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## Linking life-history traits, spatial distribution and abundance of two species of lugworms to bait collection: A case study for sustainable management plan

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### Abstract :

*Arenicola* spp. are marine benthic polychaetes dug for bait by anglers. Without regulation, this activity can lead to the decrease of lugworms' population meanwhile affecting the physical characteristics of the beach and the biodiversity. Here, we identified through morphology and genetics two species of lugworms, *Arenicola marina* and *A. defodiens*, within a Marine Protected Area of the Eastern English Channel (France). For each species, abundance and spatial distribution were assessed using a stratified random sampling and interpolation at four studied sites, as well as some life-history traits. These data were compared to lugworms' collection data to estimate its sustainability and to provide potential management measures. At one site, *A. marina* was present in large numbers on the higher and middle shore, whereas *A. defodiens* occupied the lower shore. At the other sites, both species co-occurred on the lower shore, and *A. marina* individuals were less numerous and lacking recruits. Spawning periods for *A. marina* occurred in early autumn and in late autumn for *A. defodiens*. The size at first maturity of *A. marina* was at 3.8 cm of trunk length (between 1.5 and 2.5 years old). One site (Au) appeared in need for management when linking abundance data with bait collection, where harvest of both species represented ~14% of the total amount of lugworms and was above the carrying capacity of the beach for *A. marina*. The retail value associated to lugworm harvesting within the MPA was estimated at the same level as the shrimp retail value. Our results highlight the need for some fishery regulations.

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## Highlights

- ▶ At Wimereux *Arenicola defodiens* and *A. marina* live separately (typical spatial distribution pattern).
- ▶ At Le Touquet and Fort Mahon *Arenicola defodiens* and *A. marina* live in sympatry. ▶ The size at first maturity of *Arenicola marina* is 3.8 cm of trunk length (between 1.5 and 2.5 years old).
- ▶ At Ault, the harvest of *Arenicola marina* was above the carrying capacity of the beach. ▶ The retail value associated to lugworm harvesting within the MPA was 232 447 €.

**Keywords** : *Arenicola marina*, *Arenicola defodiens*, Spawning, Population structure, Size at first maturity, Recreational fisheries, Conservation, English channel

## 66 **Introduction**

67 *Arenicola* spp. (Annelida Polychaeta), are marine benthic coastal ecosystem engineers living  
68 in burrows on intertidal and subtidal soft-sediment beaches and estuaries from the Arctic to  
69 the Mediterranean (Volkenborn, 2005). Two cryptic species of the genus *Arenicola* were  
70 recorded in the North Sea and the English Channel: *A. marina* (Linnaeus, 1758) and *A.*  
71 *defodiens* (Cadman and Nelson-Smith, 1993). They were formerly described as two varieties  
72 of the same species, *A. marina* being the “littoral” variety, and *A. defodiens* the “laminarian”  
73 variety (Luttikhuisen and Dekker, 2010). Indeed, *A. marina* rather occupies the higher shore  
74 to mid-shore in a U-shape gallery, between 10 to 40 cm below the sediment surface, while *A.*  
75 *defodiens* is present on the lower shore to subtidal area in a deeper (up to 1-meter deep) and J-  
76 shape gallery (Cadman and Nelson-Smith, 1993; Cadman, 1997). Only small morphological  
77 differences exist between the two species, the most notable being the annulations patterns of  
78 the first setigers and the shape of the gills (Cadman and Nelson-Smith, 1993). Thus, their  
79 species discrimination was proven by genetics (Cadman and Nelson-Smith, 1990) and re-  
80 confirmed recently using COI and 16S gene markers (Luttikhuisen and Dekker, 2010; Pires et  
81 al., 2015). Both species are dioecious and iteroparous (Watson et al., 1998) and their benthopelagic  
82 lifecycle (Farke and Berghuis, 1979a; Reise, 1985), has only been described for *A.*  
83 *marina*. For this species, after the spawning event in early autumn, and before the recruitment  
84 in spring, young stages experience two successive dispersal phases, with a temporary  
85 settlement in between, where at a ‘post-larval’ stage the worm lives in a mucus tube attached  
86 to various substrates (sheltered soft-sediment, macroalgae or mussel beds) (Farke and  
87 Berghuis, 1979a,b; Reise, 1985; Reise et al., 2001).

88 *Arenicola* spp. play a key role in bioturbation of soft sediments (Kristensen, 2001) and in  
89 local trophic networks (Reise, 1985; Clarke et al., 2017). Moreover, despite lugworms are not  
90 considered yet as a fisheries species (as not directly consumed), they represent a high  
91 commercial marine value showing an important biomass extraction according to Watson et al.  
92 (2017a), who estimated a global landing for polychaete bait (including lugworms) up to  
93 120 000 tonnes, representing £5.9 billion in 2016. Lugworm collection by professional or  
94 recreational fishermen may impact the size and age structure of a population, such as its  
95 abundance and distribution (Blake, 1979; McLusky et al., 1983; Olive, 1993) with possible  
96 population crashes caused by overexploitation (Olive, 1993). In addition, bait diggers can  
97 affect the physical characteristics of the beach perturbing the other associated fauna  
98 (invertebrates, wading birds, etc.) (Beukema, 1995; Clarke et al., 2017; Watson et al., 2017b).

99 In consequence, several authors call for a management (Watson et al., 2017a), and  
100 particularly, a sustainable management of these species (Clarke et al., 2017).

101 Fisheries management can be defined as "the integrated process of information gathering,  
102 analysis, planning, consultation, decision-making, allocation of resources and formulation and  
103 implementation, with enforcement as necessary, of regulations or rules which govern fisheries  
104 activities in order to ensure the continued productivity of the resources and the  
105 accomplishment of other fisheries objectives" (FAO, 2002a). In other words, this consists in  
106 maintaining its population at healthy levels, which is, in terms of population's dynamics, a  
107 population with sustainable birth, growth and survival rates (Beverton and Holt, 1957). The  
108 management can be implemented through education, or through enforced harvest regulations  
109 (Watson et al., 2015). The latter are in general applied either on the fishermen themselves,  
110 implementing licenses or fees, gear or fishing methods restrictions, closing times, season or  
111 area restrictions, either on the resource, limiting the length or quantity (bags) of the collected  
112 species mainly (FAO, 2012). Both controls are used to limit the overall mortality, or the  
113 mortality of specific individuals in the population, based on its features (FAO, 2012).

114 Several kinds of regulations for bait collection have already been enforced around the world,  
115 either for recreational or professional fishermen: licensing has been implemented in the  
116 United States and the United Kingdom (Watson et al., 2015), quotas have been implemented  
117 in Portugal (Xenarios et al., 2018) and some areas have been closed in the UK (Olive, 1993;  
118 Rogers, 1997). For *Arenicola* spp. the last two options have already been implemented in  
119 some European places: a limitation to 100 individuals in a defined area in the North of France  
120 (Direction interrégionale de la mer Manche Est-mer du Nord, 2015) or the closure of areas  
121 where the lugworm population crashed in the UK (Olive, 1993; Rogers, 1997). Although  
122 protecting lugworms, the main purpose of these management methods is sometimes rather to  
123 protect the habitat features or the wading birds disturbed by fishermen (Watson et al., 2017b).

124 Besides, these management measures are merely restrictions, often taken without any  
125 considerations of the life history traits of the local populations (Watson et al., 2017a). Studies  
126 linking bait collection data to abundance, spatial distribution and life history traits of lugworm  
127 are scarce. Xenarios et al. (2018) assessed the sustainable levels of some polychaetes species  
128 (*Diopatra neapolitana*), only taking into account the harvest effort, and Blake (1979)  
129 combined the harvest effort to population data (e.g. density and size structure). Nevertheless,  
130 the only study of this kind dealing with lugworms (Blake, 1979) was performed before the

131 knowledge of the co-occurrence of two potential species of the genus *Arenicola* inhabiting the  
132 intertidal area (Cadman, 1997).

133 In this study, we have assessed the abundance and the spatial distribution of several local  
134 populations of *Arenicola* spp. within a newly created MPA from temperate coastal areas  
135 located in the Eastern English Channel, as well as some life-history traits such as spawning  
136 period, size at first maturity, population structure and recruitment period. Additional data on  
137 lugworms' collection by recreational bait diggers within the MPA was included in order to  
138 estimate the potential sustainability of the different lugworms' population and to provide  
139 relevant potential management measures when needed.

## 140 **1. Material and Methods**

### 141 1.1. Study Area

142 The study area is located in the Eastern English Channel and is part of a marine protected area  
143 (MPA): the Parc naturel marin des estuaires picards et de la mer d'Opale created in 2012 (Fig.  
144 1). The coastline is mainly composed of hydrodynamically exposed sandy beaches of fine to  
145 medium sands (0.05 to 0.5 mm grain size), as well as some rocky shores, and includes three  
146 major estuaries of muddy sands (2 to 3 % silt): the Somme, the Authie and the Canche  
147 estuaries (Rolet et al., 2014, 2015). The tidal regime is semi-diurnal and macrotidal and,  
148 amplitude may exceed 8 m, with the largest amplitudes occurring around 2 days before the  
149 full moon (Migné et al., 2004; Rolet et al., 2015). Sampling sites (Fig. 1) were chosen at four  
150 locations along the shore of the MPA, where recreational fishermen had often been observed  
151 digging worms, in order to assess the need for management of this activity: 1) Wimereux  
152 (Wx) (50°46'14" N and 1°36'38" E), 2) Le Touquet (LT) (50°31'07" N and 1°35'42" E), 3)  
153 Fort Mahon (FM) (50°20'31" N and 1°34'11" E) and, 4) Ault (Au) (50°06'07" N and 1°26'58"  
154 E). LT and FM are composed of large exposed sandy beaches, when Wx and Au are a mixture  
155 of sandy beaches and rocky shores mainly colonized by algae and mussels on the intertidal  
156 and subtidal areas.

### 157 1.2. Spatial distribution and abundance of *Arenicola* spp.

#### 158 1.2.1. Sampling strategy

159 Spatial distributions of lugworms were investigated on the sandy shore in April-Mai 2016 at  
160 the four sites (Wx, LT, FM and Au) during spring tide periods. Formerly, lugworms  
161 distributions were assessed by samplings on uniformly distributed points along transects  
162 (Beukema and De Vlas, 1979; Beukema, 1995). However, on the studied sites, distributions

163 of lugworms were highly aggregative (with spots of faecal casts and spaces without faecal  
164 casts next to them). Therefore, a stratified random sampling approach was chosen (Fagan and  
165 Nelson, 2017), in order to improve the performance of the spatial interpolation methods (Li  
166 and Heap, 2008). At each site, the area was subdivided into a grid of equally-sized rectangle  
167 boxes: a grid of 100 m x 50 m divided into 18 boxes at Wx and at Au, and, a grid of 100 m x  
168 70 m divided into 24 boxes at LT and at FM (Fig. 1). In each box, a random sampling point  
169 was computed (Fig.1), where the abundance of lugworms (both species combined) was  
170 assessed by counting the number of faecal casts in three quadrates placed randomly, of 0.0625  
171 m<sup>2</sup> (when densities were higher than 10 faecal casts), or of 1 m<sup>2</sup> (when densities were lower  
172 than 10 faecal casts). Every 3 to 5 sampling points, lugworms were dug using either an Alvey  
173 bait pump (Decathlon ltd, extracting the worm by suction), a fork or a shovel, and the  
174 proportion of each species was calculated at the different bathymetries to correct the number  
175 of individuals belonging to each species.

#### 176 1.2.2. *Species identification*

177 Species identification was determined morphologically by the observation of the annulations  
178 pattern on the second chaetigerous segment (two annulations for *Arenicola defodiens* and  
179 three for *A. marina*) (Cadman and Nelson-Smith, 1993). Subsamples of tissue of each worm  
180 were kept in a solution of absolute ethanol at -20°C. The DNA of 3 random individuals of *A.*  
181 *marina* and 3 random individuals of *A. defodiens* was then extracted using the  
182 NucleoSpin®Soil kit according to manufacturer's instruction (Macherey-Nagel), amplified  
183 and sequenced by Genoscreen ltd (Institute Pasteur de Lille, France) in order to confirm the  
184 presence of the two different species within the MPA. Fragments of the mitochondrial  
185 cytochrome oxidase I-encoding gene (COI mt DNA) (~ 670 pb) were amplified using the  
186 universal primers: LCO 1490 (5'-GGTCAACAAATCATA AAG ATA TTG G-3') and HCO  
187 2198 (5'-TAAACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al.,1999).  
188 Polymerase Chain Reaction (PCR) was performed according to Pires et al. (2015): an initial  
189 denaturing step of 3 min at 94°C, followed by 34 cycles at 94°C for 1 min, 45°C for 30s for  
190 hybridization, then 2 min at 72°C, and a final extension for 5 min at 72°C. COI sequences  
191 were manually checked using bioedit Ver. 7.0.0. (Hall, 1999). Each COI sequence was then  
192 deposited in GenBank (Supplementary Material: Table A) and aligned with other COI  
193 sequences of *A. marina* and *A. defodiens* (retrieved from GenBank), as described by Pires et  
194 al. (2015). This multiple alignment of COI sequences was exported to the software MEGA v7

195 (Kumar et al., 2016) using ClustalW, in order to construct a molecular phylogenetic tree  
196 analysis based on the maximum likelihood method (Supplementary Material: Fig. B).

