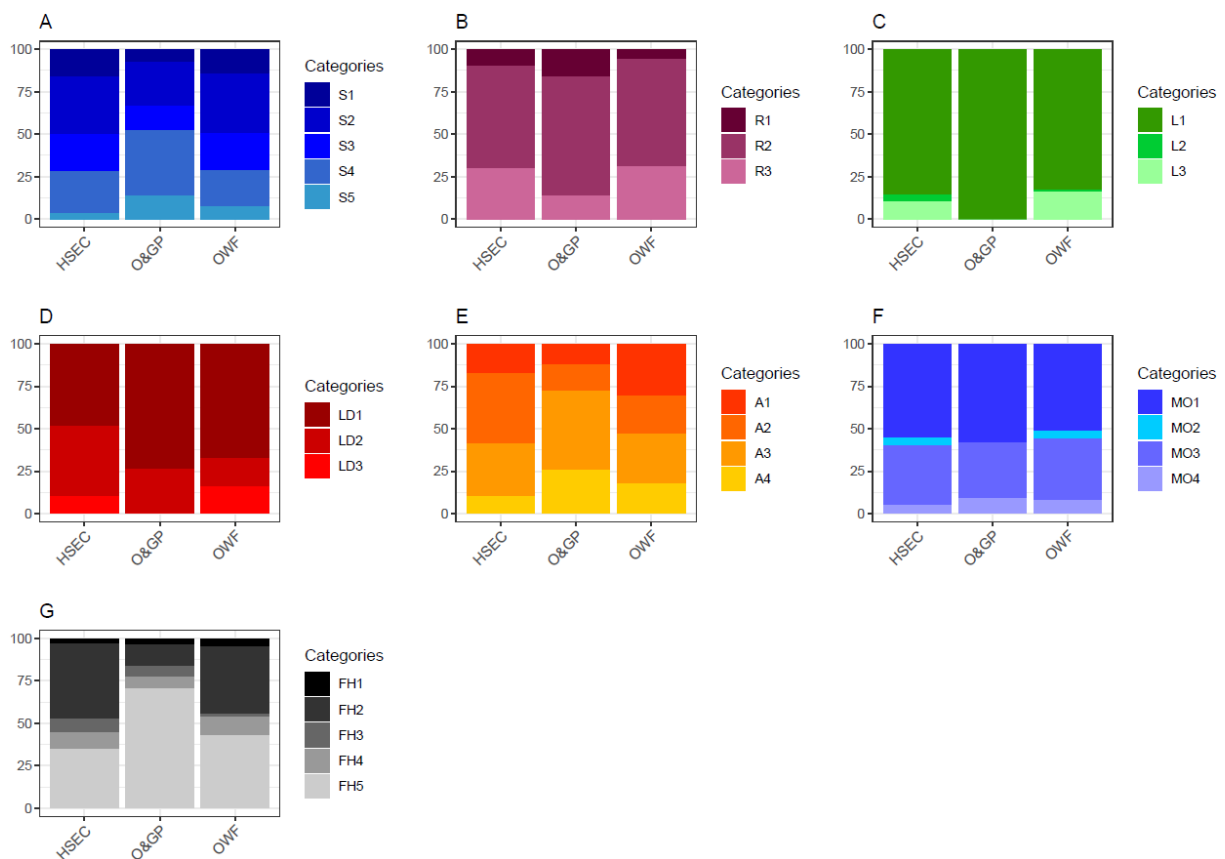
281 3.2. Biological trait profiles of hard substrates

282

283 When categories of each of the seven biological traits were compared among the habitats, at
284 least one of the categories differed among habitats, except for the mobility trait ($P > 0.05$)
285 (Fig. 5, Supplementary Material I). For the reproduction trait, category hermaphrodite was
286 represented less in O&GP than in the other two habitats. Benthic, direct larval development,

287 and the feeding mode associated to direct development mode were not represented in O&GP.
 288 The percentage of planktotrophic larvae was higher in OWF and O&GP than in HSEC. For
 289 the life span trait, category < 2 years dominated in OWF but not in the other two habitats. Life
 290 span category 2–5 years was absent in O&GP. For the diet of the colonisers, category
 291 suspension feeder was represented less in O&GP than in the other two habitats, and category
 292 carnivore was represented less in HSEC than in the other two habitats.