### 197 1.2.3 Data analyses

198 To assess the spatial distribution and abundance of *Arenicola spp.*, first, the total number of  
199 lugworms at each point was estimated by the number of faecal casts (Farke et al., 1979),  
200 assuming that one worm produced 0.84 cast.tide<sup>-1</sup> in *A. marina* (Supplementary Material: Fig.  
201 C). We assumed that both species produce approximately the same amount of casts per tide.  
202 The relative proportions of *A. marina* and *A. defodiens* were recorded for each collection  
203 point taking into account the bathymetry (height above chart datum). Since only few  
204 individuals could be collected in spring 2016, the data from autumn and winter 2015 was also  
205 used (Table 1). Bathymetries were obtained from the interregional project “CLAREC, INSU –  
206 CNRS M2C-UNICAEN” (<http://www.unicaen.fr/dataclarec/home/elevations.html>). When no  
207 bathymetry record was available (FM), we used the distance from the shoreline as a proxy.  
208 The shoreline HISTOLITT® was taken from the SHOM, the hydrographic and oceanographic  
209 service of the French navy (<http://diffusion.shom.fr/loisirs/trait-de-cote-histolittr.html>). The  
210 existence of a correlation between the proportions of the two species and the bathymetry or  
211 the shoreline distance was investigated (Spearman correlation test) at each site separately.  
212 When a correlation between the proportion of *A. marina* and *A. defodiens* and bathymetry  
213 could be established (Wx), a fitting model was adjusted on Matlab R2015b using the Curve  
214 Fitting Toolbox and a sigmoid model inspired by Cadman (1997) (Supplementary Material:  
215 Fig. D). The number of individuals of each species was then calculated following the fitted  
216 model at each collection point’s bathymetry. When no particular correlation was noticed (LT,  
217 FM) (Supplementary Material: Fig. E), the number of individuals of each species was  
218 calculated from the overall proportion of the individuals of both species from autumn 2015 to  
219 spring 2016. Eventually, when the number of individuals of *A. marina* and *A. defodiens* was  
220 assessed in every point of the grid, it was then interpolated on QGIS 2.18.0 (QGIS  
221 development team, 2016) using the inverse distance weight (IDW) method. Interpolations  
222 were superimposed to EUNIS habitat communities maps obtained from Rolet et al. (2014)  
223 and from additional samplings performed according to Rolet et al. (2014) at FM and Au in  
224 Spring 2016, which is based on species identification of the macrofauna and on the particle  
225 size analysis (Supplementary Material: Table F). The number of individuals of each species  
226 was obtained on the whole grid from the interpolation and then reduced to 1 m<sup>2</sup> to get the

227 mean density. The significance of the difference of densities between sites was then estimated  
228 with a chi-squared test for each species separately, performed on R (R Core Team, 2017).

### 229 1.3. Life-history traits of the lugworm populations

#### 230 1.3.1. *Sampling strategy*

231 Spawning dates of both species were investigated for two successive breeding seasons, from  
232 September 2015 to January 2016 and from September 2016 to January 2017, at the four  
233 studied sites. Individuals were dug with a bait pump monthly on the lower shore or with a  
234 fork on the mid-shore, at low tide (Table 1). The population structure of *Arenicola marina*  
235 was investigated only at Wx (Fig. 1) within the intertidal area at three locations from the  
236 low/middle shore to the higher shore (0 m of bathymetry: 50°46'0.1" N and 1°36'20.3" E, 0.9  
237 m of bathymetry (above 0 m): 50°46'1.7" N and 1°36'14.4" E and, 2.3 m of bathymetry  
238 (above 0 m): 50°46'2.5" N and 1°36'10.6" E) in July 2017. During low tide, 30 individuals  
239 from each location were collected by digging the sediment (between 5 and 30 cm beneath the  
240 surface), either with a pump, or a fork or by sieving (0.5 mm mesh) the sediment on the  
241 higher shore for the smaller individuals. This sampling strategy was repeated in September  
242 2017 to assess the size at first maturity of *A. marina* at Wx.

#### 243 1.3.2. *Laboratory measurements*

244 After each sampling, all worms were put in separated containers filled with seawater. Worms  
245 were maintained in the laboratory during 24 h to 48 h at 15°C in a cold room to allow gut  
246 contents to devoid prior to observations (Watson et al., 2000). After identification, worms  
247 were anesthetized in three successive solutions of twice-filtered sea water (TFSW, 0.45 µm  
248 and 0.2 µm) at 1%, 2.5% and 5% of ethanol (Gaudron and Bentley, 2002). Each individual  
249 was measured (total length and trunk length) and weighted (wet weight). To assess their  
250 reproductive status, biopsies of the coelomic fluid were performed on individuals of *Arenicola*  
251 *marina* and *A. defodiens* (Table 1) with a sterile hypodermic syringe. The gametes were then  
252 rinsed twice in TFSW and kept in ethanol (96%) at 4°C. Fifty random oocytes of each female  
253 were measured under the microscope assisted by the software Motic Image Plus 2.0.

254 Reproductive structures of males (rosettes, morulae and spermatozoids) were analyzed using  
255 the same method. To assess the size at first maturity, the occurrence of gametes was searched  
256 in coelomic fluids of 106 individuals of *A. marina*.

#### 257 1.3.3. *Data Analysis*

258 *Spawning dates*

259 Spawning periods of both species were inferred by using both the oocyte diameter frequency  
260 distributions (Watson et al., 1998) and the presence of male gamete structures such as  
261 spermatozooids or morulae, only present in mature individuals (Dillon and Howie, 1997).  
262 Furthermore, observation of spontaneous spawning events in the laboratory was considered as  
263 additional evidence that lugworms were at a maturity stage and ready to release gametes. The  
264 estimated spawning periods were then compared with environmental local data such as tidal  
265 coefficients and water temperature (data provided by “Service d’Observation en Milieu  
266 Littoral, INSU-CNRS, Wimereux”, bottom coastal point: [http://somlit.epoc.u-  
267 bordeaux1.fr/fr/](http://somlit.epoc.u-bordeaux1.fr/fr/)).

268 *Population and age structures of Arenicola marina*

269 In *Arenicola* spp., no permanent structures with year marks have been found (Beukema and  
270 De Vlas, 1979) and the population structure can only be approached through the analysis of  
271 the different size of cohorts, since spawning and recruitment only happen once a year and  
272 each cohort belongs therefore to a separate year. Only the population and age structures of *A.*  
273 *marina* at Wx were assessed through the analysis of size frequencies on the trunk length (TL)  
274 frequency distributions of 5-mm size class intervals, using a Bhattacharya analysis (N = 194)  
275 performed on the specific routine in FISAT II package (FAO, 2002b) according to Romano et  
276 al. (2013). To assess the goodness of the modal separation, separation indices (SI) were  
277 computed with values of  $SI > 2$  being considered as successfully separated. Mean TLs,  
278 standard deviations and separation indices were calculated for each of the identified cohorts.  
279 Significant differences in TL of *A. marina* were assessed using a one-way analysis of variance  
280 (ANOVA) and a post-hoc Tukey test on R (R Core Team, 2017) (RStudio Team, 2016).  
281 Normality of residuals was assessed by the Shapiro test ( $p > 0.05$ ), and homoscedasticity was  
282 tested by the Bartlett test ( $p > 0.05$ ) on R (R Core Team, 2017).

283 *First size and age at maturity of Arenicola marina*

284 The first size at maturity is the size at which more than 50% of the individuals are ‘mature’  
285 (i.e. able to produce gametes, thus adult stage). Since reproductive organs are difficult to  
286 observe in *Arenicola* spp. (Cassier et al., 1997), the presence/absence of gametes in the  
287 coelomic fluid was checked at the end of the gametogenesis period (September). These  
288 observations allowed to estimate the number of individuals containing gametes (adults), and  
289 that without gametes (juveniles). The cumulated frequency of the proportion of ‘mature’  
290 individuals per trunk length (TL) class was then calculated and the size at first maturity was

291 considered the size at which the cumulated frequency equaled to 0.5 (or 50 %). The  
292 differences in TL between adult males and females of *A. marina* at Wx, and between adults  
293 and juveniles (at the same site) were assessed using a non-parametric Kruskal-Wallis (K-W)  
294 test as distributions were not normal (Shapiro test,  $p < 0.05$ , performed on R (R Core Team,  
295 2017)).

#### 296 1.4. Survey of bait collection within the MPA

297 On the whole MPA's foreshore, the number of recreational fishermen digging lugworms was  
298 assessed through on-site monitoring between one hour before and after the low tide at least  
299 once a month. Given the high variability of the number of fishermen, four sites were chosen  
300 (Wx, LT, FM and Au) that represented the different intensities of digging effort met within  
301 the MPA. The number of worms collected per fisherman was assessed as in Xenarios et al.  
302 (2018), through field surveys, between 2014 and 2016. Given the high variability of the  
303 presence of diggers along the year (Xenarios et al., 2018), categories (in terms of numbers of  
304 fishermen) were established according to the weather conditions (temperature, pluviometry,  
305 photoperiod, maximum wind strength and atmospheric pressure), the tidal conditions (tidal  
306 coefficient, tidal range and low tide time), and the availability of fishermen (French and  
307 Belgium holidays, working days, week-ends, period of the year, morning or afternoon). The  
308 mean number of diggers per category and per site and the associated standard deviation were  
309 calculated, as well as the number of occurrences of each category in one year, which gave the  
310 number of diggers per site for this category in one year, as well as for the whole MPA. The  
311 total number of diggers for each site and for the whole MPA was then calculated summing the  
312 results of each category. The lugworms' extraction levels were calculated multiplying the  
313 total number of fishing sessions per site by the mean number of worms dug out by one  
314 fisherman in one fishing session. Finally, the retail value for the whole MPA and for each of  
315 the four studied sites was assessed from the numbers of dug lugworms and from the local  
316 retail prices taken from websites and from local retailers as in Watson et al. (2017a).

#### 317 1.5. Linking abundance and spatial distribution to extraction levels of lugworms

318 At the four studied sites, the mean number of lugworms available for bait diggers was  
319 assessed from the mean densities of lugworms established in this study, the surface of the  
320 foreshore and the percentage of lugworms weighing more than 3 g (weight considered by  
321 Olive (1993) as the limit at which worms get valuable). Then, these data were compared to  
322 the estimated number of dug lugworms assessed by the survey.

## 323 2. Results

### 324 2.1. Species identification, spatial distribution and abundance

325 The 6 random individuals chosen for a molecular analysis based on the COI genes confirmed  
326 the morphological identification (barcoding) (Supplementary Material: Fig. B, Table A). A  
327 14-15 % of nucleotide divergence was found between the COI genes of *Arenicola marina* and  
328 *A. defodiens*. At Wx, a significant correlation was found between the proportion of each  
329 species and bathymetry (Spearman,  $\rho = 0.9$ ,  $p < 0.001$ ) and a relation could be established  
330 (Supplementary Material: Fig. D). It appeared that *A. marina* was present above -1 m of  
331 bathymetry and *A. defodiens* below -2 m of bathymetry, with a small transition in between,  
332 where the two species could live in sympatry. On the other studied sites, no correlation was  
333 found between the proportion of each species and bathymetry or distance from the shoreline  
334 (LT: Spearman,  $\rho = -0.09$ ,  $p > 0.1$ ; FM: Spearman,  $\rho = 0.25$ ,  $p > 0.1$ ) (Supplementary  
335 Material: Fig. E). At Wx, *A. defodiens* was found on the lower shore, on the A2.23 EUNIS  
336 habitat and *A. marina* was mainly present on the higher shore, on the A2.223 EUNIS habitat  
337 (Fig. 2; Supplementary Material: Table F). At LT and FM, both species appeared to live in  
338 sympatry. Lugworms at LT were present on the A2.23 EUNIS habitat and at FM, lugworms  
339 were found on the A5.231 EUNIS habitat (Fig. 2; Supplementary Material: Table F). At Au,  
340 *A. defodiens* was found on the lower shore, on the A2.23 EUNIS habitat (Fig. 2;  
341 Supplementary Material: Table F), but no conclusions were made regarding the distribution of  
342 *A. marina* on this site since only a single individual was collected. The mean densities of *A.*  
343 *defodiens* did not appear to vary significantly between sites (between  $0.25 \pm 0.05$  and  $0.70 \pm$   
344  $0.05$  individuals.  $m^{-2}$  at all sites) ( $CHI^2$ ,  $p = 0.96$ ) in comparison with *A. marina* ( $6.5 \pm 0.8$   
345 individuals.  $m^{-2}$  at Wx, around 0.2 individuals.  $m^{-2}$  at LT and FM), where it varied  
346 significantly ( $CHI^2$ ;  $p < 0.01$ ) (Fig. 2).

### 347 2.2. Life history traits of lugworms

#### 348 2.2.1. Spawning dates

349 For both species, the frequency distribution of the oocytes diameters evolved from a bimodal  
350 distribution for females carrying oocytes in oogenesis, with one peak of small oocytes ( $< 50$   
351  $\mu m$ ) and one peak of larger oocytes ( $> 100 \mu m$ ), to a unimodal distribution with one single  
352 peak of large oocytes ( $\sim 150 \mu m$  for *Arenicola defodiens* and  $\sim 180 \mu m$  for *A. marina*) for  
353 females where oocytes have completed vitellogenesis and are ready to be released (example at  
354 Wx for *A. defodiens* on Fig. 3, see further details in Supplementary Material: Figs. G. 1-4).

355 Spawning events of *A. marina* (Supplementary Material: Fig. H) were assumed to take place  
356 at the beginning of autumn in 2015 and 2016 when water temperatures are ~12 to 16°C. We  
357 estimated that *A. marina* spawned between September (at Wx) and mid-November (at FM) in  
358 2015, and, between September (at Wx) and October (at FM and LT) in 2016 (Supplementary  
359 Material: Figs. G.1 and G.2), possibly during spring tides. Spawning events of *A. defodiens*  
360 (Supplementary Material: Fig. H) were assumed to take place at the end of autumn and at the  
361 beginning of winter in both 2015 and 2016 for water temperatures between ~7 to 11°C. We  
362 estimated that *A. defodiens* spawned between December (at Au, FM and LT) and January (at  
363 Wx) in 2015, and between November (at LT and FM) and December (at Wx) in 2016  
364 (Supplementary Material: Figs. G.3 and G.4), possibly during spring tides. These periods of  
365 spawning were confirmed by the presence of spermatozooids within the coelomic fluid in  
366 males of both species (data not shown).

#### 367 2.2.2. Population structure and age

368 At Wx, individuals of *Arenicola marina* ranged from 0.3 to 9 cm TL. The size-frequency  
369 distribution was multimodal (5 modes, SI > 2) (Table 2, Fig. 4a), suggesting the presence of 5  
370 different age groups, the first one being the recruits' group ( $0.90 \pm 0.37$  cm TL). Since no  
371 recruits were spotted in April-May 2016 but some were observed in July 2017, recruitment  
372 may happen at the end of spring and/or beginning of summer at Wx. TL means of the three  
373 groups of TL delimited by the high (2.3 m of bathymetry), medium (0.9 m of bathymetry) and  
374 low (0 m of bathymetry) levels on the shores were significantly different (ANOVA:  $F_{(1,2)} =$   
375  $67.16$ ;  $p < 0.001$ ; Post-hoc Tukey  $p < 0.001$ ), which suggests that recruitment happens on the  
376 upper shore (Fig. 4b). Given the weight-size relationship found for *A. marina* at Wx (Fig. 4c),  
377 lugworms reached the weight of 3 g between 5 and 9 cm, which means not before reaching 3  
378 years old. At Wx, 12.6 % of the sampled *A. marina* and 100 % of the sampled *A. defodiens*  
379 had a weight superior to 3 g. 100 % of the individuals of the two species were above 3 g at the  
380 other sites, except for *A. marina* at Au, where the only individual collected weighted 2.5 g.

#### 381 2.2.3. First size at maturity of *A. marina*

382 Adult lugworms ranged from 2.5 to 6.3 cm (TL). The first size at maturity of *Arenicola*  
383 *marina* at Wx was assessed at 3.8 cm of TL (Fig. 5), which corresponds approximately to 1 g  
384 of wet weight (Fig. 4c). No significant difference was found between the lengths of males and  
385 females (K-W: 0.63,  $p > 0.05$ ), then all the data were analysed together. A highly significant  
386 difference between the size of juveniles ( $2.29 \pm 0.97$  cm) and adults ( $3.92 \pm 0.91$  cm) was

387 observed (K-W: 0.96,  $p < 0.001$ ) (Fig. 5). According to the population structure of *A. marina*  
388 from Wx, lugworms become adult between 1.5 and 2.5 years-old (Fig. 4a, Table 2).

### 389 2.3. Bait collection data and retail value

390 Most of the data presented here is available at <https://estamp.afbiodiversite.fr/donnees>. In  
391 total, 3 638 on-site observations were made within the MPA between 2014 and 2016. Among  
392 them, 88 were performed at Wx, 54 at LT, 60 at FM and 61 at Au. At these sites, 27  
393 fishermen's baskets were randomly selected in order to estimate the number of dug lugworms  
394 (10 at Wx, 5 at LT and 12 at FM). The number of recreational diggers was highly variable  
395 along the MPA's foreshore. Au was the site where more lugworms' diggers were spotted on  
396 the whole MPA, with less than 4 000 diggers recorded in 2015. On the other studied sites, the  
397 number of recreational diggers ranged from ~ 300 at FM, ~ 700 at LT to ~ 1 200 diggers at  
398 Wx (Table 3). The mean estimated catch per fishing session varied according to the studied  
399 site from ~ 21 lugworms at FM to ~ 40 lugworms at Wx (Table 3). Since no value was  
400 available at Au, we used the mean value of the three other studies sites giving ~31 lugworms  
401 per tide and per recreational fisherman (Table 3). The estimated number of dug lugworms at  
402 the studied sites ranged from ~ 6 000 lugworms at FM to more than ~ 110 000 *Arenicola* spp.  
403 at Au which led to a retail value varying between ~ 3 000 € at FM to more than ~ 49 000 € at  
404 Au in 2015 (Table 3). The total retail value of recreational arenicolid fisheries within the  
405 MPA (232 447 €) appeared to be about the equivalent to the retail value of the recreational  
406 shrimp *Crangon crangon* fisheries (215 714 to 414 727 €), and only 4 to 5 times less  
407 important than the one of the recreational mussel *Mytilus edulis* fisheries (1 203 449 €) (Table  
408 3).

### 409 2.4. Linking lugworms' life-history traits to bait collection data

410 At the four studied sites, the number of lugworms above 3 g (e.g. considered as valuable by  
411 fishermen (Olive, 1993)) ranged between ~ 700 000 *Arenicola* spp. at FM to ~ 1 300 000  
412 *Arenicola* spp. at Wx (Table 3, Fig. 6). In 2015, the number of lugworms dug by recreational  
413 fishermen represented respectively 3.6 % of the number of lugworms (both species combined)  
414 greater than 3 g at Wx, 2.9 % at LT, 0.9 % at FM, and 13.9 % at Au, and respectively 0.8 %  
415 of the total number of lugworms (both species combined) at Wx, 2.9 % at LT, 0.9 % at FM,  
416 and 13.7 % at Au (Fig. 6). At Au only, the number of dug lugworms for the year 2015  
417 (117 791 lugworms) was greater than the estimated abundance of *A. marina* (12 810  
418 lugworms in total, all weights considered), only considering recreational fisheries (Fig. 6).

419 **3. Discussion**

420 3.1. Species identification, abundances and spatial distribution

421 Our results confirmed the occurrence of both *Arenicola marina* and *A. defodiens* on the  
422 French coast of the Eastern English Channel, only mentioned by Müller (2004) while other  
423 authors only reported *A. marina* in ecological studies (e.g. Rolet et al., 2014) and may have  
424 been confusing the two species, especially in sites where they live in sympatry on the same  
425 level of the shore (on the lower shore). However, since *A. defodiens* burrows deeper into the  
426 sand, it is therefore harder to collect and previous studies may have failed in collecting this  
427 latter species, for which only bait pumps proved to be efficient. Until now, *A. defodiens* has  
428 only been described in the UK, the Netherlands and Portugal (Atlantic Ocean). In this study,  
429 we have shown the evidence of the occurrence of *A. defodiens* on the French coast of the  
430 Eastern English Channel, suggesting that this species is widely distributed on the whole  
431 French coast of both the English Channel and the Atlantic Ocean.

432 The maximum abundance of *Arenicola marina* found in this study at Wx (61 individuals. m<sup>-2</sup>)  
433 was comparable to those found in other studies in the Wadden Sea and Portugal (~ 40 to 70  
434 individuals. m<sup>-2</sup> max) (Beukema and De Vlas, 1979; Flach and Beukema, 1994; Pires et al.,  
435 2015) but did not reach the highest abundance recorded by Farke et al. (1979) (more than 150  
436 individuals. m<sup>-2</sup>). In comparison, the values found at LT and FM for this species (2.7 and 0.6  
437 individuals. m<sup>-2</sup> max respectively) appeared relatively low. This discrepancy may be linked to  
438 physical disturbances within the higher shore at these two sites caused by mechanical engines  
439 that remove debris deposited by the tide. Beukema (1995) showed that repeated mechanical  
440 harvest of lugworms using digging machines similar to what is present at LT and FM, could  
441 decrease the overall densities of worms. In these two sites no recruits were observed during  
442 the spring period and only few individuals were collected on the higher shore during the  
443 autumn. Some individuals of *A. marina* may have migrated on the lower shore, on the EUNIS  
444 habitat A2.23 (medium to fine sands with amphipods and *Scolecopsis* sp.) or even on the  
445 EUNIS habitat A5.231 (medium to fine sands with *Donax vittatus*), as lugworms may do  
446 during cold winters (Wolff and de Wolf, 1977). The trade-off made by sharing the same  
447 ecological niche with *A. defodiens* on the lower shore at FM and LT involves interspecific  
448 competition for food and habitat, higher predation rate by birds and flatfish. This would make  
449 the survival rate of *A. marina* lower, and consequently decrease its abundance in comparison  
450 with sites where *A. marina* could live not in sympatry with *A. defodiens* such as at Wx. For *A.*  
451 *defodiens*, the maximum abundance at all sites ranged from 1.6 to 2.9 individuals. m<sup>-2</sup>. This is

452 higher to what Pires et al. (2015) found in Portugal (between 0.25 and 1 individual. m<sup>-2</sup>). The  
453 similar abundance of *A. defodiens* observed at all sites might be linked to the presence of a  
454 subtidal population of this species: when, for some reason, densities of population from the  
455 foreshore decrease, the subtidal individuals could colonize the empty spaces and reload the  
456 intertidal *A. defodiens* population. Indeed, the subtidal presence of *A. defodiens* was recorded  
457 in Portugal by Pires et al. (2015) and in France on the Eastern English Channel by the present  
458 authors (unpublished data). However, the density estimation for *A. defodiens* was made from  
459 data of cast production obtained for *A. marina*, and further investigation on the cast  
460 production of *A. defodiens* is needed to conclude more accurately on the abundance of this  
461 species.

### 462 3.2. Life-history traits of lugworm

463 The spawning period of *Arenicola marina* appeared to occur at the beginning of autumn and  
464 at the end of autumn to beginning of winter (at Wx) for *A. defodiens*. There was a time lag of  
465 two weeks to two months between the two species' spawning periods, as previously described  
466 by several authors (Dillon and Howie, 1997; Watson et al., 1998, 2000), probably to avoid  
467 species hybridization which was shown to be possible by *in vitro* fertilization (Watson et al.,  
468 2008). For both species, spawning periods vary according to the year. Environmental  
469 parameters such as tidal amplitude cycles, temperature (temperature at the beginning of the  
470 gametogenesis and temperature just prior to spawning) as well as weather conditions have  
471 shown to influence spawning periods in *A. marina* (Watson et al., 2008, 2000). The  
472 combination of these environmental parameters may explain the variation of spawning  
473 periods between years. In fact, spawning periods recorded in this study for both species are  
474 likely to have occurred during spring tides (Supplementary Material: Fig. H), but not at the  
475 same water temperature. There was ~ 4°C difference between the minimum and the maximum  
476 of water temperature during the spawning period of the different sites for a respective species  
477 which might suggest that spring tides may play a role in the triggering of spawning events  
478 rather than water temperature. Watson et al. (2000) suggested for a Scottish population of *A.*  
479 *marina* that others spawning cues may be taken into account such as air temperature, air  
480 pressure, daily rainfall and/or wind speed, etc.