293



294

295 **Figure 5.** Percentage of each category of the seven biological traits selected (A) maximum
 296 body size, B) reproduction, C) larval development, D) larval diet, E) life span, F) mobility,
 297 and G) feeding habit) for the three habitats (HSEC: hard substrates in the English Channel,
 298 O&GP: oil and gas platforms, OWF: offshore wind farms)

299

300 The percentage contributions of the most represented categories of the seven biological
 301 traits varied among habitats (Supplementary Material Table J). For HSEC and O&GP, the
 302 categories represented most for maximum body size were 10–50 mm and 100–300 mm.

303 For OWF, the categories represented most were 10–50 mm and 50–100 mm. For
 304 reproduction, category gonochoric dominated in HSEC, O&GP, and OWF For HSEC,
 305 O&GP, and OWF, larval development was mainly pelagic and larval diet was mainly
 306 planktotrophic, however, lecithotrophic larva was also highly represented in HSEC. For life
 307 span, the most represented categories were 2–5 years and 5–20 years for HSEC, 5–20
 308 years and > 20 years for O&GP, and < 2 years and 5–20 years for OWF. For mobility,
 309 sessile organisms dominated in HSEC, O&GP, and OWF. For feeding habit, for HSEC and
 310 OWF, colonisers were either suspension feeders or carnivores, whereas for O&GP,
 311 carnivores dominated

312

313 3.3 Functional diversity and structure

314 FRic and RaoQ were highest for HSEC (0.68 and 0.53, respectively) and lowest for O&GP
 315 (0.07 and 0.42, respectively).

316

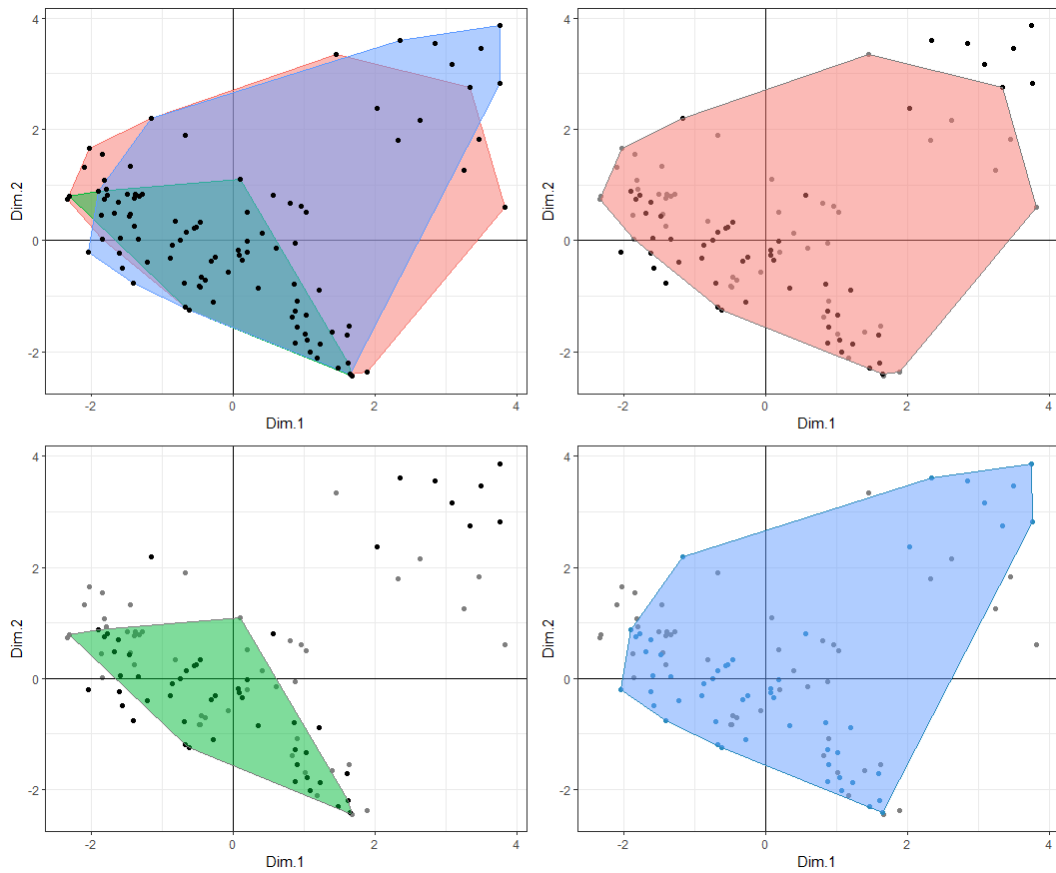
317 **Table 2.** Functional diversity indices (functional richness (FRic) and Rao's quadratic
 318 entropy (RaoQ)) based on the biological traits of the main species (n = number of species).
 319 Bold indicates the highest indicator values.