481 The size at first maturity found for *Arenicola marina* at Wx (3.8 cm) corresponds to an  
482 individual of approximately 1 g, which is close to the weight at which individuals of *A.*  
483 *marina* started developing gametes in the laboratory experiment performed by De Wilde and  
484 Berghuis (1979). Recruits of *A. marina* were only spotted at Wx and recruitment happened

485 between the end of spring and the beginning of summer, which mirrored recruitment period  
486 recorded by Flach and Beukema (1994). No recruits of *A. marina* were detected on the other  
487 sites. Since sampling for spatial distribution pattern was performed at the beginning of spring  
488 at LT and FM, we might have come too early to detect recruitment of the first cohort of *A.*  
489 *marina* on these sites and further investigation will be needed since some small individuals  
490 were then detected on the upper shore in autumn 2016 at both sites. However, another  
491 possible explanation to the uneven distribution and abundance of *A. marina* recorded at the  
492 different sites might be explained by a particularly low survival rate of the recruits at LT, FM,  
493 and Au compared to Wx, due to physical disturbance as mentioned earlier. Another  
494 hypothesis is linked to the lifecycle of *A. marina* that involves a post-larval nursery grounds  
495 composed of sheltered soft sediments, macro-algae and/or mussel beds (Farke and Berghuis,  
496 1979b; Reise, 1985). These transitory colonization habitats might have been degraded by  
497 anthropogenic disturbance at Au (Paute, 2015) or naturally absent close to LT and FM (as  
498 suggested by the subtidal macrobenthic community map for the area designed by Croguennec  
499 et al. (2011)), enhancing a post-larval mortality and subsequently a low recruitment of  
500 juveniles on the beach after the second larval dispersal phase. The low recruitment of *A.*  
501 *marina* at LT, FM and Au might also be linked again to the two phases of dispersal during its  
502 lifecycle, where, under certain weather conditions, a strong current may be directed up North  
503 (Bailly Du Bois et al., 2002; Ellien et al., 2000; Nicolle et al., 2017) during the second  
504 dispersal phase prior to the settlement of juveniles on the higher shore, favoring recruitment to  
505 North sites such as Wx (which could be considered as a sink of propagules) compared to the  
506 three others sites that are more south on the MPA (which could rather be considered as  
507 sources of propagules). Further studies on larval dispersal using a modeling approach based  
508 on biophysical model or population genetics should be applied to support this hypothesis.

### 509 3.3. Linking life-history traits, abundance and spatial distribution to bait collection data: 510 management stakes and fishery

511 At Wx, LT and FM, according to the survey carried out in 2015 on recreational fishermen,  
512 extraction levels of lugworms appeared quite low compared to the lugworm abundances  
513 calculated in this study (less than 5% of the population harvested). Moreover, the presence of  
514 numerous young individuals of *A. marina* at Wx seems to ensure a rapid renewal of the part  
515 of the population allocated to bait digging. However, 104 professional licenses have been  
516 delivered to some fishermen specialized in lugworm digging within the MPA and some of  
517 them are able to extract more than 400 worms per tide (anonymous fisherman

518 communication). The lugworm extraction may have been underestimated in this study as the  
519 survey was done only on recreational fishermen. Besides, the proportion of the lugworm  
520 population dug at Au was already quite high (13.7 % of the total number of individuals and  
521 13.9 % of the individuals heavier than 3 g). If we consider that the maximum age of *Arenicola*  
522 *defodiens* is close to the one of *A. marina*, which is around 5 to 6 years old, it means that  
523 every year, around one sixth to one fifth (e.g. 17% to 20%) of the population is renewed  
524 (Beukema and De Vlas, 1979). In this case, maybe the managers of the MPA should consider  
525 following up the population's density of this species to make sure that its abundance does not  
526 decrease over time. If so, some preventive management measures should be implemented  
527 such as forbidding or restricting the bait collection during the spawning periods and giving a  
528 minimum size limit of worm collection. Again, the numbers of *A. marina* were really low at  
529 Au compared to the total number of dug individuals, and actions should be taken to follow up  
530 and manage this species in order to allow its recovery. The species was found to be able to  
531 produce gametes (adult) between the cohort 2 and 3 (1.5 to 2.5 years old and approximately 1  
532 g) and managers should encourage local fishermen to harvest only lugworms from cohorts 4  
533 or 5 (i.e. worms that spawned at least once, older than 3 years old), where worms are larger to  
534 6.15 cm long (TL) and getting close to 3 g (Fig. 3c). Although, further study of the dynamics  
535 of population of this studied site is needed to determine the best "size limit" management  
536 strategy (Gwinn et al., 2015), especially since the weight/size/age relationships of *A. marina*  
537 were only studied at Wx, where the growth of the individuals of this species might be  
538 different from the one of the individuals of the same species at Au. However, as mentioned  
539 before, Au might not be a sink of larvae of *A. marina*. A second hypothesis is due to the  
540 natural mussels' beds of this site that is not in a good status and may lead to a mortality of the  
541 first settlers during their lifecycle (Reise, 1985; Paute, 2015). These last considerations  
542 enlighten the need for an integrated management of the different activities, species and  
543 habitats in the area.

544 The total retail value of recreational fisheries for *Arenicola* spp. within the MPA appeared to  
545 be about equivalent to the one of the shrimp *Crangon crangon*, and only 4 to 5 times less  
546 important than the one of the mussel *Mytilus edulis* (in terms of recreational fisheries). These  
547 last two species benefit within the MPA from a number of catch restrictions (length and bags  
548 limits, closing fishing areas, restrictions on catch engines, etc.) (Direction interrégionale de la  
549 mer Manche Est-mer du Nord, 2015), when no restriction exists for *Arenicola* spp.  
550 recreational fisheries within the MPA.

551 In order to give restrictions, distinguishing the two species of lugworms will be necessary,  
552 and especially, when sympatry of the two species occurs. Pires et al. (2015) suggested that  
553 there could be a difference in the shape of the faecal casts, where the faecal casts of *A.*  
554 *defodiens* are more spiral-like than those of *A. marina*. These features could be taught to  
555 anglers when fishing for one of the two species must be limited. If size limit of the bait will be  
556 needed, size of the cast diameter of the lugworms may be used as an indicator, as this has  
557 been well correlated with the size of the worm itself such as in *A. marina* (Olive, 1993;  
558 unpublished data). Again, this information could be communicated to fishermen through  
559 education (Watson et al., 2015).

560 To conclude, the management of the lugworm populations within the MPA and some fishery  
561 regulation appear crucial given their ecological and economical importance with some  
562 populations (e.g. Au) that may be threatened by human activities.

563

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745 **Table 1: Summary of the number of samples and the associated name of the collected species, date, site and type of EUNIS habitat for the**  
 746 **assessment of the biological traits of the two lugworm species at Wimereux (Wx), Le Touquet (LT), Fort Mahon (FM) and Ault (Au).**

Biological traits	Site	Species*	Number of individuals (n)	Type of EUNIS habitat **	Date	
Population structure	Wx	<i>Arenicola marina</i>	186	A2.223	May and July 2017	
Species distribution	Wx	<i>A. marina</i>	24	A2.223 + A2.23	March 2016	
		<i>A. defodiens</i>	5	A2.223 + A2.23		
	LT	<i>A. marina</i>	4	A2.223 + A2.23	April 2016	
		<i>A. defodiens</i>	1	A2.223 + A2.23		
	FM	<i>A. marina</i>	4	A2.223 + A2.23	April 2016	
		<i>A. defodiens</i>	3	A2.223 + A2.23		
	Au	<i>A. marina</i>	1	A2.23	May and June 2016	
		<i>A. defodiens</i>	11	A2.23		
Spawning period	Wx	<i>A. marina</i>	51 86	A2.223	Sept - Nov 2015 Sept - Oct 2016	
		<i>A. defodiens</i>	34 16	A2.23	Sept 2015 – Jan 2016 Oct 2016 – Dec 2016	
	LT	<i>A. marina</i>	17 8	A2.23 + A2.223	Oct – Dec 2015 Oct 2016	
		<i>A. defodiens</i>	16 12	A2.23	Oct – Dec 2015 Nov 2016	
	FM	<i>A. marina</i>	5 19	A2.23 + A2.223	Sept – Nov 2015 Oct 2016	
		<i>A. defodiens</i>	17 11	A2.23	Sept – Nov 2015 Nov 2016	
	Au	<i>A. defodiens</i>	26	A2.23	Oct – Nov 2015	
	Size at first maturity	Wx	<i>A. marina</i>	106	A2.223	Sept 2017

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749 **Table 2: Mean size and number of individuals and separation indices (SI) of every cohort**  
 750 **found with the Bhattacharya analysis**

	<b>Mean trunk length (cm)</b>	<b>Number of individuals</b>	<b>SI</b>
Cohort 1	0.90 ± 0.37	27	-
Cohort 2	2.56 ± 0.60	36	3.42
Cohort 3	4.82 ± 0.55	76	3.93
Cohort 4	6.15 ± 0.56	41	2.40
Cohort 5	8.21 ± 0.46	14	4.04
Total sample	4.12 ± 1.93	194	-

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**Table 3: Extrapolated number of dug worms (per site and on the whole MPA) and its associated retail value, and comparison with the two other major recreational fisheries of the area: *Mytilus edulis* and *Crangon crangon*, with Wx for Wimereux, LT for Le Touquet, FM for Fort Mahon, and Au for Au.**

	Sites / Species	Extraction area (km <sup>2</sup> )	Estimated number of fishing sessions / year (*)	Mean estimated catch / fishing session (*)	Estimated removed number	Estimated removed weight (kg)	Retail Price	Total retail value (€)	References
<b>Studied sites (<i>Arenicola</i> spp.)</b>	Wx	0.9	1246 ± 40	39.8 ± 32.1	49 590 ± 19 755	198 kg to 744		20 778 ± 8 277	
	LT	1.5	692 ± 39	34.0 ± 15.2	23 528 ± 5 626	353 kg to 541	4.19 € / 10 worms	9 858 ± 2 357	<a href="https://www.decathlon.fr/catalogue-sport-appats-vivants-peche-mer.html">https://www.decathlon.fr/catalogue-sport-appats-vivants-peche-mer.html</a>
	FM	1.8	311 ± 32	21.3 ± 20.5	6 624 ± 6 702	86 kg to 179		2 775 ± 2 808	<a href="https://estamp.afbiodiversite.fr/donnees">https://estamp.afbiodiversite.fr/donnees</a>
	Au	1.8	3862 ± 173	30.5 ± 25.4	117 791 ± 98 203	1.885		49 354 ± 41 147	
<b>Whole MPA</b>	<i>Arenicola</i> spp.	-	18 189 ± 2 131	30.5 ± 25.4 worms	554 765 ± 250 323 worms	9 875 ± 4 456	4.19 € / 10 worms	232 447 ± 105 885	<a href="https://www.decathlon.fr/catalogue-sport-appats-vivants-peche-mer.html">https://www.decathlon.fr/catalogue-sport-appats-vivants-peche-mer.html</a>
	<i>Mytilus edulis</i>	-	74 287 ± 3 054	3.6 ± 0.2 kg	-	267 433 ± 12 280	around 4.5 € / kg	1 203 449 ± 55 260	Local fishermen and <a href="http://www.manger-la-mer.org">http://www.manger-la-mer.org</a>
	<i>Crangon crangon</i>	-	12 652 ± 1 440	1.1 kg	-	13 917 ± 1 584	15.5 to 29.8 € / kg	215 714 ± 24 552 to 414 727 ± 47 203	FranceAgriMer (2017) and local fish retailers

774 **Figure captions**

775

776 **Figure 1.** Location of the four studied sites within the MPA where spatial distribution,  
777 abundance, life-history traits and survey of bait collection were carried out.