Habitat	n	FRic	RaoQ
Hard substrates in the English Channel	68	0.68	0.53
Offshore wind farms	56	0.54	0.50
Oil and gas platforms	28	0.07	0.42

320

321 In the MFA, the first two axes of the correlation circle explained 27.7% (14.8% and 12.9%,
 322 respectively) of the variability in the data set (Fig. 6). Eight categories had a high
 323 contribution: organisms with pelagic larval development, direct development, a
 324 planktotrophic larval diet, and sessile and crawling adult organisms with a life span less than
 325 2 years or 5–20 years.

341



342

343 **Figure 7.** Functional polygons of the three habitats, top left is the overlap of hard
344 substrates in the English Channel (red), oil and gas platforms (green), and offshore wind
345 farms (blue), species are represented by points. Dimensions 1 and 2 explained 14.8%
346 and 12.9% of the variance, respectively.

347 Overlap analyses revealed that HSEC functional polygon is covered by 35.1% and
348 91.6% of the O&GP and OWF functional polygons respectively. O&GP functional
349 polygon is covered by 96.9% and 94.5% of HSEC and OWF functional polygons
350 respectively. Finally, OWF functional polygon is covered by 85.3% of HSEC and 27.1%
351 of O&GP functional polygons respectively (Supplementary materials L).

352 4. Discussion

353 Installation of OWFs is known to influence marine ecosystems, such as by for instance
354 causing the reef effect (Wilhelmsson and Malm, 2008) or stepping-stone effect (De Mesel et

355 al., 2015), or by rendering habitats more complex (i.e. transition from soft substrates to hard
356 substrates) (Degraer et al., 2020). As an example to anticipating the impact of colonisation by
357 benthic organisms on artificial man-made structures, we applied our method to the English
358 Channel marine ecosystem, in relation to the French energy transition objectives, that plans to
359 install seven OWFs within the EC in the next decade. This requires predicting the influence of
360 OWFs on marine ecosystems, particularly on benthic communities in the EC. The present
361 study focused specifically on the reef effect of benthic species and showed that community
362 structure was more similar between the two human-made structures (OWFs and O&GP),
363 whereas functional diversity was more similar between the communities of OWF and HSEC.
364 Beyond the French case, our results could be of interest for the whole English Channel.

365

366 4.1 Comparison of communities in the three habitats

367 The list of colonisers highlighted similarities and differences in community structure among
368 the three habitats: the species composition of HSEC differed from those of OWF and O&GP,
369 which were more similar to each other. However, the community structure analysis was based
370 only on the presence/absence of species in each habitat, and thus provided a qualitative
371 overview of the composition of assemblages. Natural and artificial substrates have been
372 compared (Coolen et al., 2020; Pinto et al., 2021) to identify parameters that can explain
373 differences in their communities. Several hypotheses were explored, such as the substrate's
374 type (e.g. rock vs. steel), complexity (e.g. surface area, rocks, crevices (Atilla et al., 2005;
375 Coolen et al., 2015)). Zupan et al. (2023) showed that the age and type of substrate had
376 significant effects on species composition. The type of substrate (concrete, steel and
377 complexity) is a well-known factor in the marine environment according to multiple
378 colonisation experiments with different types of substrates that influenced the assemblage of
379 colonisers (Taniguchi and Tokeshi, 2004; Burt et al., 2009; Gaudron et al., 2010; Osman,

380 2015). The type of substrate could explain the differences in species composition of HSEC vs.
381 those of OWF and O&GP as HSEC samples are often located on seabed, while OWF and
382 O&GP samples are usually taken at mid-water depth. A recent study showed the impact of
383 depth on marine species richness and diversity in benthic colonisers (Coolen et al., 2022).

384 Another hypothesis is that biofilm that develops on hard substrates can influence the
385 substrates that larvae choose during colonisation (Hadfield, 2010). It can also influence
386 metamorphosis during the transition from larval to post-larval stages (Shitema, 2012). Thus, it
387 would be interesting to study the biofilm composition of hard substrates to identify whether it
388 can explain community differences. Tan et al. (2015) compared biofilm composition on
389 natural (i.e. rocky shores) and artificial (i.e. seawall) substrates, and observed no difference in
390 biofilm composition, but did observe a difference in the relative abundance of biofilm
391 organisms. Other environmental factors could explain the differences in species composition
392 of HSEC vs. those of OWF and O&GP. For example, depth is known to influence species
393 richness on hard substrates, with maximum richness from 15 or 25 m to 75 m in depth (Clarke
394 and Lidgard., 2000; Van der Stap et al., 2016; Coolen et al., 2020). Distance to shore can also
395 impact species diversity (Van der Stap et al., 2016; Reeves et al., 2018). However, the spatial
396 aspect should be considered, as OWF and O&GP were not present in the EC during our study.
397 Although species assemblages of OWF and O&GP (mainly in the North Sea) differed from
398 that of HSEC, 84 taxa were common to all three habitats. These species are likely to colonise
399 the future Dunkirk OWF and, more broadly, all OWFs installed in the EC in the near future.
400 Interestingly, 73 taxa were common to HSEC and OWF, which increases the number of
401 potential colonisers of the Dunkirk OWF to 157. From a broader perspective, this means that
402 a fraction of benthic organisms already present in the area where the offshore parks are
403 located will potentially colonise them. The use of the functional profile of colonisers could
404 then allow identifying this fraction of colonisers thanks to their functional traits. But this

405 [method](#) is likely to overestimate the colonisers potential, because the number of taxa observed
406 in the literature was always less than 157 (e.g. 78 species by Kerckhof et al. (2012), 63 by
407 Kerckhof et al. (2010), 121 by Karlsson et al. (2021), 85 by Vanagt et al. (2013), 70 by
408 Leonhard and Pedersen (2004), and 55 by Bouma and Lengkeek (2013)). [In this study, the](#)
409 [case of the future OWF of Dunkirk is particularly interesting because it is located in the](#)
410 [transition zone between the eastern French EC, where no OWF currently exists \(but seven are](#)
411 [planned\), and the southern North Sea where numerous OWF are already implemented. The](#)
412 [methodology and the results obtained for the French case study could be of interest to any](#)
413 [other future OWF.](#)