778

779 **Figure 2.** Spatial distributions of the two species *Arenicola marina* and *A. defodiens* at the  
780 four studied sites: Wimereux (Wx), Le Touquet (LT), Fort Mahon (FM) and Ault (Au), and  
781 associated bathymetries (height above chart datum) or distance from the shoreline and EUNIS  
782 habitats.

783

784 **Figure 3.** Evolution of the oocyte diameter frequencies of *Arenicola defodiens* at Wimereux  
785 between October 2015 and January 2016, measured on 50 random oocytes of n individuals.

786

787 **Figure 4.** Length-frequency distributions of the trunk lengths of all specimens of *Arenicola*  
788 *marina* obtained from Wimereux in summer 2017 analysed using FISAT II. Normal curves  
789 represent each detected cohort (C.1 to C.5) (A), spatial distribution of the different sizes along  
790 the shore level (low = 0.1 m of bathymetry, medium = 0.9 m of bathymetry and high = 2.3 m  
791 of bathymetry) (B) and associated length-weight relationship (C). Since recruitment happens  
792 once a year at the same period, each cohort represents an age group. Cohort C.1 comprises the  
793 newly recruits, born in autumn 2016, C.2 the 1.5 years old individuals, born in autumn 2015,  
794 etc.

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796 **Figure 5.** Sizes in juveniles and adults of *Arenicola marina* at Wimereux (A), relative  
797 proportion of adults per size class (B) and its associated cumulated frequency (C).

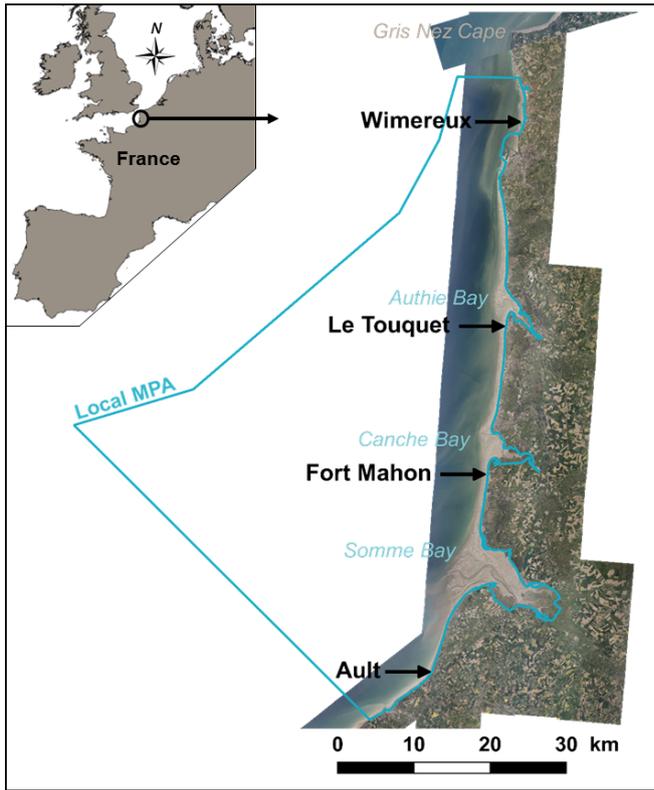
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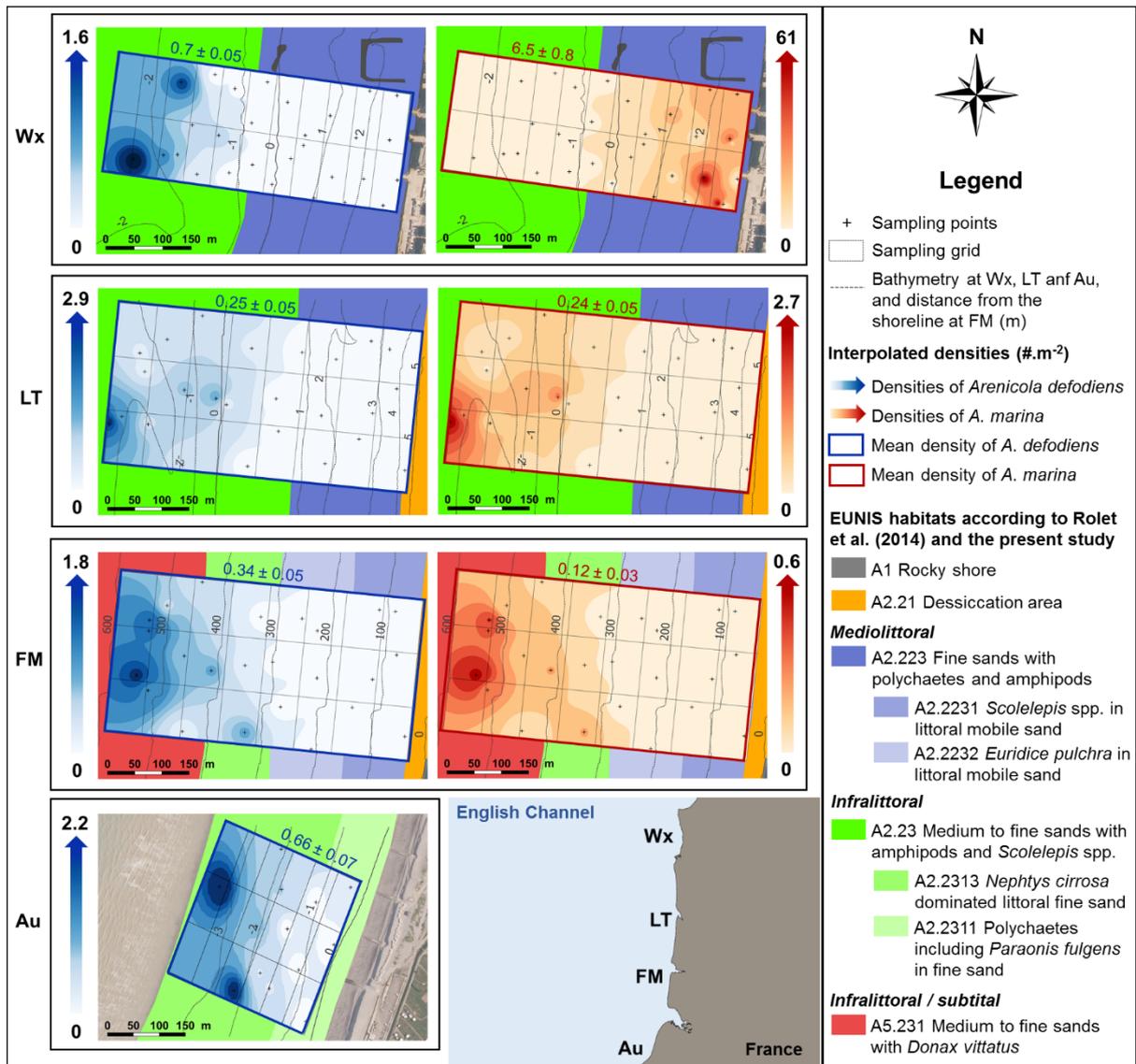
799 **Figure 6.** Comparison of the total number of individuals, number of individuals above 3 g and  
800 number of lugworms harvested in 2015 by recreational fishermen respectively for *Arenicola*  
801 *marina*, *A. defodiens*, and both species combined at Wimereux (Wx), Le Touquet (LT), Fort  
802 Mahon (FM) and Ault (Au).

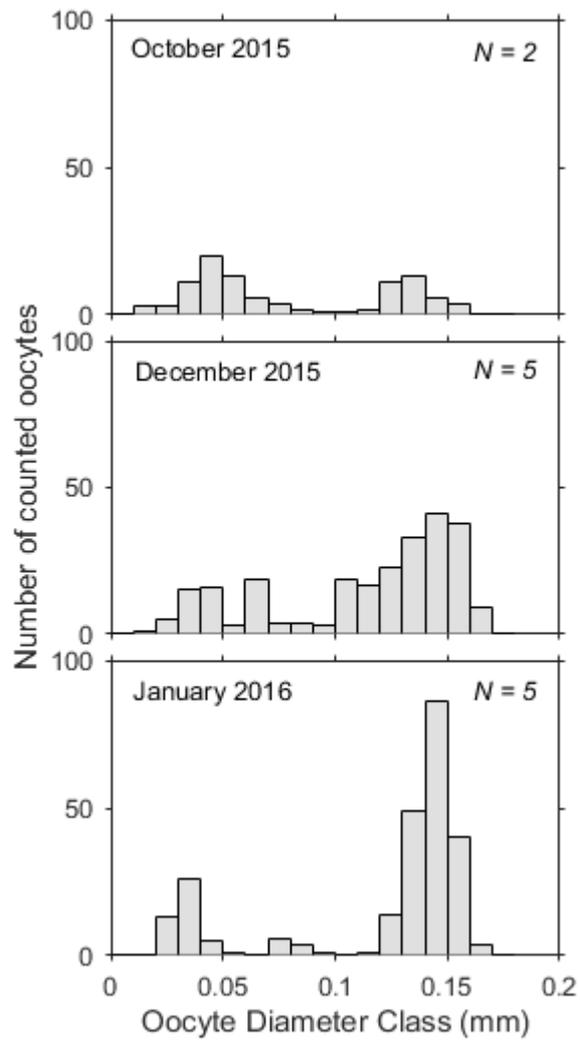
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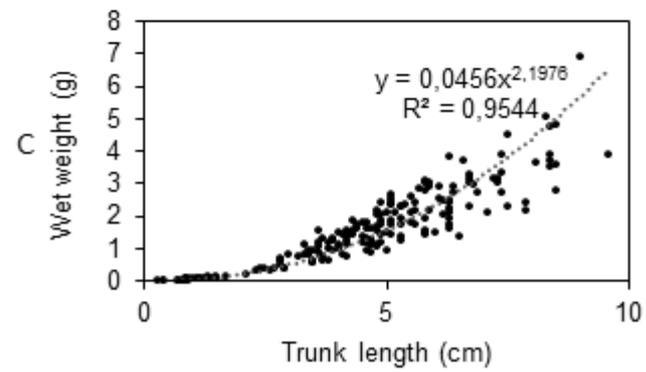
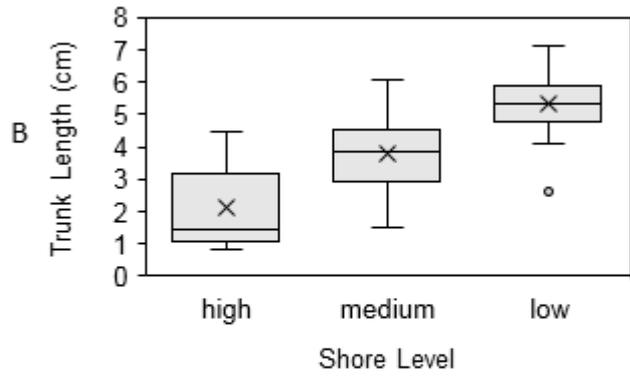
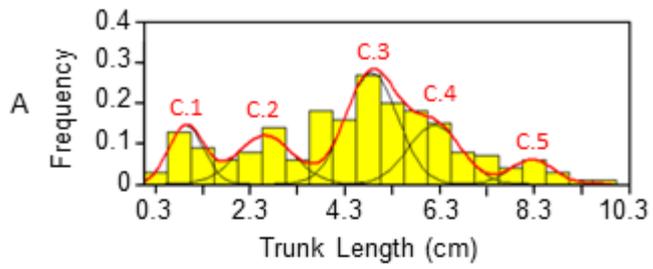
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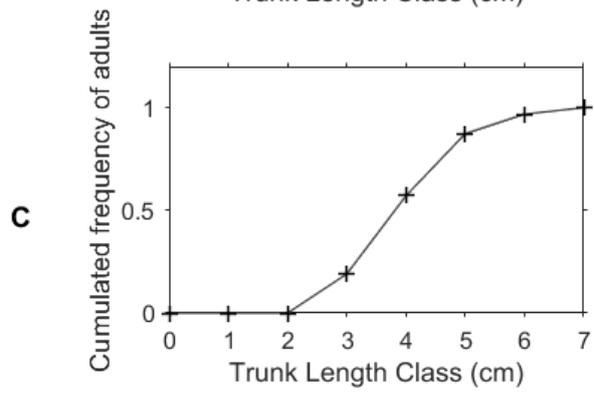
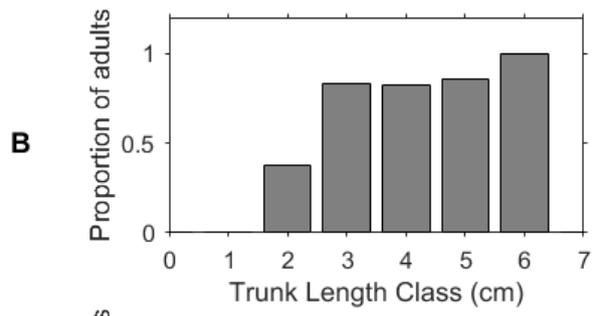
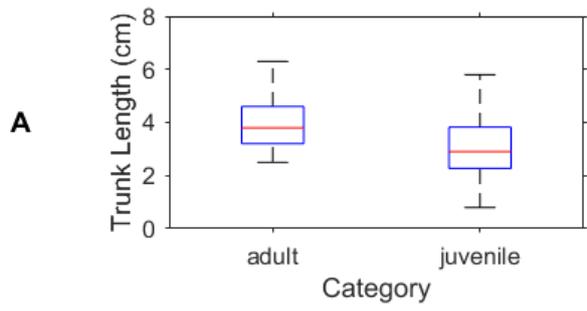
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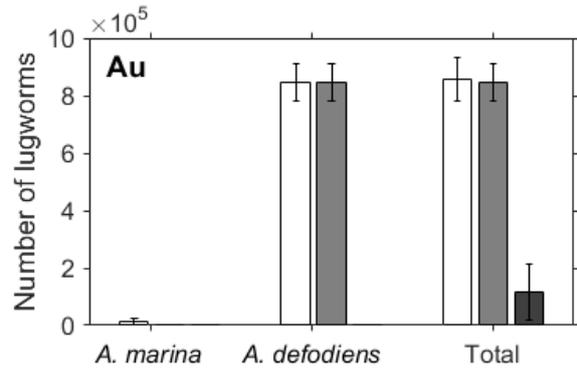
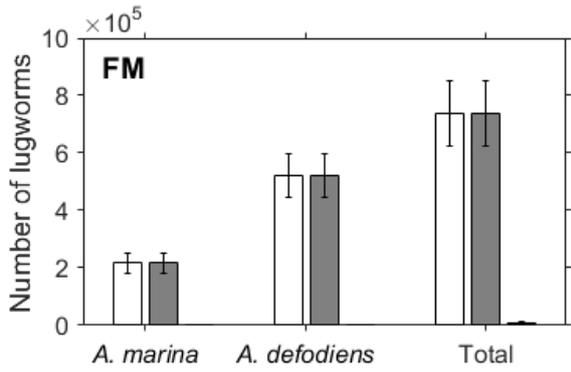
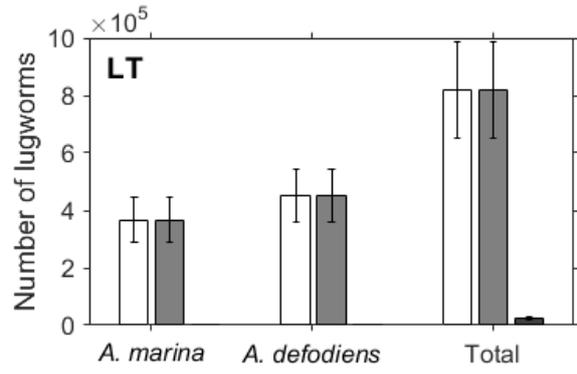
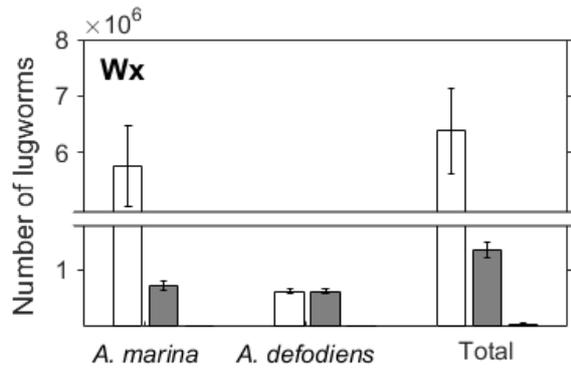












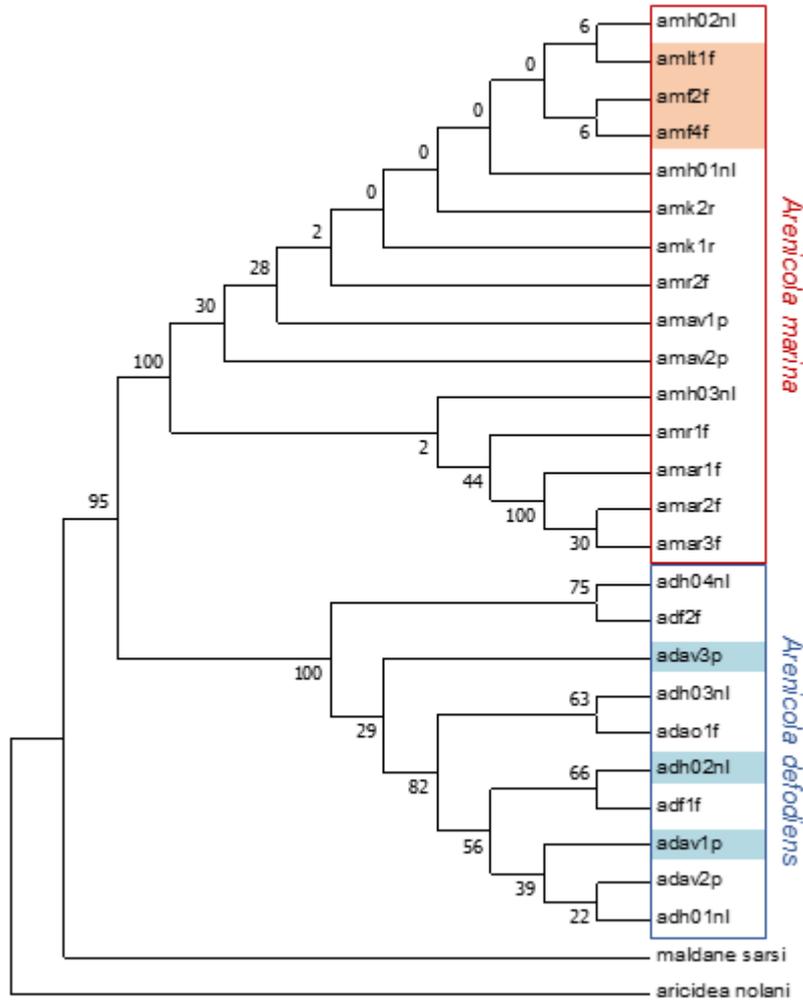
Total number of individuals  
 Number of individuals above 3 g  
 Number of lugworms harvested in 2015

## Supplementary Materials

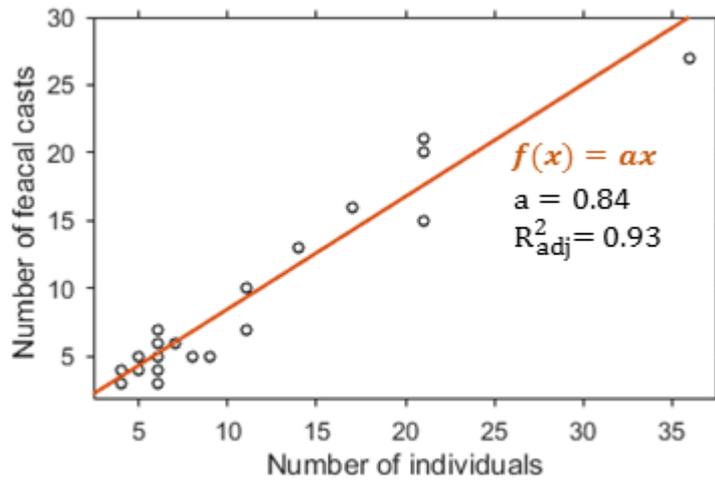
**Table A.** COI gene sequences used in the phylogenetic analyses in this study (in bold) and in the literature. For each haplotype, the species, acronym, GenBank accession number, and location (with GPS coordinates when available) are given.

Species	Acronym	Genbank accession number	Location	Latitude	Longitude	Literature
<i>Arenicola marina</i>	AmAv1P	KM042097	Ria de Aveiro, Portugal	40° 36' 48.76"N	8° 44' 27.63"W	Pires et al., 2015
<i>A. marina</i>	AmAv2P	KM042098	Ria de Aveiro, Portugal	40° 36' 13.29"N	8° 44' 10.31"W	Pires et al., 2015
<i>A. marina</i>	AmR1F	JQ950326	Roscoff, France	48° 43' 40.21"N	3° 59' 16.21"W	Pires et al., 2015
<i>A. marina</i>	AmR2F	JQ950327	Roscoff, France	48° 43' 40.21"N	3° 59' 16.21"W	Pires et al., 2015
<i>A. marina</i>	AmAr1F	HQ023444	Arcachon, France	44° 39' 51"N	1° 09' 38"W	Carr et al., 2011
<i>A. marina</i>	AmAr2F	HQ023443	Arcachon, France	44° 39' 51"N	1° 09' 38"W	Carr et al., 2011
<i>A. marina</i>	AmAr3F	HQ023441	Arcachon, France	44° 39' 51"N	1° 09' 38"W	Carr et al., 2011
<i>A. marina</i>	AmK1R	GU672432	Kandalaksha Bay, Russia	66° 33' 07.2"N	33° 6' 43.2"E	Hardy et al., 2011
<i>A. marina</i>	AmK2R	GU670812	Kandalaksha Bay, Russia	66° 33' 07.2"N	33° 6' 43.2"E	Hardy et al., 2011
<i>A. marina</i>	Amh01NL	GQ487319	Netherlands	-	-	Luttikhuizen and Dekker, 2010
<i>A. marina</i>	Amh02NL	GQ487320	Netherlands	-	-	Luttikhuizen and Dekker, 2010
<i>A. marina</i>	Amh03NL	GQ487321	Netherlands	-	-	Luttikhuizen and Dekker, 2010
<b><i>A. marina</i></b>	<b>AmF2F</b>	<b>MF405759</b>	<b>Fort-Mahon, France</b>	<b>50°20'24.629" N</b>	<b>1°32'35.286" E</b>	<b>This study</b>
<b><i>A. marina</i></b>	<b>AmF4F</b>	<b>MF405760</b>	<b>Fort-Mahon, France</b>	<b>50°20'24.629" N</b>	<b>1°32'35.286" E</b>	<b>This study</b>
<b><i>A. marina</i></b>	<b>AmLT1F</b>	<b>MF405761</b>	<b>Le Touquet, France</b>	<b>50°31'12.887" N</b>	<b>1°34'16.803" E</b>	<b>This study</b>
<i>A. defodiens</i>	AdAv1P	KM042099	Ria de Aveiro, Portugal	40° 40' 36.70"N	8° 40' 34.90"W	Pires et al., 2015
<i>A. defodiens</i>	AdAv2P	KM042100	Ria de Aveiro, Portugal	40° 42' 43"N	8° 40' 39"W	Pires et al., 2015
<i>A. defodiens</i>	AdAv3P	JQ950325	Ria de Aveiro, Portugal	40° 41' 20"N	8° 42' 54"W	Pires et al., 2015
<i>A. defodiens</i>	Adh01NL	GQ487323	Netherlands	-	-	Luttikhuizen and Dekker, 2010
<i>A. defodiens</i>	Adh02NL	GQ487325	Netherlands	-	-	Luttikhuizen and Dekker, 2010
<i>A. defodiens</i>	Adh03NL	GQ487324	Netherlands	-	-	Luttikhuizen and Dekker, 2010
<i>A. defodiens</i>	Adh04NL	GQ487322	Netherlands	-	-	Luttikhuizen and Dekker, 2010
<b><i>A. defodiens</i></b>	<b>AdAO1F</b>	<b>MF405762</b>	<b>Ault-Onival, France</b>	<b>50°06'45.026" N</b>	<b>1°27'09.686" E</b>	<b>This study</b>
<b><i>A. defodiens</i></b>	<b>AdF1F</b>	<b>MF405763</b>	<b>Fort-Mahon, France</b>	<b>50°20'24.629" N</b>	<b>1°32'35.286" E</b>	<b>This study</b>
<b><i>A. defodiens</i></b>	<b>AdF2F</b>	<b>MF405764</b>	<b>Fort-Mahon, France</b>	<b>50°20'24.629" N</b>	<b>1°32'35.286" E</b>	<b>This study</b>

- 1 **Figure B.** Maximum Likelihood tree of COI sequences of arenicolid species with
- 2 bootstrapping values. The specimens sequenced in this study are highlighted and acronyms
- 3 are described in Table A.