414

415 4.2 Biological traits of species on hard substrates

416 Over the past decade, the functional trait-based approach has been widely adopted and seen as
417 a complementary to species-based approaches (Degen and Faulwetter, 2019). Biological trait
418 analysis of colonisers of the three habitats highlighted that gonochoric reproduction, pelagic
419 larval dispersal, and sessile juveniles/adults were the categories represented most in each of
420 the three habitats. However, dominant traits differed among the habitats, including maximum
421 body size, larval diet, life span, and adult feeding. Colonisers were smallest for OWF (i.e.
422 maximum body size of 50-100 mm), mostly intermediate for HSEC (i.e. 10–50 or 100–300
423 mm), and largest for O&GP (i.e. 100–300 or 10–50 mm). A similar trend was observed for
424 life span, which was shortest for OWF colonisers (i.e. < 2 or 5–20 years), intermediate for
425 HSEC (i.e. 2–5 or 5–20 years), and longest for O&GP colonisers (i.e. 5–20 or > 20 years).
426 According to the literature, the maximum body size and life span of colonisers provide
427 information on the stage of the community (Bolam and Eggleton, 2014; Bremner, 2008; Cain
428 et al., 2014; Costello et al., 2015; Emmerson, 2012; Micheli and Halpern, 2005; Norkko et al.,
429 2013; van der Linden et al., 2016). As OWF colonisers were smaller and had a shorter life

430 span, the OWF community could be considered fast growing, highly productive, and less
431 sensitive to disturbance, which indicates a younger community. Due to their larger body size
432 and longer life span, O&GP colonisers could be considered slow growing, less productive,
433 and more sensitive to disturbance. Biological traits of the HSEC community could be
434 intermediate because the substrates are of different types (i.e. intertidal rocky shore, pebbles,
435 shipwrecks, concrete) and ages (i.e. 4 to ca. 80 years). [The first theory about](#) benthic
436 community succession on offshore marine structures was that it follows the same rules as that
437 in other ecosystems, with pioneer, intermediate, and climax stages (Kerckhof et al., 2010).
438 Degraer et al. (2020) identified these three stages of succession on wind turbines on the
439 Belgian coast [in the North Sea](#), with the pioneer stage from 0–2 years, the intermediate stage
440 from 3–5 years, and the climax stage from 6 years after installation. [But a recent study \(Zupan](#)
441 [et al., 2023\) showed that after 11 years communities are still changing and two other theories](#)
442 [are put forward, first several stable or climax communities theory \(Sutherland, 1974\) and the](#)
443 [repeated successional pathway of the cycle climax theory \(Oshurkov, 1992\).](#) Therefore, the
444 age of the community should be considered when using a functional trait profile. Pioneer
445 species are generally small due to harsh abiotic conditions and relatively low nutrient
446 availability (MacArthur and Wilson, 1967; Thornton, 2007; Dykman et al., 2021), whereas
447 species at the climax stage are relatively larger, with slower growth, and influence the
448 establishment of other species (Hirata, 1986; Tilman, 1988, Teixido et al., 2004). Therefore,
449 according to their functional profiles, OWF assemblages in the present study were in the
450 transition between pioneer and intermediate stages of succession, whereas O&GP
451 assemblages were at the climax stage. These observations for a mean age of the OWFs (3
452 years) and O&GP (21 years) during sampling agree with the succession observed by Degraer
453 et al. (2020). Our results suggest that O&GP can be used as long-term predictions of

454 communities of OWF colonisers at the climax stage, [information during the younger stages](#)
455 [are needed to fully support this statement.](#)

456 Our results also revealed relevant information on feeding habits. In the study of
457 Degraer et al. (2020), offshore hard substrates were generally dominated by suspension
458 feeders, but our study showed that carnivores dominated in OWF and O&GP. This could be
459 due to having used a qualitative approach instead of a quantitative approach based on biomass
460 or abundance, which were not available for this study. The main functional traits of species in
461 a targeted habitat could be used to predict colonisation of human structures. More concretely,
462 the functional profile of OWF colonisers defined in the present study could be used to identify
463 which potential colonisers already living in the EC could colonise the seven future OWFs
464 based on their functional traits.