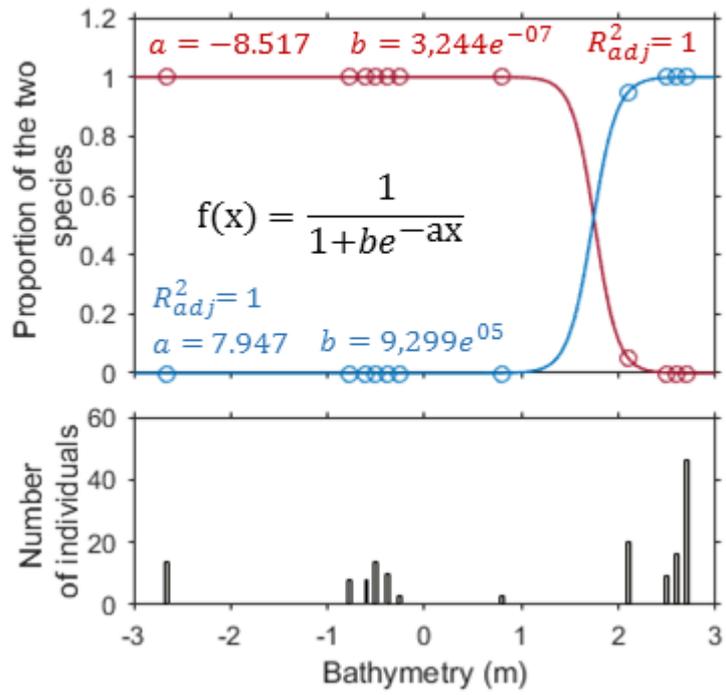


5 **Figure C.** Linear relation between the number of faecal casts produced and the number of  
6 individuals of *Arenicola marina*.



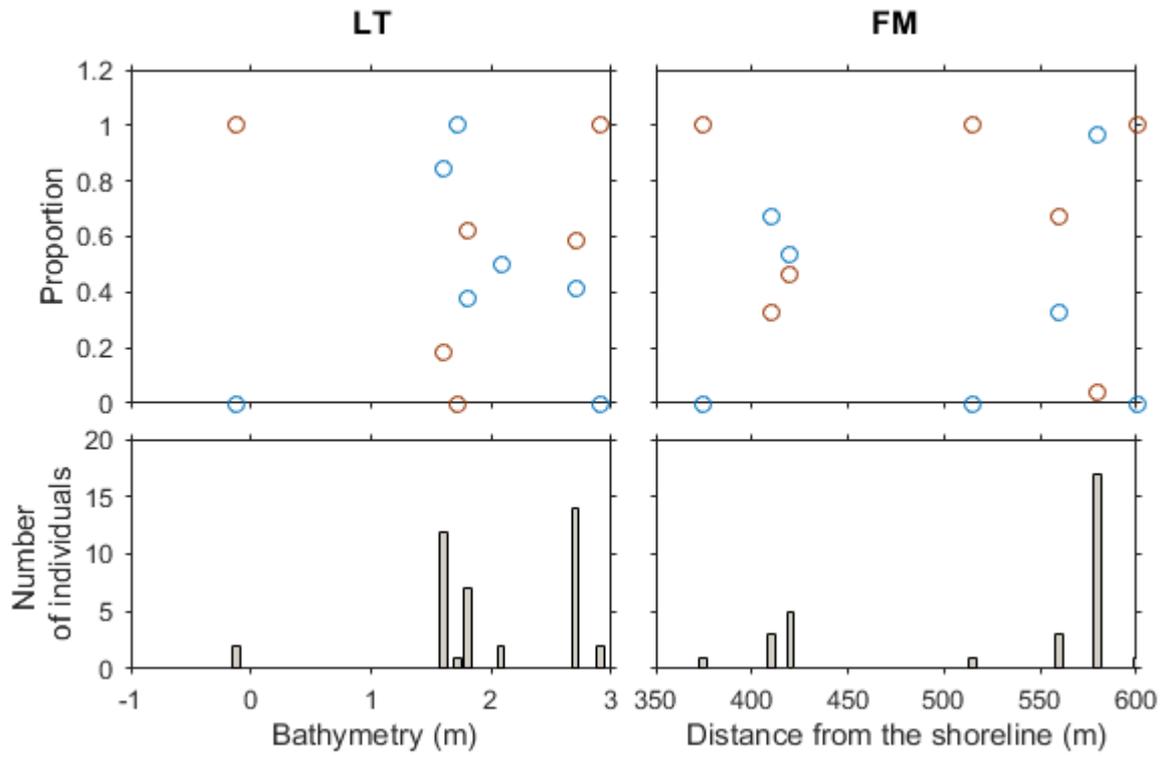
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9 **Figure D.** Proportion of *Arenicola marina* (red dots) and *A. defodiens* (blue dots) according  
10 to bathymetry at Wimereux and the associated fitting transition curves and functions, as well  
11 as the number of lugworms collected at each point to calculate the proportion (weight of the  
12 different proportion points).



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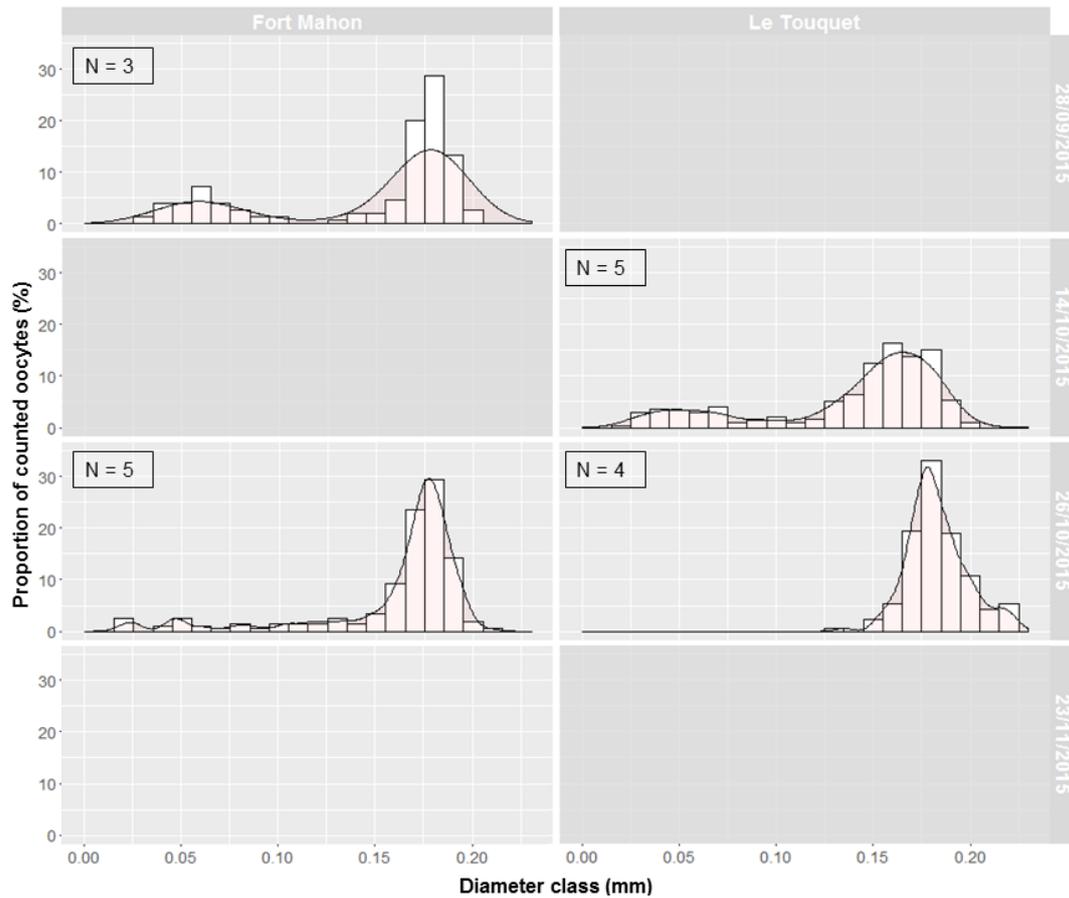
14 **Figure E.** Proportion of *Arenicola marina* (red dots) and *A. defodiens* (blue dots) according  
15 to bathymetry or distance from the shoreline and the related number of individuals used to  
16 calculate the proportion at Le Touquet (LT) and Fort Mahon (FM).



19 **Table F.** EUNIS habitats found at Fort Mahon and Ault based on particle size analysis and  
 20 species identification at these sites

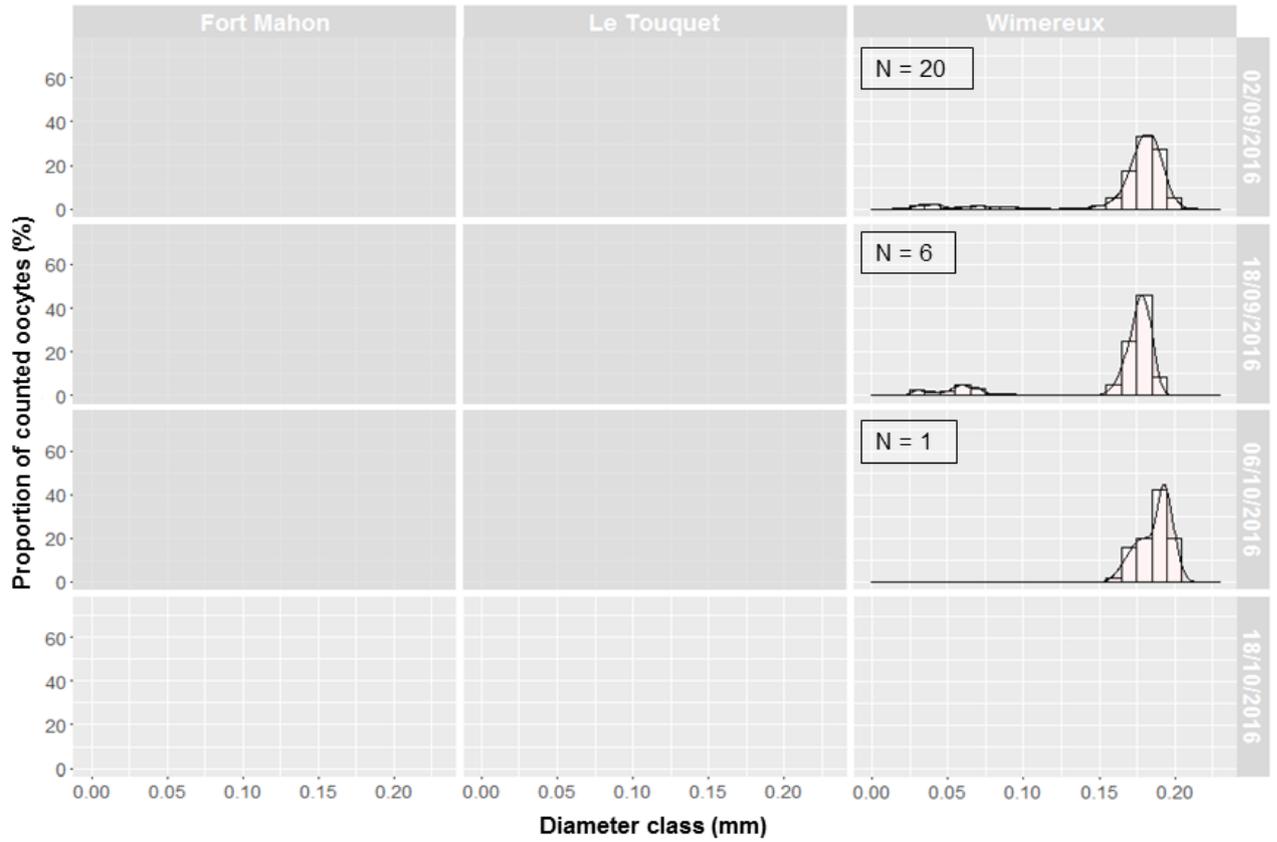
Site	GPS location	Species abundancy (%)	Particle size analysis (%)		Corresponding EUNIS habitat		
Fort Mahon (FM)	1°32'31.68" E 50°20'24.89" N	<i>Donax vittatus</i>	73	mudstones	0	A5.231 Medium to fine sands with <i>Donax vittatus</i>	
		<i>Urothoe poseidonis</i>	10	fine sands	70.7		
		<i>Nephtys cirrosa</i>	8	medium sands	23.6		
		<i>Spio martinensis</i>	5	coarse sands	1.9		
		<i>Urothoe brevicornis</i>	5	fine gravels	1.8		
		<i>Notrotopis falcatus</i>	4	coarse gravels	2.1		
		<i>Lanice conchilega (juveniles)</i>	4				
		<i>Eurydice pulchra</i>	3				
		<i>Vaunthompsonia cristata</i>	2				
		<i>Gastrosaccus spinifer</i>	1				
		<i>Spio sp.</i>	1				
		<i>Nephtys hombergii</i>	1				
		<i>Eteone picta</i>	1				
Fort Mahon (FM)	1°32'39.03" E 50°20'24.36" N	<i>Nephtys cirrosa</i>	57	mudstones	0	A2.2313 <i>Nephtys cirrosa</i> dominated littoral fine sands	
		<i>Eurydice pulchra</i>	21	fine sands	53.1		
		<i>Portumnus latipes</i>	14	medium sands	43.6		
		<i>Nephtys hombergii</i>	7	coarse sands	1.8		
Fort Mahon (FM)	1°32'47.60" E 50°20'23.32" N			fine gravels	1	A2.2232 <i>Eurydice pulchra</i> in littoral mobile sand	
		<i>Eurydice pulchra</i>	60	mudstones	0		
		<i>Scolelepis squamata</i>	39	fine sands	34.2		
		<i>Haustorius arenarius</i>	0.3	medium sands	63.5		
		<i>Urothoe poseidonis</i>	0.3	coarse sands	1.6		
		<i>Bathyporeia pilosa</i>	0.3	fine gravels	0.5		
Fort Mahon (FM)	1°32'54.07" E 50°20'22.79" N	<i>Scolelepis squamata</i>	81	mudstones	0	A2.2231 <i>Scolelepis</i> spp. in littoral mobile sand	
		<i>Bathyporeia pilosa</i>	13	fine sands	35.4		
		<i>Carcinus maenas</i>	2	medium sands	62.1		
		<i>Ophelia rathkei</i>	2	coarse sands	1.4		
		<i>Haustorius arenarius</i>	2	fine gravels	0.3		
Ault (Au)	1°27'09.49" E 50°06'43.13" N and 1°27'04.04" E 50°06'44.05" N	<i>Nephtys cirrosa</i>	50	mudstones	0.1	A2.2313 <i>Nephtys cirrosa</i> dominated littoral fine sand	
		<i>Bathyporeia pelagica</i>	19	fine sands	58.0		
		<i>Portumnus latipes</i>	6	medium sands	38.3		
		<i>Haustorius arenarius</i>	6	coarse sands	1.9		
		<i>Nephtys hombergii</i>	6	fine gravels	0.9		
	Ault (Au)	1°27'15.07" E 50°06'42.31" N	<i>Lanice conchilega</i>	6	coarse gravels	0.9	A2.2311 Polychaetes, including <i>Paraonis fulgens</i> , in littoral fine sand
			Oligochaete	6			
			<i>Paraonis fulgens</i>	31	mudstones	0.1	
			<i>Gastrosaccus spinifer</i>	19	fine sands	30.8	
			<i>Eurydice pulchra</i>	19	medium sands	66.3	
Ault (Au)	1°27'15.07" E 50°06'42.31" N	<i>Nephtys hombergii</i>	13	coarse sands	0.8		
		<i>Bathyporeia pelagica</i>	13	fine gravels	0.4		
		<i>Bathyporeia pilosa</i>	6	coarse gravels	1.6		