465

466 4.3 Functional diversity and structure

467 The functional diversity indices showed greater functional similarity between the assemblages
468 of OWF and HSEC, which differed from those of O&GP. HSEC had the highest functional
469 diversity indices, but those of OWF were higher than those of O&GP, which had the smallest
470 functional volume (perhaps mainly due to the absence of species with direct larval
471 development [within the main species list](#)) and thus seemed to be an unstable habitat (Tilman,
472 2001). For HSEC and OWF, arthropods and molluscs were the main species with direct larval
473 development. Although not on the list of main species used for functional trait analysis,
474 arthropods with direct larval development were present in O&GP (e.g. in Amphipoda,
475 Decapoda, and Isopoda [Orders](#)), but they were not identified to the species level.

476 Taxonomic resolution can influence the results of functional analysis of a community.
477 According to Poff et al. (2006), family-level resolution can result in loss of information,
478 particularly for families with genera that have multiple trait characteristics. Thus, genus-level

479 resolution could detect biological or ecological responses more accurately. While the species
480 level is the highest resolution and can detect the smallest biological or ecological responses, it
481 is also sensitive to redundancy due to congeneric species that are functionally equivalent and
482 thus considered ecologically equivalent (Wiggins and Mackay, 1978). This most accurate
483 level was able to detect subtler biological and ecological responses than using family or
484 genus, which are less accurate (Poff et al., 2006). However, identifying taxa to the species
485 level can also be negative because it may result in excluding many individuals that cannot be
486 identified, as in our study, which may have biased comparison of the ecological functioning
487 of the three habitats. Repeating the biological trait analyses in this study after removing
488 species with a direct development trait showed the same trends as the original biological trait
489 analyses (i.e. smaller functional indices and volumes for O&GP than for the two other
490 habitats) (Supplementary Material K).

491 Overall, HSEC seems to be the most stable and resilient of the three habitats studied.
492 At the mean age of OWF (i.e. 3 years) our study indicates a high functional diversity
493 supported by the functional indexes values and high overlap values of the functional
494 polygons. OWF had a functional diversity similar to those of the communities already present
495 in HSEC. As Coolen et al. (2022) and Zupan et al. (2023) demonstrated that the greatest
496 specific richness and diversity were reached around 6 years, the maximum functional
497 similarity between OWF and HSEC could be reached at this period. Conversely, using O&GP
498 as a long-term reference indicates that community functional diversity may decrease on
499 OWFs during years. This agrees with Kerckhof et al. (2019), who observed that mussels and
500 anemones dominated long-term communities colonising wind turbines. Because Zupan et al.
501 (2023) recently challenged the idea that OWFs will tend to a stable climax stage as their
502 longest monitoring program, the current state of knowledge requires further studies on long-
503 term colonisation of artificial substrates.

504

505

506 **5. Conclusion**

507 Installing an OWF creates a new habitat that benthic organisms can colonise. Focusing on
508 functional traits helped to identify species responses to environmental disturbances and their
509 effects on ecosystems (Carmona et al., 2016), which is relevant for studying the influence of
510 OWFs on ecosystems. Our case study indicated how this new artificial substrate could
511 influence benthic communities and their functioning. As functional traits can be used across
512 species and geographic ranges (Bernhardt-Römermann et al., 2011), we compared different
513 communities that form many habitats (i.e. OWF, O&GP, and HSEC) in different areas (i.e.
514 EC, North Sea, and Irish Sea). Based on functional trait profiles, we identified 157 taxa that
515 could colonise future OWFs built in the EC. Qualitative analysis of OWFs in the North Sea
516 showed that their functional diversity is relatively similar to that of hard substrates already
517 present in the EC during the intermediate successional stage of the community. It would be
518 interesting to replicate this approach using abundance and biomass data and to apply it to all
519 of the species sampled to quantify the functional diversity of OWFs.

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526

527

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533

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