21 **Figure G.1.** Oocyte diameter distributions of the collected females of *Arenicola marina* (N is  
22 the number of females) at Fort Mahon and Le Touquet in autumn 2015. When boxes appear  
23 darker, the sites were not sampled at the corresponding date.

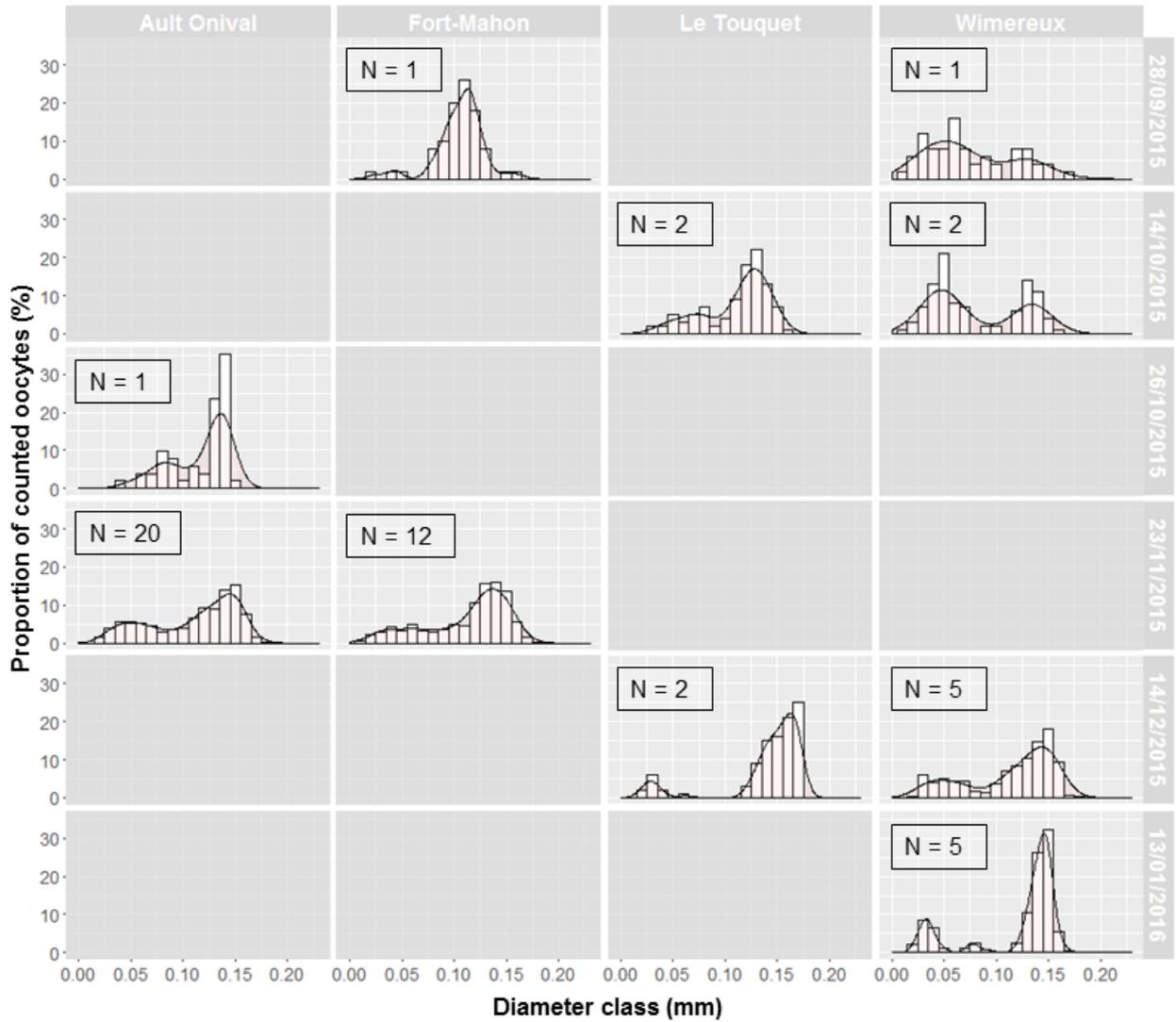


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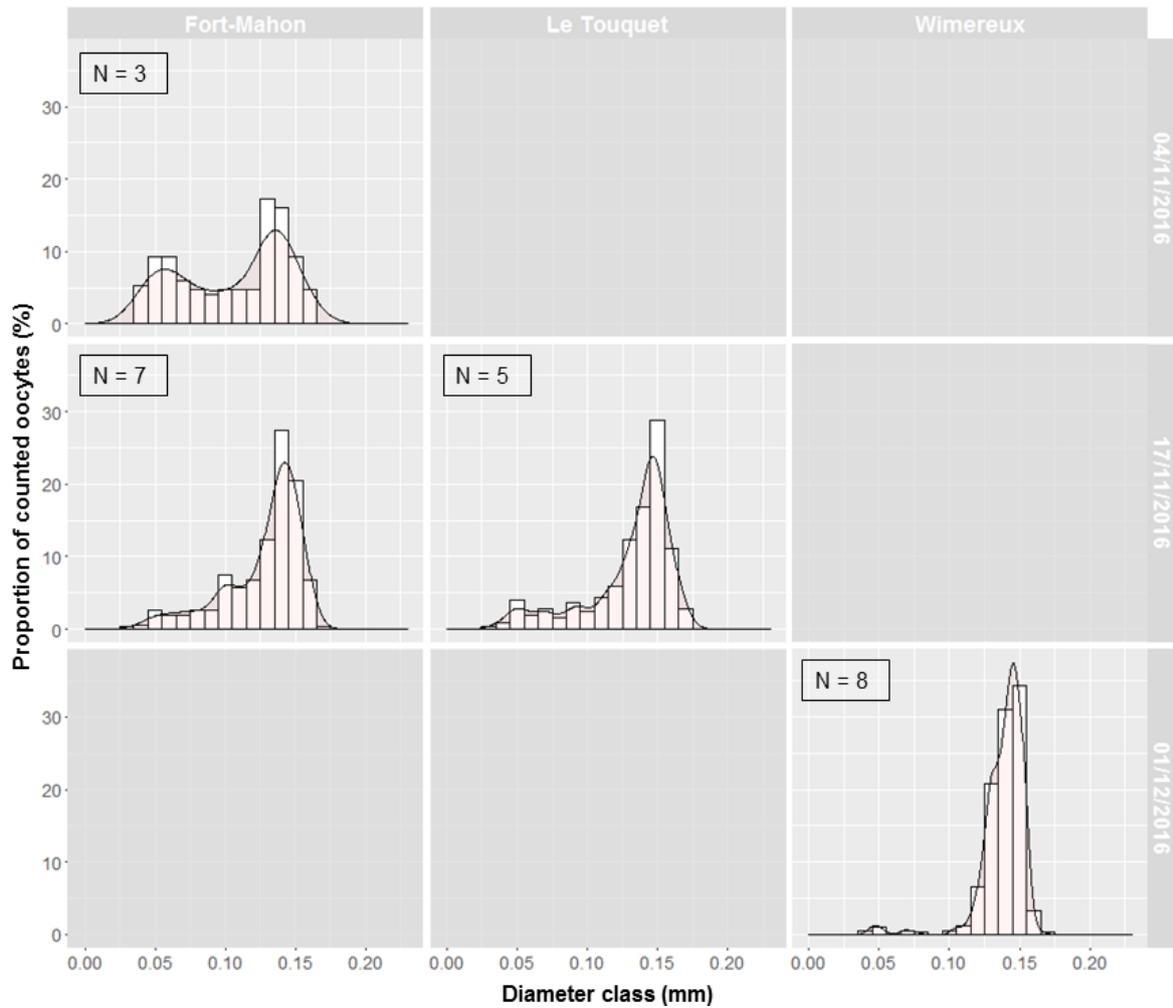
25 **Figure G.2.** Oocyte diameter distributions of the collected females (N is the number of  
 26 females) of *Arenicola marina* at Fort Mahon, Le Touquet and Wimereux in autumn 2016.  
 27 When boxes appear, darker the sites were not sampled at the corresponding date.



29 **Figure G.3.** Oocyte diameter distributions of the collected females (N is the number of  
 30 females) of *Arenicola defodiens* at all sites in autumn and winter 2015/2016. When boxes  
 31 appear darker, the sites were not sampled at the corresponding date.



33 **Figure G.4.** Oocyte diameter distributions of the collected females (N is the number of  
34 females) of *Arenicola defodiens* at Wimereux, Le Touquet and Fort Mahon in autumn and  
35 winter 2016/2017. When boxes appear darker, the sites were not sampled at the  
36 corresponding date.



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38

39 **Figure H.** Inferred spawning dates of *Arenicola marina* (red) and *A. defodiens* (blue) at all  
 40 sampled sites in 2015 (darker) and 2016 (lighter) and associated tide coefficients (in black)  
 41 and water temperatures (in green).

